

A Review on Endophytic Microorganisms as Fertilizer and their Growth Promoting Activity

Sakshi¹ and Priyanka Sen Guha^{1*}

¹Department of Biotechnology, Brainware University, Kolkata 700125

*Corresponding Author. Email: psg.bt@brainwareuniversity.ac.in

Received on: August 04, 2023 | Accepted on: September 11, 2023 | Published on: September 29, 2023

Abstract

Endophytes are microbes that live in plants asymptotically and are primarily bacteria and fungi. Endophytic microorganisms frequently serve useful functions, such as transferring nutrients from the soil to plants, controlling plant growth, enhancing plants' ability to withstand stress, reducing pathogen virulence, enhancing plants' ability to resist illness, and stifling the growth of rival plant species. Further, it has been demonstrated that endophytic microbes are capable of: (i) removing nutrients from soil and transferring them to plants through rhizophagy and other nutrient-transfer symbioses; (ii) reducing oxidative stress on hosts; (iii) protecting plants from disease; (iv) deterring herbivores from eating plants; and (v) suppressing rival plant growth. This study indicates that endophytic bacteria may be able to significantly reduce the demand for agrochemicals (fertilizers, pesticides, etc.) due to their efficient functions. The inhibition of reactive oxygen, which is utilised to extract nutrients from microorganisms in roots, could cause an increase in atmospheric carbon dioxide levels to decrease the effectiveness of the rhizophagy cycle.

Keywords: Endophytes, Rhizophagy, Symbioses, Nutrients, Plant growth.

1. Introduction

An endophyte is any microbial community that inhabits inside the plant tissues as well as on the surface. The endophytic microbial community plays a very important role in plant growth promotion and as a unique fertilizer for agriculture fields. A plant endophyte serves as an integral part of plants, enhancing the plant's ability to acquire nutrients, defending the plant from pathogens and insects, increasing stress tolerance in plants, modulating plant development, and suppressing weed growth (Compant et.al.2010). These bacteria have the potential to reduce the environment impact of agriculture by reducing the need for pesticides. Farmers can benefit greatly from understanding

the role of endophytes in plant growth and health. The benefit is mostly economical since endophytes acts as fertilizer and reduces the need for chemical pesticide application (Kandel et al. 2017). Studies have shown that even a 20% reduction in such applications results in enormous savings. But most importantly, it is ecofriendly and also results in significant improvements in crop quality. This means healthier food for people and ultimately a healthier world. A number of studies have shown that endophytic microbes are capable of concentrating nutrients from soil and transferring them to plants, increasing plant growth and development, reducing host oxidative stress,

protecting plants from diseases, and suppressing the growth of competitors (Johnston et al. 2011).

2. Microbes Impacts On Plant Growth

2.1 Endophytes influence how plants develop

It is likely that endophytes ability to modify seedling development is a result of plants evolving in constant symbiosis with bacteria that colonize plant tissues. Another example of how bacteria and plants have co-evolved is the widespread ability of many microorganisms to create plant signal molecules like nitric oxide and growth regulators like auxins and ethylene (Verma et.al 2018). Trials have shown that seedlings of grass species that have had most of their endophytic bacteria removed do not exhibit root gravitropism (i.e., roots do not grow downward) and have less or no root hairs, internal colonizing microorganisms causes the roots to regain their gravitropic response, which increases plant stature and root hair production. According to several investigations, root hairs grow longer until all bacteria have been expelled (White et al. 2012). Nitric oxide or ethylene synthesis is carried out by microbial protoplasts that gather at the top of the elongating hair shaft's tip, which is a type of epidermis may cause root hair to lengthen, although this has not been verified. It is uncertain what the intracellular bacteria make or break down to start the gravitropic response in seedling roots. It has also been demonstrated that endophytic bacteria in plants promote root development and increase root branching, both of which contribute to greater plant growth (Paungfoo et al. 2010). Although the synthesis of growth regulators by microbes is often credited with these benefits of endophytes on root growth, improved nutrient uptake from bacteria may also contribute to improved plant growth.

2.2 Nutrient transfer symbioses

Microorganisms that fix atmospheric nitrogen in plant tissues are examples of endophytic microorganisms that provide nutrients to plants. Actinorhizal and rhizobial symbioses are endophytes that sequester nitrogen and are known as endophytes that sequester bacteria in low oxygen nodules, where nitrogen is fixed and transported to root tissues, due to the sensitivity of nitrogenases to oxygen (Prieto et.al.2017). Microbes that live both inside endophytic tissues and outside in the soil constitute another kind of nutritional endophytic symbiosis. This type of symbiosis is created by mycorrhizal fungi and dark septate endophytes with many different plant groups. These fungi's hyphae develop endophytically in the roots, and their mycelia that extend into the soil gather nutrients and transport them back to the plants. The release of nutrients from insects by microbes that move between plants and decaying insects is another way to obtain nutrients. This cycle involves insects eating plants and storing nutrients like nitrogen in their bodies (Beltran et.al.2014). When these insects are degraded by microorganisms that are symbiotic with plants, the nutrients are transferred to the plants.

2.3 Cycle of rhizophagy and nutrient uptake

Among the various nutrient uptake methods, the "rhizophagy cycle" or "rhizophagy symbiosis" is very crucial. It occurs when microbes (usually bacteria or yeasts) cycle between an endophytic/intracellular protoplast phase in root cells and a free-living walled phase in the soil (Figure 1) (C) (White et.al 2018). In the free-living soil phase, microorganisms take up nutrients, and in the endophytic/intracellular protoplast phase, nutrients are oxidatively removed from bacteria. Because nitrogenases are inhibited by the large quantities of reactive oxygen produced from root cell plasma membranes onto microorganisms, any nitrogen fixation by bacteria engaged in the rhizophagy

cycle most likely takes place in the free-living soil phase. By way of root exudates (such as proteins, carbs, vitamins, and organic acids) located at the root tip meristem, plants feed microorganisms during the rhizophagy cycle (Figure 2). Just below the exudate zone, meristematic root cells with immature cell walls are internalized with microbes (Soares et.al.2015). Unknown internalization processes of microorganisms into root cells. Once bacteria have internalized, the root cells secrete superoxide onto them in the periplasmic space between the cell wall and plasma membrane, which is created by root cell plasma membrane bound NADPH oxidase (Nicotinamide Adenine Dinucleotide Phosphate Oxidase) (Figure 2(B)). Exposure to reactive oxygen (superoxide) produced by root cells causes intracellular germs to break down cell walls; bacteria develop protoplast phases known as "L-forms," while fungus form protoplast phases known as "mycosomes." This protoplast phase can be connected to the bacteroids of rhizobia, another microbe phase involved in nutrition exchange with host cells (Gond et.al 2015). The suppression of superoxide formation in plant roots using high carbon dioxide is what prevents bacteria in root cells from transitioning to protoplast stages. Older microbe cells/protoplasts are frequently completely oxidized—swelling and disappearing as cells mature (Figure 2(B)). In root cells, protoplast forms of microbes reproduce sequentially as they "bud" or "bleb."

Microbe protoplasts circulate swiftly (circulation estimated at 8–11 s⁻¹) along the edge of root cells due to the action of cyclosis. Cyclosis causes microbe protoplasts to reproduce more often, and fewer initial intracellular microbe cells result in the production of more small protoplasts. Electrolyte seeps from internal bacterial protoplasts when they are exposed to reactive oxygen, and oxidised bacterial components may enter plant root cells across the plasma membrane. The constant migration of microorganisms across the root cell's plasma membrane may reduce the nutritional gradients between its protoplasts. Increased efficiency in the transmission of nutrients between the cell and the microorganism. Root hairs lengthen as a result of the buildup of living intracellular bacteria in the root hair tip (perhaps via nitric oxide signaling), and pores that form in the root hair tips occasionally allow microbe protoplasts to escape. In the rhizosphere, bacteria rebuild their cell walls as they infiltrate soil populations (Figure 2(C, D)). What triggers root hairs to regularly release microbial protoplasts is unknown. The most likely process of ejection, which violently expels microbe protoplasts from the hair, may involve potassium loading into the vacuole at the base of the hair cell and subsequent enlargement in the hair vacuole that propagates from the hair base to the tip (Verma et.al.2018).

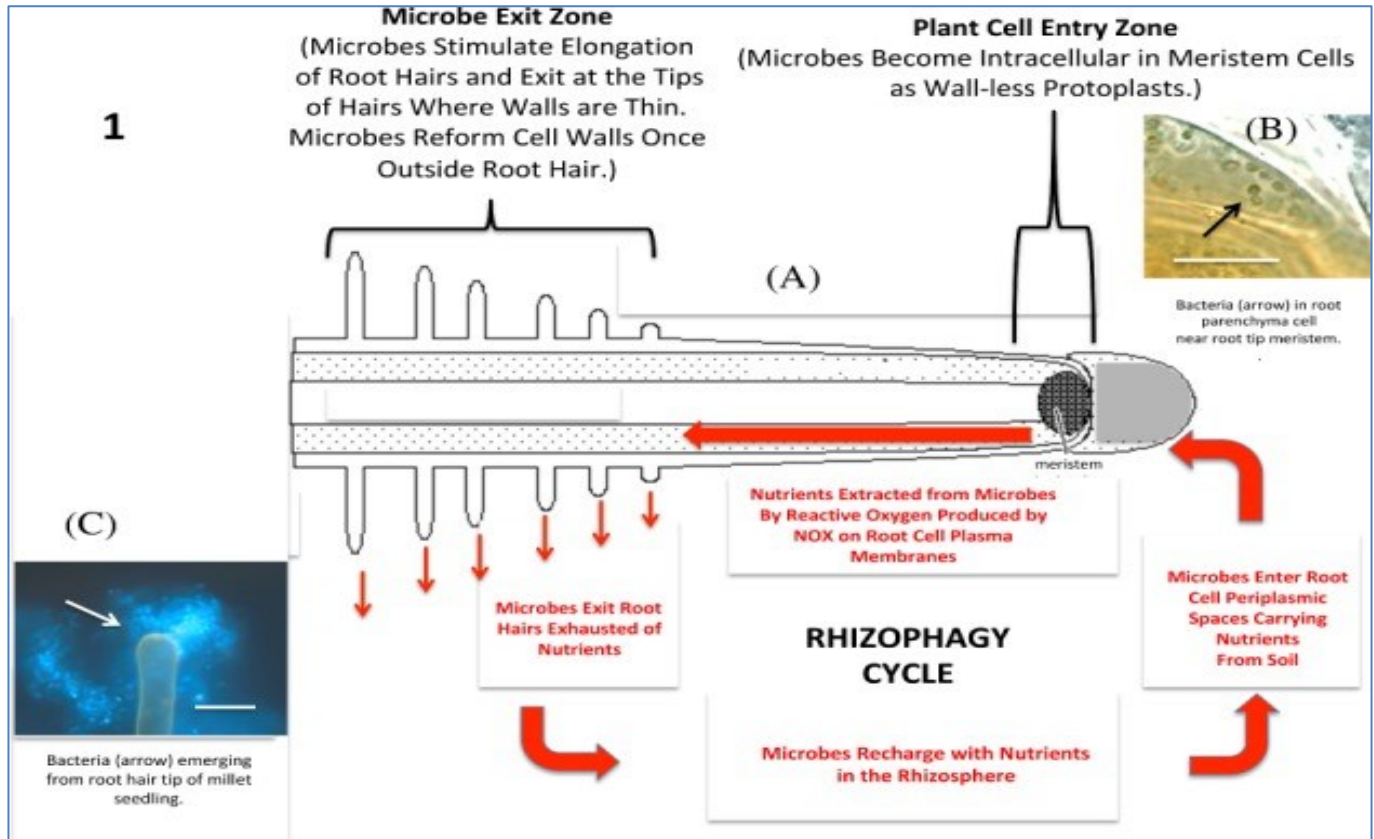


Figure 1 An illustration of the rhizophagy cycle is provided. Microorganisms enter root cells at the meristem at the root's tip and exit root cells at the terminals of growing root hairs, as shown in the diagram of the rhizophagy cycle in (A). Microorganisms involved in the rhizophagy cycle alternate between an intracellular endophytic phase and a free-living soils phase; the former involves obtaining soil nutrients, whereas the latter involves oxidatively extracting them. An agave seedling is depicted in (B) with bacteria (arrow) in the periplasm of a parenchyma cell near the root tip meristem (bar = 20 m; coloured with DAB and subsequently aniline blue). (C) The root hair tip of a grass seedling showing bacteria emerging from it (arrow; bar = 20 m; dyed with fluorescent nucleic dye SYTO 9). (White et.al 2018)

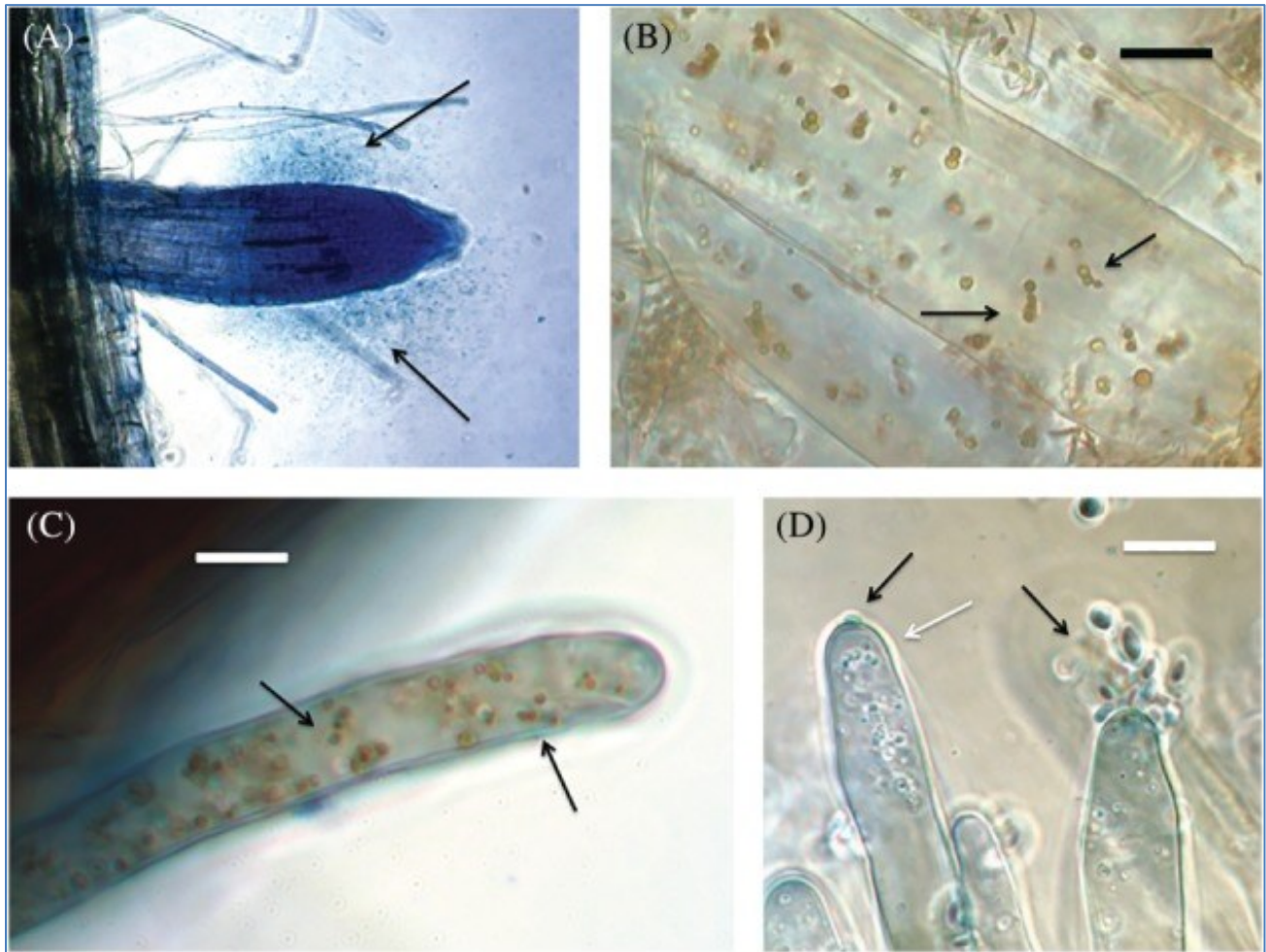


Figure 2 Shows bacteria in plant roots. (A) A cloud of bacteria (shown by arrows) is present surrounding the root tip meristem of the invasive reed grass *Phragmites australis*. (B) A root parenchyma cell from *P. australis* labelled with DAB and subsequently aniline blue to reveal bacterial replicating protoplasts (arrows) in the periplasm. (C) Bacterial protoplasts (arrows) are visible in the periplasm of a *Cynodon dactylon* grass root hair after being dyed with DAB and aniline blue. (D) After being stained with DAB, endophytic yeast (*Rhodotorula* sp.) was injected into the root hairs of a clover (*Trifolium repens*), showing yeast protoplasts inside the root hairs (white arrow) and yeast being ejected from root hair tips (black arrows) (White et.al 2019).

As part of the rhizophagy cycle, plants raise microbes to act as nutrient carriers and stimulate plant development. One study found that around 30% of the nitrogen in grass plants came through rhizophagy. According to gene responses in plants, plant antioxidants and nitrate transporters are commonly among the genes elevated in plants after endophyte infection. These increased genes may be brought on by roots' heightened oxidative reactions and larger levels of nitrate liberated during protein degradation (Redman et.al 2002). Another experiment using tomato seedlings found that raising the carbon dioxide level inhibited the generation of superoxide and the extraction of nutrients from microorganisms. This restriction of the rhizophagy cycle reduced the uptake of potassium, calcium, and Sulphur by seedlings. It's plausible, nevertheless, that rhizophagy cycle. However, it's probable that the cycle of rhizophagy is essential for acquiring rare micronutrients (including iron, copper, and zinc). Numerous bacteria migrate across the earth, eating nutrients. They effectively sequester micronutrients through the use of siderophores and other techniques. Metals also adhere to microbe cell walls because they have a positive

charge whereas the latter have a net negative charge (Irrizary et.al.2018). Contrary to nodule-forming symbioses, the rhizophagy cycle appears to be present in the majority of vascular plants. It is likely an essential mechanism for plants to absorb nutrients.

2.4 Plants utilizing microbes for mining soil metals.

Plant roots release organic acids such acetic acid, citric acid, and malic acid. Among the metals that these organic acids have a great affinity for are iron, zinc, copper, and magnesium. High affinity transporters are found in many bacteria, including *Bacillus* species, and they enable the recognition and uptake of these organic acid-metal complexes. The organic acid-metal complexes provide bacteria with access to both carbon and mineral resources, both of which are advantageous to their nutritional status. The bacteria' entry into the root cells allows plants to remove the metals from them (Pawlowski et.al.2012). Plants likely get the essential soil elements they need for survival and growth from the rhizophagy cycle, which harvests metals from soil microbes (Figure 3).

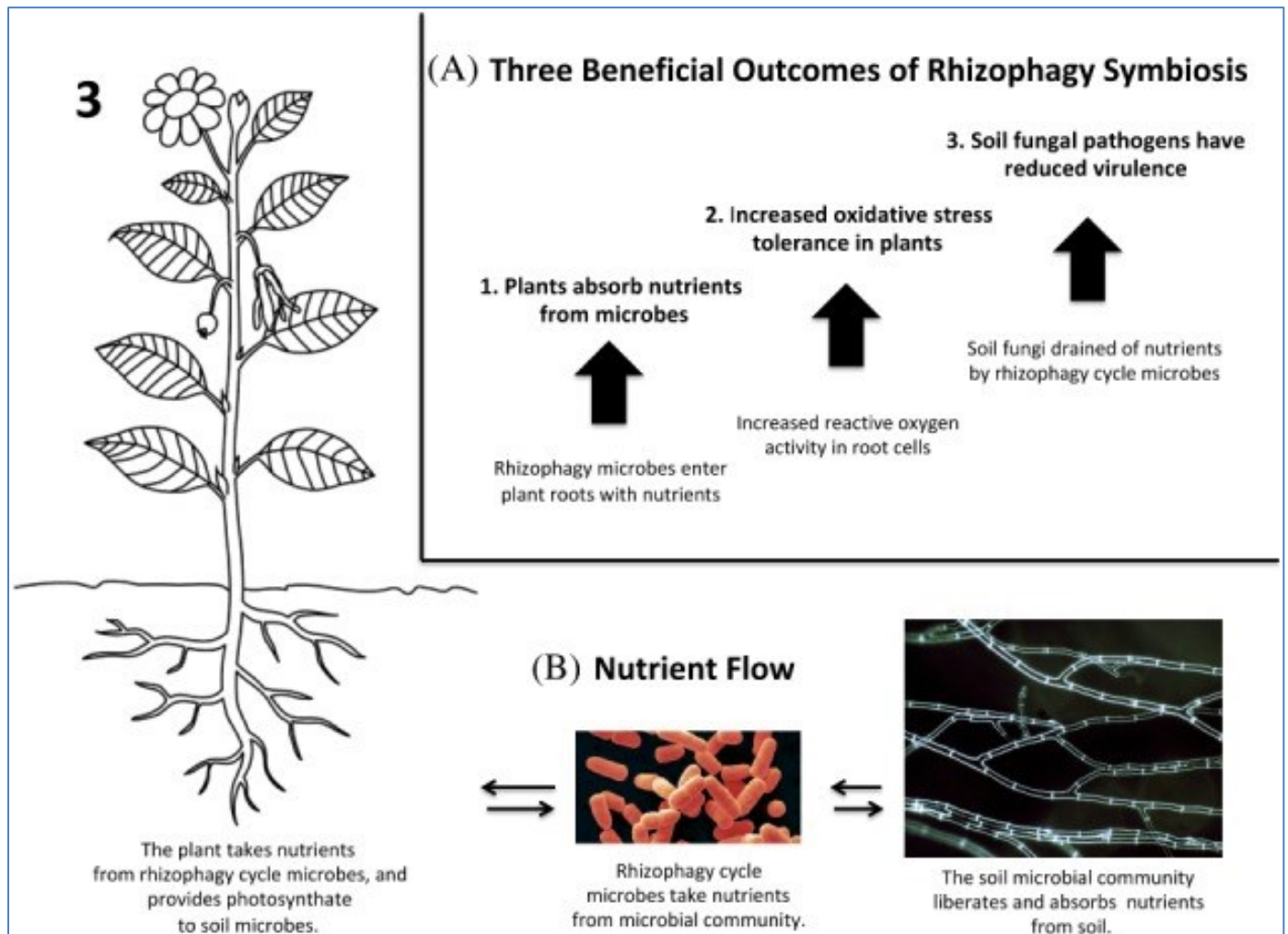


Figure 3 Rhizophagy symbiosis positive impacts and nutrient flow (A,B). Some advantages of this procedure include the ones listed below: Plants take up nutrients from internalised microbes, reactive oxygen production in roots increases plant resistance to oxidative stress, and rhizophagy microbes' nutrient scavenging from soil fungi lowers the virulence of potential pathogens in the soil microbial community. (B) Rhizophagy microorganisms serve as a middleman in the movement of nutrients from plant roots to the soil microbial community and back to the plant, mediating the flow of rich plant nutrients such as those produced during photosynthetic processes. (White et.al. 2019)

2.5 Rhizophagous microbes ingest nutrients from other soil organisms

By causing nutrient leakage from their cells, rhizophagy bacteria, such as *Bacillus* species, can deprive other soil microorganisms of their food supply. Because of this, they are able to transmit nutrients from the soil's microbial community to the plant (Figure 3(B)). Rhizophagy microorganisms scavenge nutrients from other microbes by using 'hemolysins' (biosurfactants) to break pores in the target germs' membranes and allow the nutrients to leak out. Lipopeptides called hemolysins, which are frequently found in *Bacillus* species, serve as biosurfactants that increase membrane porosity and result in nutrient loss from afflicted organisms, generally fungi. *Bacillus* species and other bacteria colonize the hyphae of soil fungi in the soil, resulting in membrane leakage. A diverse and robust microbial community is vital for the soil because some microorganisms can get nutrients from soil bacteria (Pawłowski et.al.2012). In a way, soil nutrients and fixed nitrogen migrate from soil microorganisms to plants, and then photosynthesized carbon dioxide from plant roots flows out to the microbial community of the soil (Figure 3B). Other nutrients in the rhizosphere may also be soluble or made available to the plant by bacteria in the rhizophagy symbiosis.

3. Endophyte Applications In Agriculture

3.1 Domestication of plants and the eradication of endophytic microorganisms

To support growth and provide defence against biotic and abiotic challenges, plants in natural communities have symbiotic relationships with endophytic microorganisms. However, long-term cultivation and domestication may cause symbiotic microorganisms to disappear. An annual wild tobacco plant *Nicotiana attenuata* was used in a cropping experiment, and it was discovered that The decrease of symbiotic

microbes and a rise in illness brought on by the fungus *Fusarium* and *Alternaria* were observed after 7 years of continuous culture and seed cleaning (Coba et.al. 2017). By recapturing those bacteria from tobacco's wild populations and applying them to seedlings in culture, disease resistance was produced. Natural seed-vectored bacteria were eliminated by acid treatment of cotton seeds to destroy fibres, leaving cotton. Youngsters are more susceptible to illness and stress. The acquisition of microorganisms from uncultivated cotton family plants' seeds significantly increased the stress and disease tolerance of cotton seedlings. The loss of symbiotic bacteria from cotton seeds may be the cause of the high prevalence of illnesses and pests that afflict cotton. Because of rigorous cultivation and modification, crops like maize no longer have the exterior seed structures that originally carried microorganisms like hulls in primitive teosinte. In comparison to earlier flint-type Indian maize or tropical maize, Due to the loss of symbiotic endophytes from hybrid maize varieties, current hybrid varieties need higher inputs of nitrogen and insecticides to produce yields. The microbially rich seed husk of Bermuda grass (*Cynodon dactylon*) is commonly removed, and the plant is then treated with fungicides, depriving grass seedlings of their native endophytes. This occurs in a number of different types of grass seeds. It's likely that many crop species have lost their symbiotic endophytic microbes since we don't know how long-term usage of inorganic fertilizers, fungicides, or other agrochemicals impacts endophytic bacteria in crop plants. The function of the seed community of microbes may change as a result of the loss of specific members of the natural endophytic community, potentially making seeds less able to grow and survive (Marschner et.al.1994). It may be required to collect endophytic microorganisms from wild relatives of crops in order to compensate for losses of vital endophytic microbes and lessen

dependency on agrochemicals in crop agriculture and reintroduce them into agricultural systems—possibly as seed treatments.

3.2 Mechanisms for the control of illness by endophytes

One of the various ways endophytes benefit plants is by inhibiting pathogen fitness and growth. This encompasses a number of processes, such as host defence gene upregulation, synthesis of antimicrobial metabolites, development of systemic resistance, or increased resistance in plants against infections, as well as direct antagonistic competition with pathogens for space and resources. According to a growing body of research, endophytes (fungi and bacteria) defend host plants from ailments and other pests from seed development to the end of the plant's life (Behie et.al.2013). A number of antifungal compounds, including phenazine-1-carboxylic acid, 2, 4-diacetylphloroglucinol, pyrrolnitrin, pyoleutin, and volatiles, are produced by the bacterial endophytes *Pseudomonas aeruginosa* and *P. fluorescens*. Because they create a variety of physiologically active chemicals that may function as phytopathogen inhibitors, similar substances containing hydrogen cyanide that significantly slow down the growth of fungus and *Bacillus* species are essential disease-controlling organisms. They create a range of lipopeptides that cause fungal hyphal membranes to leak, significantly reducing their pathogenicity as plant infections. This could have the effect of quenching the quorum, causing pathogenic fungus to remain inactive and not spread disease. Many of the antifungal substances made by endophytes target the fungi's membranes, causing nutrition leakage and decreasing the virulence of the fungi (White et.al.2014). Additionally, endophytic symbionts may increase plant resistance and shield plants against a variety of diseases, especially by enhancing salicylic acid production through induced systemic defence

(ISR). Through enhancing the ethylene or PR proteins, as well as the salicylic acid, Jasmonate, and JA pathways.

3.3 Endophytes alter oxidative stress tolerance in plants

Plant cells respond to environmental stressors by producing reactive oxygen species, such as superoxide, hydroperoxyl radicals, hydrogen peroxide, and hydroxyl radicals. Plant proteins, nucleic acids, and membranes may become oxidatively damaged as a result of ROS emission within plant tissues and cells. Some endophytes increase abiotic and biotic stress tolerance. Plant defence mechanisms are engaged at the beginning of endophytic colonization, releasing ROS (Atsatt et.al.2014). A qPCR investigation revealed that bacteria in the initial phases of colonization increased the transcript levels of genes that degrade ROS, such as glutathione reductase and superoxide dismutase. Further reducing oxidative damage to plants caused by pathogens that create or produce ROS may be achieved by upregulating host ROS-degrading genes. Tissues of infected tall fescue grass show higher levels of osmoprotective mannitol and other antioxidant fungal carbohydrates are present in the endophytic fungus *Epichloa coenophiala*, which aids in protecting plants from oxidative stress (Hill et.al.2013). Numerous plants have been demonstrated to develop abiotic stress resistance when exposed to the endophytic fungus the Indian *Piriformospora*. Within 24 hours of being exposed to polyethylene glycol to mimic drought stress, Chinese cabbage (*Brassica rapa*) infected with *Piriformospora indica* displayed upregulation of the antioxidant enzymes peroxidases, catalases, and superoxide dismutases in the leaves. The expression of the drought-protective genes DREB2A, CBL1, RD29A, and ANAC072 was elevated in the leaves of plants harboring endophytes. A meta-genome analysis of rice endophytes revealed the existence of several genes that encode enzymes

involved in defence against excessive ROS, such as glutathione synthases and glutathione S-transferases. The stems of poplar trees were found to have the endophytic bacterium *Enterobacter* sp. 638. In addition to several superoxide dismutases, including as SOD A, SOD B, and SOD C, it also contained genes for catalases, hydroperoxide reductases, thiol peroxidases, and hydroperoxide reductases. *Pestalotiopsis microspora* endophytes have produced the strong antioxidant chemicals pestacin and isopestacin. According to reports, endophytes can lessen the oxidative stress that metal-contaminated soil causes in plants. In Ni-contaminated substrates, the endophytic *Paecilomyces formosus* infection of soybean greatly reduced lipid peroxidation and boosted the synthesis of superoxide dismutase, catalase, peroxidase, and polyphenol oxidase (Warner et.al. 2002).

3.4 Endophyte-mediated anti-herbivory, section

To stop insects and other herbivores from consuming plants, several endophytes produce chemicals. Species of the fungus *Epichloa* live inside the aerial portions of plants, such as the leaves, culms, and seeds, and they generate a range of alkaloids that discourage herbivores from feasting on them. These endophytes have been used to help commercial forage and turf grasses become more pest-tolerant. However, only grasses and sedges contain endophytes from this group of species. It has also been demonstrated that fungi endophytes of the morning glory family produce ergot alkaloids, which render morning glory plants extremely hazardous to herbivores (Barun et.al 1991). Similar to this, endophytic fungus in the genus *Undifilum* generate the deadly alkaloid swainsonine, a potent poison, in plants generally known as "locoweeds" in the family Fabaceae. Toxin and anti-herbivore substance. These few instances imply that endophytes that prevent

insect pests from feeding may be more widespread than is currently known. As a result of a more thorough examination of fungal and bacterial endophytes in plants, many other endophytes that could be exploited in crops to reduce insect pest feeding or boost plant tolerance to feeding may be found (White et.al. 2014).

3.5 Transgenic endophytes

Transgenically altering the genomes of endophytes may be a beneficial tactic and an alternative to genetically altering the host plant. Genes added to endophytic microorganisms may bestow novel traits that are beneficial for the development of human or animal pharmaceuticals as well as the biocontrol of plant diseases and host plant growth (Shehata et.al.2017). For example, the endophytic bacterium *Clavibacter xyli* subsp. *Cynodontis*, which lives in the xylem of numerous plant species, was genetically altered to control insects. Another instance involves the transformation of an endophytic *Burkholderia pyrrocinia* JKSH007 with the Bt endotoxin gene to produce an insecticidal protein that is specific to the second instar of *Bombyx mori* silkworms. Furthermore, an antifungal gene was added to an endophytic *Pseudomonas putida* WCS358r strain and were introduced into wheat, which caused a decline in the number of harmful *Fusarium* spp. in the soil. It appears plausible that future crop management strategies could make use of transgenically altered endophytes (Meyers et.al.2014). The confinement of endophytic bacteria to certain plants, however, may be challenging or impossible due to their mobility.

3.6 Obstacles to and developments in the use of endophytes in agriculture

The advancement of research into the uses of endophytes in crops has been hampered by a general lack of knowledge about the common occurrence of communities of endophytic

microorganisms in plant tissues. The lack of attempts to comprehend the roles of endophytes in promoting plant growth and improving plant health can also be attributed to the general and widespread belief that the majority of microorganisms on plants are pathogenic or have minimal effects. An important step forward in our understanding of the significance and functionality of endophytes has been made possible by the steady accumulation of research over the past few decades that has shown that endophytes are widespread in plants and have a favorable impact on their growth and health (Holland et.al.1997). In recent years, the search for beneficial endophytes and other the development and marketing of plant biostimulants, particularly endophytes, has been a key focus of certain businesses, which has improved the use of microorganisms in agricultural applications. Recent regulatory texts in the European Union and the 2018 Agriculture Improvement Act (commonly known as the 2018 Farm Bill) in the United States specifically addressed biostimulants and their regulation to support the development of uses for microorganisms in agriculture (Kogan et.al.1997). The scientific, legal, and regulatory environment appears to be in place for some significant upcoming breakthroughs in endophytic microbe products and applications in agriculture.

4. Conclusion

In commercial crop plants, microbial endophytes and soil microorganisms could be used to directly improve plant health and increase productivity (Rodriguez et.al.2019). Endophytes may also have advantages when they lessen infections, insect damage, and weedy plant competition. With current agricultural techniques, it might be difficult to increase crop yield without endangering the health of agricultural soils and degrading the quality of food with agrochemicals

(Johnston et.al.2016). A major decrease in the use of chemicals in crop production may result from the present attempts to discover microbial crop stimulants. Endophytes might make it easier to grow crops without using as many pesticides, fungicides, insecticides, or herbicides (Santhanam et.al.2015). We anticipate a change in cultivation methods that will place a greater emphasis on cultivating plants in a way that maximizes their interactions with endophytes and soil microorganisms. Microbe amendments to soils and plants that function to provide nutrients to plants (for example, through the rhizophagy cycle) while also suppressing pathogen virulence, discouraging insect feeding, and reducing growth of competing weeds can result in enhancing microbial diversity with agricultural practises that are more considerate of natural processes (Irrizarry et.al.2017). To achieve this future, we must have a better understanding of how microorganisms' function in soils and in plants. We must further our understanding of how to maximize microbial functions in order to increase crop protection and productivity.

References

1. Atsatt PR and Whiteside MD, Novel symbiotic protoplasts formed by endophytic fungi explain their hidden existence, lifestyle switching, and diversity within the plant kingdom. *PLoS ONE* 9:e95266, 2014.
1. Braun V and Focareta T, Pore-forming bacterial protein hemolysins (cytolysins). *Crit Rev Microbiol*, 1991, 18, 115–158.
2. Beltrán-García MJ, White JF, Prado FM, Prieto KR, Yamaguchi LF, Torres MS *et al*, Nitrogen acquisition in *Agave tequilana* from degradation of endophytic bacteria. *Sci Rep*, 2014, 4, 6938.

3. Behie SW and Bidochaka MJ, Insects as a nitrogen source for plants. *Insects*, 2013, 4, 413–424.
4. Coba de la Peña T, Fedorova E, Pueyo JJ and Lucas MM, The Symbiosome: legume and rhizobia co-evolution toward a nitrogen-fixing organelle? *Front Plant Sci*, 2017 8, 2229.
5. Compant S, Clement C and Sessitsch A, Plant growth-promoting bacteria in the rhizo- and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. *Soil Biol Biochem*, 2010, 42, 669–678.
6. Gond SK, Bergen M, Torres MS and White JF, Effect of bacterial endophyte on expression of defense genes in Indian popcorn against *Fusarium moniliforme*. *Symbiosis*, 2015, 66, 133–140.
7. Irizarry I and White JF, *Bacillus amyloliquefaciens* alters gene expression, ROS production, and lignin synthesis in cotton seedling roots. *J Appl Microbiol*, 2018, 124, 1589–1603.
8. Hill PW, Marsden KA and Jones DL, How significant to plant N nutrition is the direct consumption of soil microbes by roots? *New Phytol*, 2013, 199, 948–955.
9. Hardoim PR, van Overbeek LS, Berg G, Pirttilä AM, Compant S, Campisano A *et al*, The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiol Mol Biol Rev*, 2015, 79, 293–320.
10. Holland MA, *Methylobacterium* and plants. *Recent Res Dev Plant Physiol*, 1997, 1, 207–213.
11. Johnston-Monje D and Raizada MN, Conservation and diversity of seed associated endophytes in *Zea* across boundaries of evolution, ethnography and ecology. *PLoS ONE* 6: e20396, 2011.
12. Kandel SL, Joubert PM and Doty LS, Bacterial endophyte colonization and distribution within plants. *Microorganisms*, 2017, 5, 77.
13. Kogan AK, Grachev SV, Eliseeva SV and Bolevich S, Carbon dioxide--a universal inhibitor of the generation of active oxygen forms by cells (deciphering one enigma of evolution) PAH. 2017, 2, 204–217.
14. Marschner H and Dell B, Nutrient uptake in mycorrhizal symbiosis. *Plant Soil*, 1994, 159, 89–102.
15. Myers S, Zanobetti A, Kloog I, Huybers P, Andrew D, Leakey B *et al*, Increasing CO₂ threatens human nutrition. *Nature*, 2014, 510, 139–142.
16. Ongena M and Jacques P, *Bacillus* lipopeptides: versatile weapons for plant disease biocontrol. *Trends Microbiol*, 2008, 16, 115–125.
17. Paungfoo-Lonhienne C, Rentsch D, Robatzrk S, Webb RI, Sagulenko E, Nasholm T *et al*, Turning the table: plants consume microbes as a source of nutrients. *PLOS ONE*, 2010, 5, e11915.
18. Prieto KR, Echaide-Aquino F, Huerta-Robles A, Valerio HP, Macedo-Raygoza G, Prado FM *et al*, Endophytic bacteria and rare earth elements; promising candidates for nutrient use efficiency in plants, in *Plant Macronutrient Use Efficiency*, ed. by Hossain M, Kamiya T, Burritt D, Tram L-SP. and Fujiwara T. Academic Press, Cambridge, MA, 2017, 285–302.
19. Pawlowski K and Demchenko KN, The diversity of actinorhizal symbiosis. *Protoplasma*, 2012, 249, 967–979.
20. Rodriguez RJ, Woodward C, Kim YO and Redman RS, Habitat-adapted symbiosis as a

- defense against abiotic and biotic stresses, in *Defensive Mutualism in Microbial Symbiosis*, ed. by White JF., Jr and Torres MS. CRC Press, Boca Raton, FL, 2009, 335–346.
21. Redman RS, Sheehan KB, Stout RG, Rodriguez RJ and Henson JM, Thermotolerance generated by plant/fungal symbiosis. *Science*, 2002, 298, 1581.
 22. Santhanam R, Luu VT, Weinhold A, Goldberg J, Oh Y and Baldwin IT, Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. *Proc Natl Acad Sci U S A*, 2015, 112, E5013–E5020.
 23. Soares MA, Li H, Bergen M and White JF, Functional role of an endophytic *Bacillus amyloliquefaciens* in enhancing growth and disease protection of invasive English ivy (*Hedera helix* L.). *Plant and Soil*, 2015, 405, 107–123.
 24. Shehata HR, Dumigan C, Watts S and Raizada MN, An endophytic microbe from an unusual volcanic swamp corn seeks and inhabits root hair cells to extract rock phosphate. *Sci Rep*, 2017, 7, 1347.
 25. Verma SK, Kingsley K, Bergen M, English C, Elmore M, Kharwar RN *et al*, Bacterial endophytes from rice cut grass (*Leersia oryzoides* L.) increase growth, promote root gravitropic response, stimulate root hair formation, and protect rice seedlings from disease. *Plant Soil*, 2017, 422, 223–238.
 26. Verma SK and White JF, Indigenous endophytic seed bacteria promote seedling development and defend against fungal disease in browntop millet (*Urochloa ramosa* L.). *J Appl Microbiol*, 2018, 124, 764–778.
 27. Warner JB and Lolkema JS, Growth of *Bacillus subtilis* on citrate and isocitrate is supported by the Mg²⁺-citrate transporter CitM. *Microbiology*, 2002, 148, 3405–3412.
 28. White JF, Crawford H, Torres MS, Mattera R, Irizarry I and Bergen M, A proposed mechanism for nitrogen acquisition by grass seedlings through oxidation of symbiotic bacteria. *Symbiosis*, 2012, 57, 161–171.
 29. White JF, Torres MS, Somu MP, Johnson H, Irizarry I, Chen Q *et al*, Hydrogen peroxide staining to visualize intracellular bacterial infections of seedling root cells. *Microsc Res Tech*, 2014, 77, 566–573.
 30. White JF, Kingsley KL, Kowalski KP, Irizarry I, Micci A, Soares MA *et al*, Disease protection and allelopathic interactions of seed-transmitted endophytic pseudomonads of invasive seed grass (*Phragmites australis*). *Plant Soil*, 2017, 422, 195–208.
 31. White JG, Kingsley KL, Verma SK and Kowalski K, Rhizophagy cycle: an oxidative process in plants for nutrient extraction from symbiotic microbes. *Microorganisms*, 2018, 6, 95. 10.3390/microorganisms6030095.
 32. White JF, Torres M, Sullivan R, Jabbour R, Chen Q, Tadych M *et al*, Occurrence of *Bacillus amyloliquefaciens* as a systemic endophyte of vanilla orchids. *Microscopy Res Tech*, 2014, 77, 874–885. 10.1002/jemt.22410.
 33. White, James & Kingsley, Kathryn & Verma, Rajan & Obi, Nkolika & Dvinskikh, Sofia & Elmore, Matthew & Verma, Satish K. & Gond, Surendra & Kowalski, Kurt & Zhang, Qiuwei.. Review: Endophytic Microbes and Their Potential Applications in Crop Management. Pest Management Science. 2019.