Wheat Microbiome: Potentiality of Alleviating Drought Stress

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KEYWORDS

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ABSTRACT

Climate change is a major threat that affects global crop production. Global warming impacts crop production through abiotic stresses. Drought is one of the biggest threats to wheat cultivation. In this regard, various technologies, such as breeding programs and genetic engineering, are being applied to cope with this threat. Such methods are expensive and time-consuming. Myriad adaptive mechanisms are used by wheat plants to cope with drought stress. However, plant associations with microbiomes have gained attention lately. There is much evidence of both endopytic and rhizospheric bacteria in promoting the growth of wheat plants under drought. Their effects on plants are either by triggering direct or indirect responses to mitigate drought stress. Such responses exist at physiological, morphological, biochemical, and molecular levels. Biochemical such as the production of phytohormones, extracellular polymeric substances (EPS), siderophore, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, antioxidants, osmolytes, and volatile organic compounds, in addition to solubilization of minerals and nitrogen fixation, or at molecular levels such as activation of stress genes and transcription factors. Or through many morphological and physiological responses, such as increasing relative water content (RWC) and root length and weight. Thus enhancing growth and tolerance for drought. This review highlights the potential of rhizospheric and endophytic bacteria to alleviate drought stress in wheat plants through different mechanisms, which are a sustainable and environmentally friendly way to mitigate drought.

1. Introduction

Wheat (Triticum spp.) is considered one of the most essential food crops all over the world (Tadesse et al., 2016). Recently, the production of wheat has not met consumer demand, resulting in hunger and price instability worldwide. According to FAO, the demand for wheat is expected to increase by 60% with a predicted world population of 9 billion (FAO, 2012). To meet these demands as a result of this dramatically increasing population, an increase of approximately 25%–70% above current production levels may be sufficient to meet 2050 crop demand in general and approximately 1.6% for annual wheat production (Tadesse et al., 2016).

Different abiotic stresses can reduce crop yield, therefore, they control the distribution of plant species. Abiotic stress and its effects on plants are a focus of interest because of the potential impact of climatic change on rainfall patterns and temperature extremes, the salinization of agricultural lands by irrigation, and the overall need to maintain or increase agricultural productivity on marginal lands. In their environment, plants may be exposed to several distinct abiotic stresses, either concurrently or at different times throughout the growing season (Tester and Bacic, 2005).

The most common abiotic stresses that plants may face are a decrease in the availability of water (drought), extremes of temperature, including freezing, decreased availability of essential nutrients from the soil (or excessive levels of toxic ions during salt stress), and excess light (especially when photosynthesis is restricted). Wheat is susceptible to drought stress, particularly until the heading or germination stage and during the grain filling period (Ali, 2019). After a period of water deficiency, many physiological, biochemical, and phenological changes occur. An increase in root/shoot ratio due to drought is a result of a higher level of abscisic acid, which, together with auxin, cytokine, and gibberelic acid, represses the development of shoots and stimulates the growth of roots (Talaat, 2019). Recent studies found that the root microbiome is crucial for nutrient uptake, in addition, stressed plants were found to affect beneficial microbiome assembly (Bakker et al., 2018).

Plant growth is affected by soil microorganisms. Recently, several studies were conducted to identify the relations and interactions between soil and plant (Averill et al., 2014). Plants have evolved to cope with biotic and abiotic stresses in association with soil microorganisms (Lemanceau et al., 2017). Plants are in association with a large number of microorganisms in the rhizosphere, leaf surfaces, endosphere, and other parts such as pollen and nectar, which collectively are known as the plant microbiome (Liu et al., 2017). Together with the plant, they form a holobiont (Liu et al., 2018). The ecophysiology of plant-microbe interaction is very complicated and interwoven. Therefore, a fully understood of these multiple fine-tuning signals and their integration that generated through plant-microbe interactions is required for sustainable crop improvement (Chen et al., 2022).

The revolution in molecular biology led to the development of the omics technique, which recently gained prominence in diversity studies of microbes, enabling researchers to uncover soil microbial communities across different soil habitats (Alawiye and Babalola, 2019). The term 'metagenomics' was first coined in 1998 and encompasses the qualitative and quantitative characterization of all genetic material sampled from a defined environment (Handelsman, 2005). This can be achieved by sequence analysis of the total isolated genomic DNA from that sample (Hugenholtz and Tyson, 2008). Metagenomes can use either targeted sequencing, e.g. ribosomal DNA or shotgun sequencing, covering the entire genomic sequence, which is carried out by next generation sequencing (NGS)-based OMICS technologies, such technology can differentiate between bacterial endophyte metagenomes and any contaminating plant genomic sequences (Fadiji and Babalola 2020). Recently, Next Generation Sequencing (NGS) has been deployed to uncover the nature and role of rhizosphere and endophytic microbiomes in different environments (Zhang et al., 2020a). This review will, thus, focus on both wheat root endophyte and rhizosphere bacterial microbiomes and the mode of action of the wheat microbiome in enhancing wheat plant performance under drought.

2. Wheat Microbiome

Many definitions were given to the microbiome by researchers. Schlaeppi and Bulgarelli (2015) have defined microbiota or microbiome, as a set of genomes of the microorganisms in some habitat. It’s also been defined as the microbial communities associated with any plant that can live, thrive, and interact with various tissues such as roots, shoots, leaves, flowers, and seeds (Turner et al., 2013). The plant microbiome is not stable; it depends on and is stimulated by the host, stresses, and surrounding environment (Timm et al., 2018). Variations in the microbiome are not a passive response of plants but rather an outcome of millions of years of evolution; plants are more likely to seek cooperation with microbes to fight stresses (Chen et al., 2018). As a matter of fact, plants use the ‘cry for help’ strategy under biotic or abiotic stress (Bakker et al., 2018). Plants take advantage of beneficial microbes in their environments using a range of chemical stimuli to enhance their capacity to cope with stresses (Bakker et al., 2018).

Plant roots are surrounded by complex communities of microorganisms, which include bacteria, fungi, algae, viruses, archaea, cynobacteria, and protozoa (Verma and Suman, 2018), and are considered the host’s second genome (Wei et al., 2019). In addition, roots are the primary site for import and export molecules this results in a “rhizosphere” that supports higher bacterial numbers than do bulk soils (Hinsinger et al., 2009). Root rhizosphere is a hot spot zone for mutualistic host-microbe interactions (Muller et al., 2016). These interactions are classified as rhizospheric and endophytic (as shown in Fig. 1).

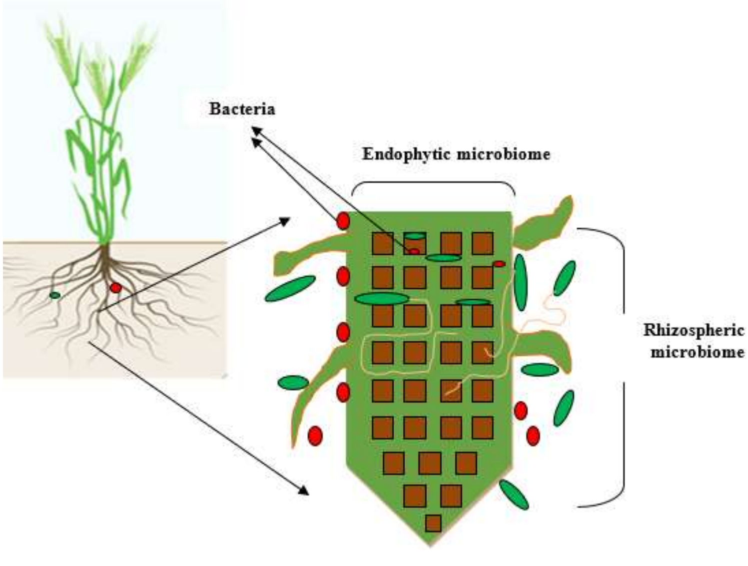

Figure 1: Assemblage of microbes in and around wheat plant.

Microbes benefit from root exudates, which provide energy sources in the form of sugars and organic acids (Van Dam and Bouwmeester, 2016). While plants benefit from mineral mobilization (Plociniczak et al., 2016), improving growth, drought and salt tolerance (Naveed et al., 2014), and protection against soil-borne pathogens (Chen et al., 2018). The complexity of these interactions has led researchers to focus on the pathogenicity of some microbes (Philippot et al., 2013).

The composition of the soil rhizosphere microbial community is affected by many factors, such as ambient conditions, soil properties, and background microbial composition (Qiao et al., 2017). Moreover, the variations in temperature, humidity, and precipitation significantly influence wheat microbiome composition. Azarbad et al. (2018) found that the water regime primarily rules the bacterial and fungal community structure in the wheat rhizosphere. Further, the geographic distance (Fan et al., 2017) and seasonal changes (Schlatter et al., 2019) spatially determine the wheat microbial community structure. More fungi and fewer bacteria were observed in wheat grown under water stress (Azarbad et al., 2018). In fact, plants are able to shape this community, it was found that different plant species host specific communities when grown on the same soil (Bazghaleh et al., 2015).

Certain microbes prefer certain plants as dictated by plant molecular signaling, root morphology, rhizosphere deposits, and root exudates (Philippot et al., 2013). Furthermore, the ever-changing rhizosphere microbiome affects microbe-driven soil functions and plant growth and productivity (Schlaeppi and Bulgarelli, 2015).

Some microbes are present as endophytes inside roots (Gehring et al., 2006). Many of these microorganisms remain unknown and uncultured (Amann et al., 1995). The majority of rhizospheric microorganisms are fungi (Staniek et al., 2008), followed by bacteria (Santoyo et al., 2016). However, they fluctuate between the internal space and plant surface during colonization (Hallman et al., 1997). In fact, the mechanisms by which microorganisms are able to exist and survive in plant tissues are still not fully understood. Nonetheless, endophytes are able to move between tissues inside the plant host (Annah et al., 2015). Both rhizospheric and endophytes are available in huge densities, times more than those for host plant cells (Buee et al., 2009). The first step of bacterial colonization involves a dispersal phase in which bacteria are able to recognize primary metabolites in root exudates. Depending on their chemotaxis, they migrate toward the rhizoplane (root surface) and attach themselves to it (Liu et al., 2017). Subsequently, bacteria formed microcolonies or biofilm on the root surface, and through wounds or fissures formed at the base of lateral roots, endophytic bacteria colonized the root endoshpere. Intracellular entry is achieved by endophytic bacterial secretion of cellulase and other enzymes that degrade plant cell walls (Liu et al., 2017).

Current microorganism-plant interaction studies are limited to symboitic relationships, leaf pathogens, and mycorrhizal fungi. On the contrary, rhizospheric microbiomes and their role in different plant functions like growth, health, and tolerance against abiotic and biotic stresses are still under investigation (Ahlawat et al., 2018). Plants are usually colonized by more than one type of endophyte. Thus, the high species number and the high amount of microbial biomass in small populations result in multitrophic interactions between bacteria, micro- and macroscopic fungi, microfauna, plants, and the environment (Gan et al., 2017).

Wheat plants interact mostly with either common microbes or niche-specific microbes. Arthrobacter nicotianae, Bacillus amyloliquefaciens, B. sphaericus, B. subtilis, Paenibacillus amylolyticus, P. polymyxa, Micrococcus luteus, Pseudomonas aeruginosa, and P. azotoformans are the most commonly reported microbes in the wheat phyllosphere, rhizosphere, and endophyte (Verma and Suman 2018). Actinobacteria, Bacteroidetes, Firmicutes, Proteobacteria, and Gemmatimonadetes are the main taxonomic bacterial phyla. According to Verma and Suman (2018), bacterial microbiomes, viz. Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria, which occupy a major portion, and three classes of bacteria, namely, Alphaproteobacteria, Betaproteobacteria, and Gammaproteobacteria (Mahapatra et al., 2020), are present in wheat (as shown in Fig. 2). Moreover, Proteobacteria are the predominant endophytes in roots and Firmicutes and Actinobacteria in shoots (Robinson et al., 2016).

The developmental stages of wheat plants influence microbiome profiles (Comby et al., 2016). In fact, the microbiome profile of wheat is both spatially and temporally dynamic (Chen et al., 2022). Thus, understanding and recognizing microbiome profiles, interactions, and influence factors aid in improving inoculation methods and wheat cultivation enhancement under both biotic and abiotic stresses. Furthermore, it allows us to explore approaches for the manipulation of the microbiome to improve wheat growth and yield. On the other hand, determining the microbiome structures of rhizospheric and endophytic bacterial species is a key to leveraging crop production in a sustainable way.

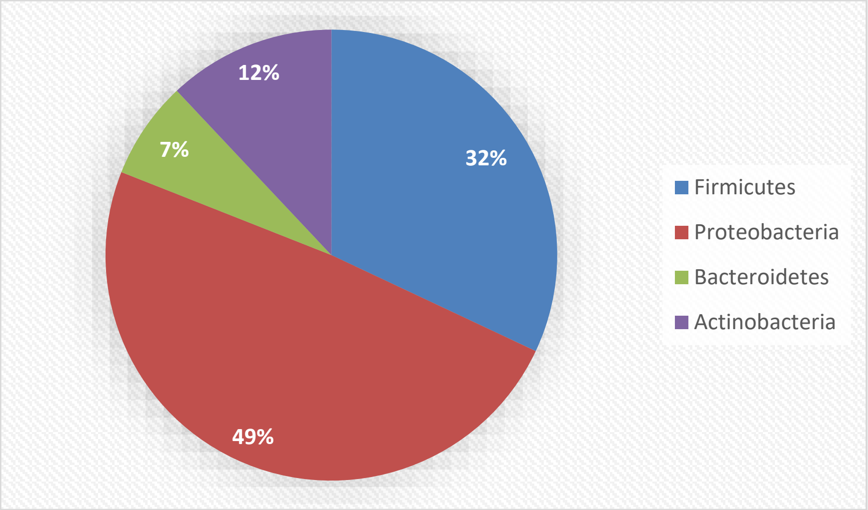

Figure 2: Abundance of wheat microbiomes belonging diverse phylum (Mahapatra et al., 2020)

3. Wheat Rhizosphere Microbiome

Over 100 years ago, the rhizosphere was described as the area around a plant root that is inhabited by a unique population of microorganisms (Hiltner, 1904), while Liao (2023) defined it as the area of soil surrounding the root system. Rhizosphere soil serves as a bridge, enabling the exchange of materials and energy between microbes and plants (Bakker et al., 2018). Plant genetic makeup (Turner et al., 2013; Lu et al., 2018) as well as soil physical and chemical properties influence the rhizosphere microbiome abundance and diversity among plant species (Lundberg et al., 2012). Different stresses influence root exudates and hence determine the nature of rhizospheric microbial communities (Lakshmanan et al., 2012). It can be concluded that the rhizospheric microbiome may be regulated by plants in their favor by enhancing the growth of microorganisms that are considered beneficial to their growth and health (Cook et al., 1995). Nonetheless, others would consider root exudates simply as plant waste material (Dennis et al., 2010). Agriculture practices also affect the rhizospheric microbiome community (Souza et al., 2015).

Genotype-specific microbiome was investigated by Naz et al. (2014) in two wheat cultivars, and the rhizospheric bacterial diversity was determined at the flowering stage using 16S rRNA rhizosphere libraries, and a huge variation at phylum, class, order, family, and genera levels was detected.

Many of rhizospheric colonized belonging to the genera Pseudomonas (Grichko and Glick, 2001; Sorty et al., 2016), Azotobacter (Sahoo et al., 2014) Azospirillum (Creus et al., 2004), Rhizobium and Pantoea (Sorty et al., 2016), Bacillus (Tiwari et al., 2011; Sorty et al., 2016) Enterobacter (Grichko and Glick, 2001; Sorty et al., 2016), Burkholderia (Barka et al., 2006) and cyanobacteria (Singh et al., 2011), their growth promotion and mitigation of abiotic stresses in plant has been documented. Jorquera et al. (2012) hypothesized that the rhizosphere microbiomes positively influence the survival of some plant species under extreme stress conditions. Rhizobacteria improve and support the growth of plants exposed to flooding (Grichko and Glick, 2001). Under salinity, halotolerant bacteria grow in the company of the host plant and modulate plant traits, which help the plant grow. This was proved by Upadhyay et al. (2009) in wheat grown under saline conditions, 24 rhizobacterial isolates out of 130 were found to be tolerant against high levels of sodium chloride. Moreover, 24 of the isolates produced IAA, 10 were phosphorus solubilizers, 8 were siderophores producers, 6 were gibberellin producers, and 2 had the nif H gene. Bacillus was predominant in the soil-saline condition. The same finding was reported by Siddikee et al. (2010).

In the rhizosphere of Salicornia brachiate, an extreme succulent halophyte flowering plant, Jha et al. (2012) reported several new halotolerant diazotrophic bacteria (Brachybacterium saurashtrense sp.nov., Zhihengliuella sp., Brevibacterium casei, Haererehalobacter sp., Halomonas sp., Vibrio sp., Cronobacter sakazakii, Pseudomonas spp., Rhizobium radiobacter, and Mesorhizobium sp.). In addition, these bacteria also have activities like indole acetic acid production, phosphate solubilization, and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase. In Triticum aestivum, Majeed et al. (2015) indicated that plant inoculation with plant growth-promoting rhizobacteria (PGPR) strains provided a significant increase in shoot and root length and shoot and root biomass. A significant increase in shoot N contents (up to 76%) and root N contents (up to 32%) was observed over the un-inoculated control.

Srivastava et al. (2020) performed 16S rRNA gene amplification sequencing to reveal the bacterial community in the wheat rhizosphere. It was found that the dominant phyla were Proteobacteria (68%), followed by Firmicutes (13%), Bacteroidetes (3%), Actinobacteria (3%), and Acidobacteria (3%). On the other hand, Mahoney et al. (2017) concluded that wheat (Triticum aestivum) cultivars are involved in shaping the rhizosphere by differentially altering the bacterial OTUs consistently across different sites, and these altered bacterial communities may provide beneficial services to the host. Furthermore, these differences were proven by previous evidence that wheat and other plant species differ in the organic compounds they deposit into the soil rhizosphere (Zuo et al., 2014). Differences in root phytochemicals could have been attributed to the observable differences (Zuo et al., 2014). Pseudomonas sp. and Acinetobacter sp. were reported to enhance the production of IAA and ACC deaminase in salt-affected soil in barley and oats (Chang et al., 2014).

3.1 Wheat Rhizoshperic Bacteria

Many rhizospheric bacteria have been reported for their beneficial role in enhancing wheat growth under drought stress. Physiological status, productivity, and nutrient status were improved in wheat inoculated with Serratia marcescens and Pseudomonas sp. under drought stress; both species showed attributes such as production of ACC deaminase, siderophore, exo-polysaccharide, IAA, ammonia, and efficiently solubilized zinc and phosphate (Khan and Singh, 2021). Similarly, Pseudomonas azotoformans enhances various biochemical mechanisms, such as photosynthetic pigment efficiency, antioxidative enzymatic activities, and the production of exopolysaccharides (EPS), indole-3 acetic acid (IAA), and ACC deaminase in wheat under drought conditions (Ansari et al., 2021). Moreover, Variovorax paradoxus, Ochrobactrum anthropi, Pseudomonas fluorescens, and P. palleroniana alleviate water stress in wheat via ACC deaminase activity (Chandra et al., 2019). Phosphorus (P) uptake, growth indices, and grain yield were significantly increased in wheat under water-deficit stress via Pseudomonas helmanticensis and P. baetica (Karimzadeh et al., 2021).

Plant responses to stress are mediated by phytohormones (Kang et al., 2014). Rhizobacteria Bacillus subtilis, Arthrobacter protophormiae, and Dietzia natronolimnaea reduce ABA/ACC content, enhance IAA content, and modulate the expression of a regulatory component (CTR1) of the ethylene signaling pathway and the DREB2 transcription factor in wheat under drought conditions (Barnawal et al., 2017). Furthermore, Bacillus sp. and Enterobacter sp. improved wheat growth under water deficits by increasing the production of salicylic acid (SA) and indole-3-acetic acid (IAA) (Jochum et al., 2019). Pseudomonas fluorescens and P. palleroniana enhanced the growth of wheat under water stress via Indole-3-acetic acid (IAA) production and antioxidant enzyme activity (Chandra et al., 2018). Moreover, Klebsiella sp., Enterobacter ludwigii, and Flavobacterium sp. improved drought tolerance in wheat; their abilities to increase phosphate solubilization, production of EPS, IAA, and siderophore, and enhance ACC deaminase activity offer a potential use as plant-growth-promoting rhizobacteria (PGPR) (Gontia-Mishra et al., 2016). Li H et al. (2020) found that rhizobacteri Streptomyces pactum can enhance the osmotic adjustment and antioxidant capacity of wheat plants under drought via induction of abscisic acid (ABA) accumulation and up-regulation of drought resistance-related gene expression such as EXPA2, EXPA6, P5CS, and SnRK2.

Indole-3-acetic acid (IAA), indole-3-carboxylic acid (ICA), and indole-3-lactic acid (ILA) produced by the rhizobacteria genus Bacillus, Enterobacter, Moraxella, and Pseudomonas; B. amyloliquefaciens; B. muralis; B. thuringiensis; B. simplex; and E. aerogenes; M. pluranimalium; and P. stutzeri improved shoot length, spike length, seed weight, tillers, and number of spikelets in wheat under drought conditions (Raheem et al., 2018).

Chakraborty et al. (2013) found that rhizospheric bacteria Bacillus safensis and Ochrobactrum pseudogregnonense increase root and shoot biomass, height of plants, yield, and chlorophyll content in wheat under water stress. Moreover, relative water content (RWC) and antioxidant response were higher. Similarly, rhizospheric bacteria Pseudomonas putida and Bacillus cereus also increased the activity of antioxidant enzymes; plants exhibit higher proline content; improved water status by increasing RWC; and alleviated oxidative stress in wheat Triticum aestivum under severe drought stress (Lozo et al., 2023).

Plants can cope with stress through the production of osmolytes such as proline (Ghosh et al., 2021). Timmusk et al. (2014) reported that rhizobacteria Bacillus thuringiensis enhanced wheat drought stress tolerance through increasing proline content and the production of the volatiles benzaldehyde, β-pinene, and geranyl acetone. Further, Rashid et al. (2022) reported that Bacillus megaterium and Bacillus licheniformis induced drought tolerance in wheat by enhancing relative water content, chlorophyll and carotenoid content, proline content, and activation of defense-related antioxidant enzymes.

Production of extracellular polymeric substances (EPS) such as exopolysaccharides by rhizobacteria enhances the water holding capacity of soil. EPS forms a soil aggregation around the root, which improves growth under drought conditions (Ansari et al., 2019). Rhizobactreia EPS producers Planomicrobium chinense, Bacillus cereus, and Pseudomonas fluorescens increase biomass (leaf area and root/shoot length), enhance soil structure, and reduce soil water loss in wheat under drought (Khan et al., 2017). Similarly, rhizospheric bacteria Planomicrobium chinense and Bacillus cereus produced proline, indole-3-acetic acid (IAA), hydrogen cyanide (HCN), ammonia (NH3), and exopolysaccharides (extracellular polymeric substances) in wheat under drought conditions. Khan and Bano (2019) recommended the integrative use of a combination of both strains, which appears to be a promising and eco-friendly strategy for reducing moisture stress in wheat plants. Moreover, Bacillus subtilis and Azospirillum brasilense also produced EPS, osmolytes, stress hormones, and antioxidant enzymes; these products impart drought tolerance in wheat (Ilyas et al., 2020). Further, Rhizobium leguminosarum, Mesorhizobium ciceri, and Rhizobium phaseoli improved wheat seedling and growth under water-deficit conditions by producing EPS and activating antioxidant enzymes (Hussain et al., 2014).

Among the tolerate mechanisms and strategies of drought in plants are antioxidants. Antioxidants are essential compounds for plants to promote growth under both biotic and abiotic stress (Sies, 1997); these compounds can reduce oxidative stress by scavenging reactive oxygen species (ROS). Antioxidants are divided into enzymatic (e.g., guaiacol peroxidase, superoxide dismutase (SOD), ascorbate peroxidase (APX), mono dehydro-ascorbate reductase, ascorbate dehydrogenase, and glutathione reductase) and non-enzymatic (e.g., glutathione, carotenoids, tocopherols, and flavonoids) (Gill et al., 2010). Rhizobacteria Bacillus subtilis increased the activity of antioxidant enzymes (superoxide dismutase, peroxidase, and catalase) and improved wheat growth under drought (Sood et al., 2020). Similarly, Bacillus paramycoides and Bacillus paranthracis enhanced the production of drought-fighting molecules like superoxide dismutase, peroxidase, catalase, and proline in wheat under water deficit conditions (Yadav et al., 2022b). Many studies on the effects of rhizospheric bacteria on wheat under drought for their plant growth promotion showed a potential for using these bacterial strains for drought mitigation (Table 1).

Table 1: Contributions of rhizobacteria in alleviation of drought stress in wheat (Triticum aestivum).

Rhizobacteria	Effects	References
Acinetobacter sp.	Phosphorous and zinc solubilization, production of hydrogen cyanide (HCN), EPS and improve root morphology.	Latif et al., 2022
Azospirillum lipoferum	Fixing and producing the highest amounts of N and auxin, P solubilizing and ACC-deaminase activities.	Arzanesh et al., 2011
Azospirillum brasilense	Upregulation of some stress-related genes (APX1, SAMS1, and HSP17.8), increase activity of enzymes involved in the plant ascorbate–glutathione redox cycle.	Kasim et al., 2013
	Increase RWC of roots, shoots and leaves, higher contents of pigments (chlorophyll a and b) and ascorbic acid, and protein patterns of roots. Lower leakage of electrolytes and less accumulation of MDA and hydrogen peroxide.	Kasim et al., 2021
	Induce the levels of phytohormones, improve activities of enzymes, antioxidants and EPS.	Furlan et al., 2017
Bacillus sp.	Growth promoting effect and increase IAA.	Wang et al., 2014
	Enhance leaf wilting, drooping and yellowing, TaWdreb2 and TaBADHb genes were highly expressed.	Fang et al., 2023
Bacillus altitudinis	Produce EPS, increase root dry weight, chlorophyll content, SOD and proline.	Yadav et al., 2022a
Bacillus amyloliquefaciens	Production of ACC deaminase, improve the chlorophyll a, chlorophyll b, photosynthetic rate, transpiration rate, grain weight, and grain N, P and K.	Danish and Zafar-ul-Hye, 2019
	Upregulation of some stress-related genes (APX1, SAMS1, and HSP17.8), increased activity of enzymes involved in the plant ascorbate–glutathione redox cycle.	Kasim et al., 2013
	Molecular modifications in wheat, induce tolerance genes.	Abd El-Daim et al., 2018
Bacillus cereus	Increasing root and shoot length and both fresh and dry weight of root and shoot.	Sati et al., 2023
Bacillus megaterium	Production EPS, improvement in plant height, root length, biomass, chlorophyll and carotenoid content, MSI, leaf RWC, total soluble sugar, total phenol, proline, and total soluble protein, improvement in enzymatic activities of several antioxidant enzymes such as POD, CAT, and APX, decrease in electrolyte leakage, H_2O_2 and MDA contents.	Shankar and Prasad, 2023
Bacillus paramycoides	Produce EPS, increase root dry weight, chlorophyll content, SOD and proline.	Yadav et al., 2022b
Bacillus subtilis	Increase RWC, reduce ethylene production, induced ROS.	Mockevičiūtė et al., 2023
Bacillus tequilensis	Enhance chlorophyll content and antioxidant properties such as proline, peroxidase and polyphenol oxidase.	Patel et al., 2022
Bacillus velezensis	Increase chlorophyll content.	Abd El-Daim et al., 2019
	Increasing root and shoot length and both fresh and dry weight of root and shoot.	Sati et al., 2023
Bifidobacterium animalis B. bifidum B. longum	Increase RWC, reduce ethylene production, induced ROS.	Mockevičiūtė et al., 2023
Blastococcus sp.	Enhance leaf wilting, drooping and yellowing, TaWdreb2 and TaBADHb genes	Fang et al., 2023

	were highly expressed.	
Chryseobacterium sp.	Phosphorous and zinc solubilization, production of HCN and EPS, and improving root morphology.	Latif et al., 2022
Cronobacter sakazakii	ACC-deaminase activity, P/Zn/K-solubilization, calcite degradation, IAA, and siderophore production. Improve plant growth, leaf area, and biomass. Expression of cytosolic ascorbate peroxidase (cAPX) and ribulose-bisphosphate carboxylase (rbcL) genes.	Zia et al., 2021
Ensifer meliloti	Improve plant dry weight and spike weight, higher P and N in shoots and spikes and higher sugar accumulation.	Raklami et al., 2021
Enterobacter bugandensis	Improve plant growth and chlorophyll content, increase osmolyte content (proline and total soluble sugar), RWC, CAT and SOD activity, and decrease lipid peroxidation, expression of genes encoding antioxidant enzymes (CAT, APX, and GPX), osmolyte synthesis (P5CS, P5CR, and TPS1), biosynthesis of stress hormone genes (NCED, WZE, SAMS, ACS1, and ACO encoding proteins for the biosynthesis of abscisic acid and ethylene) and calcium transporter (TPC1), regulation of the ethylene biosynthesis gene and modulation of TPC1 gene expression.	Arora and Jha, 2023
Enterobacter cloacae	Increase leaf RWC, SPC, amount and activity of enzymatic and non-enzymatic antioxidants, including POD, SOD, Phe, Fla, and Anth. Enhance the inhibition of free radicals by DPPH and clear ROS. Production EPS, improvement in plant height, root length, biomass, chlorophyll and carotenoid content, MSI, leaf RWC, total soluble sugar, total phenol, proline, and total soluble protein, improvement in enzymatic activities of several antioxidant enzymes such as POD, CAT, and APX, decrease in electrolyte leakage, H_2O_2 and MDA contents.	Vafa et al., 2022 Shankar and Prasad, 2023
Herbaspirillum seropedicae	Induce the levels of phytohormones in treated plants, improve activities of enzymes, antioxidants and EPS.	Furlan et al., 2017
Klebsiella sp.	Phosphorous and zinc solubilization, production of HCN and EPS, and improving root morphology.	Latif et al., 2022
Klebsiella aerogenes	Antioxidant activities, production of IAA, EPS and siderophore. Phosphate solubilization.	Shaffique et al., 2023
Lactobacillus casei L. delbrueckii L. diacetylactis L. plantarum Lactococcus lactis	Increase RWC, reduce ethylene production, induced ROS.	Mockevičiūtė et al., 2023
Pantoea agglomerans	Increase in plant height, root length, shoot dry weight, root dry weight, chlorophyll, SOD activity and in the concentration of shoot N, P and K.	Naderi et al., 2022
Proteus mirabilis	ACC-deaminase activity, P/Zn/K-solubilization, calcite degradation, IAA, and siderophore production. Improve plant growth, leaf area, and biomass. Expression of cytosolic ascorbate peroxidase (cAPX) and ribulose-bisphosphate carboxylase (rbcL) genes.	Zia et al., 2021
Pseudomonas sp.	Growth promoting effect and increase IAA.	Wang et al., 2014
Pseudomonas aeruginosa	Increase fresh weight, dry weight, lengths of roots, shoot and photosynthetic contents, enhancement in total soluble sugars, total soluble proteins, calcium, potassium, phosphate, and nitrate contents.	Lalarukh et al., 2022
Pseudomonas baetica	Increase root and shoot length and both fresh and dry weight of root and shoot. Increase RWC, chlorophyll index, proline content, plant height, shoot dry weight, thousand grain weight, and the concentration of shoot and grain P.	Sati et al., 2023 Shirmohammadi et al., 2020
Pseudomonas balearica	ACC-deaminase activity, P/Zn/K-solubilization, calcite degradation, IAA, and siderophore production. Improve plant growth, leaf area, and biomass. Expression of cytosolic ascorbate peroxidase (cAPX) and ribulose-bisphosphate carboxylase (rbcL) genes.	Zia et al., 2021
Pseudomonas helmanticensis	Increase RWC, chlorophyll index, proline content, plant height, shoot dry weight, thousand grain weight, and the concentration of shoot and grain P.	Shirmohammadi et al., 2020
Pseudomonas stutzeri	Enhance chlorophyll content and antioxidant properties such as proline, peroxidase and polyphenol oxidase.	Patel et al., 2022
Rahnella aquatilis	Improve plant dry weight and spike weight, higher P and N in shoots and spikes and higher sugar accumulation.	Raklami et al., 2021
Rhizobium leguminosarum	Improve the growth parameters (fresh and dry aerial weight, chlorophyll content, and RWC), down regulated DREB2 and CAT1 genes.	Barquero et al., 2022
Rhizobium sullae	EPS production and increase in water holding capacity of soil in rhizosphere.	Kaci et al., 2005
Rhodopseudomonas palustris Rhodopseudomonas sphaeroides	Increase RWC, reduce ethylene production, induced ROS.	Mockevičiūtė et al., 2023
Serratia sp.	Growth promoting effect and increase IAA.	Wang et al., 2014
Serratia marcescens	Increase leaf RWC, SPC, amount and activity of enzymatic and non-enzymatic antioxidants, including POD, SOD, Phe, Fla, and Anth. Enhance the inhibition of free radicals by DPPH and clear ROS.	Vafa et al., 2022
Staphylococcus pasteuri	Increase root and shoot length and both fresh and dry weight of root and shoot.	Sati et al., 2023
Stenotrophomonas sp.	Growth promoting effect and increase IAA.	Wang et al., 2014
Stenotrophomonas maltophilia	Increase RWC of roots, shoots and leaves, higher contents of pigments (chlorophyll a and b) and ascorbic acid, and protein patterns of roots. Lower leakage of electrolytes and less accumulation of MDA and hydrogen peroxide.	Kasim et al., 2021
Streptococcus thermophilus,	Increase RWC, reduce ethylene production, induced ROS.	Mockevičiūtė et al., 2023

ACC - 1-aminocyclopropane-1-carboxylate; EPS - exopolysaccharide; HCN - hydrogen cyanide; IAA - indole 3-acetic acid; NH3 - ammonia; RWC – relative water content; ABA- abscisic acid; SOD - superoxide dismutase; ROS – relative oxygen species; POD- peroxidase; CAT- catalase; APX- ascorbate peroxidase; SPC- soluble protein content; Phe- phenol; Fla- flavonoid; Anth- anthocyanin; DPPH-2-2-Diphenyl picryl hydrazyl; CAT1; catalase gene; DREB2; dehydration-responsive element-binding protein 2; MSI- membrane stability index;

MDA- malondialdehyde.

4. Wheat Endophytes Microbiome

Endophytes are microorganisms that form symptomless infections within healthy plant tissues. Such infections are termed "endophytic", particularly when they are believed to be mutualistic or at least non-pathogenic, or ‘‘latent infections’’, where latent pathogens are involved (Larran et al., 2007). Endophytic microbiomes invade plants through wounds and root hairs. They may systematically colonize the plants (Compant et al., 2010). Pang et al. (2022) found that wheat endophytic bacteria showed organ- and growth-stage diversity, which may reflect their adaptations to different plant tissues. Generally, in comparison between an above-ground plant organ and a root or other underground tissues, the last seems to have a higher abundance of endophytes (Robinson et al., 2016). Moreover, wheat bacterial endophyte communities are more abundant and heterogeneous in roots compared to leaves (Robinson et al., 2016). The movement of endophytic bacteria from roots to leaves is still unclear in many plants. Most bacteria in the plant endosphere are assumed to have a “facultative endophyte” lifestyle, and at a stage in their life cycle, they exist outside the host plants (Hardoim et al., 2008). In fact, endophytes often originate from soil, initially infecting the roots of the host plant and colonizing the plant apoplast.

Endophytic bacteria thrive symbiotically inside different healthy plant parts. They do not normally cause any visible disease symptoms. Although endophytic bacteria are adapted to living inside specific plant genotypes, many reports reveal that endophytic community structure is influenced by abiotic and biotic factors such as environmental conditions, microbe-microbe interactions, and plant-microbe interactions (Ryan et al., 2008).

Research on endophytes has shown a potential for plant growth promotion by a number of mechanisms, including phytostimulation, through the production of indole acetic acid or the synthesis of the enzyme aminocyclopropane-1-carboxylic acid deaminase (Zhang et al., 2020b); biofertilization, through the solubilization of minerals (Gupta et al., 2012) or bacterial nitrogen fixation (Thaweenut et al., 2010); and pathogen control, through priming of the plant defense system (Pavlo et al., 2011) or production of antimicrobial metabolites (Ren et al., 2013). A fully understanding of endophytes community structure, colonization, and establishment is imperative to utilizing these beneficial traits. The use of endophytic bioinoculants for their plant growth-promoting and disease-control properties is now applicable and registered, and even for the development of sustainable agriculture production.

Multi-omics techniques have significantly improved the understanding and exploration of the role of the plant microbiome (Shahzad et al., 2018). Regardless of the low cultivability (0.001–1%) of the endophytic microbiome (Eevers et al., 2018), cultivation-independent techniques based on the isolation of all the 16S rRNA present in plants permit the detection of both cultivable and non-cultivable endophytes (Eevers et al., 2018; Hardoim et al., 2015; Verma and Suman, 2018). Six bacterial phyla that typically dominate in the endophytic structure were identified using next-generation sequencing (NGS) techniques: Proteobacteria, Actinobacteria, Firmicutes, Bacteroidetes, Acidobacteria, and Deinococcus-Thermus (Hardoim et al., 2015; Rahman et al., 2018). At the class level, Gammaproteobacteria was found to be the most abundant (Hardoim et al., 2015), followed by Alphaproteobacteria (Hardoim et al., 2015; Rahman et al., 2018) and Bacilli (Comby et al., 2009).

Plant and bacterial genotypes, as well as biotic and abiotic environmental factors, influence the presence of different endophytic species. While the population of endophytes mostly depends on tissue type and season of isolation in a single host plant (Kuklinsky et al., 2004), Many studies focus on the differences in responses of bacterial communities to host, location, growth stage, field management strategies, and soil conditions for wheat. Thus, such research provided a better insight into this field.

In Triticum aestivum L. (cv. ‘Hondia’) and Triticum spelta L. (cv. 'Rokosz'), Kuzniar et al. (2019) suggested that the endophytic core microbiome is associated with plants throughout their whole life. This finding confirms the fact that plant organs can determine the actual endophytic community. Ziarovska et al. (2020) suggested that the changes in variability of bacterial endophytes are associated preferentially with the drought stress varietal characteristics of the analyzed wheat instead of the applied stress conditions.

Endophytes have been noticed to have a significant role in the effect of drought stress on the host plants. Seeds and roots of quinoa, rice, and the halophyte Limonium sinense are colonized by bacterial endophytes of Bacillus sp., Pseudomonas sp., Klebsiella sp., Serratia sp., Arthrobacter sp., Streptomyces sp., Isoptericola sp., and Microbacterium sp. to help accumulate substances similar to glycine and betaine that lead to better resistance to salinity and drought (Jha et al., 2011). Under heat stress, inoculation of Bacillus amyloliquefaciens and

Azospirillum brasilence in Triticum aestivum reduced the regeneration of reactive oxygen species and the pre-activation of heat shock transcription factors (El-Daim et al., 2014). While in Zn toxicity, Pseudomonas aeruginosa improved biomass, nitrogen and phosphor uptake, and total soluble protein production in Triticum aestivum (Islam et al., 2014).

Many studies show that endophyte can trigger a wide array of molecular morpho-physiological and biochemical responses (including photosynthesis), which all play a key role in mitigating and resisting drought (Verma et al., 2021). These responses result in improving both root length and volume, enhancing nutrient uptake, and protecting and enhancing the photosynthesis machinery, either directly by endophyte production of phytohormones or indirectly by triggering host gene expression and physiology (Li X et al., 2019). Subsequently, the uptake and conservation of plant water are targeted, and cellular-level tolerance traits are activated. Among the direct and indirect effects of endophytes, auxin-producing microorganisms promote root growth in host plants under water-limiting conditions (Qiang et al., 2019). On the other hand, indirectly, endophytes stimulate the production of auxin in their hosts, resulting in a modification of root architecture by increasing root length, number, volume, and biomass, which improves plant abilities to mine water under drought conditions (Liu and Wei, 2019).

Endophytes can also produce and modulate the production of abscisic acid (ABA) in the host (Zhou et al., 2021). Directly secreted ABA functions as an elicitor to activate a signaling cascade, resulting in resistance responses against drought stress in the host (Zhou et al., 2021). Other endophytes indirectly modulate drought by increasing the concentration of ABA within the host; this results in lowering both stomatal conductance and density, which contribute to improved water use efficiency under drought (Rho et al., 2018). Endophytes can alert the expression of cuticular wax biosynthesis genes (for example, BiP, KCS, KAR, FAR, FabG, desB, SSI2, fadD, and ABCB1), which is an important trait for drought adaptation (Zhao et al., 2022). Furthermore, endophytes activate diverse cellular level tolerance traits and increase reactive oxygen species scavenging capacity under drought; such responses can reduce the damage to cellular membranes and macromolecules (Tsai et al., 2020). Endophyte can also induce the accumulation of compatible solutes like glycine, betaine, soluble sugars, proline, and organic acids; these solutes are capable of lowering osmotic potential and turgor maintenance under drought (Zhao et al., 2022).

Endophyte activates transcription of drought-responsive genes in the host plant (Sherameti et al., 2008).

4.1 Wheat Endophytic Bacteria

Bacillus, Pseudomonas, and Pantoea are common bacterial endophytic genera that occur frequently in agricultural crops, including wheat species (Comby et al., 2009). In addition, Robinson et al., 2016, demonstrated that the following were also endophytic representatives: Devosia, Rhizobium, Duganella, Variovorax, Serratia, Brevundimonas, Aeromicrobium, Agreia, Agromyces, Arthrobacter, Microbacterium, Cellulomonas, Rhodococcus, Plantibacter, Flavobacterium, Pedobacter, Stenotrophomonas, and Paenibacillus, which were present in the roots and shoots of T. aestivum cv. ‘Hereward’. Moreover, it was shown that there is a difference between wheat root and leaf in the composition of endophyte communities. Proteobacteria were prevalent in roots, whereas Firmicutes and Actinobacteria representatives dominated in leaves (Robinson et al., 2016). Endophytic bacteria Burkholderia phytofirmans reduce the effect of drought stress on wheat grown under limited irrigation conditions (Naveed et al., 2014). As we mentioned earlier, chlorophyll content is decreased under drought exposure in wheat, which affects the photosynthesis rate (Wasaya et al., 2021). Endophytic bacteria Bacillus marisflavi, Bacillus thuringiensis, and Bacillus subtilis improved chlorophyll content, photosynthetic rate, CA activity, and relative water content in wheat (Triticum aestivum) under water-deficit conditions (Aslam et al., 2018). Similarly, endophytic bacteria Rhizobium leguminosarum, Mesorhizobium ciceri, and Rhizobium phaseoli improved the growth, biomass, and drought tolerance index of the wheat under simulated drought (Hussain et al., 2014). The production of phytohormones by endophytics aids in stress mitigation. Actinobacteria Streptomyces coelicolor, S. olivaceus, and S. geysiriensis enhanced wheat growth under water stress conditions through the production and accumulation of IAA (Yandigeri et al., 2012). Endophytic bacteria: Bacillus lentus, Bacillus subtilis, and Bacillus cereus increased levels of superoxide dismutase and catalase improved water use efficiency in wheat under drought (Meenakshi et al., 2019). Table 2 shows a group of endophytic bacteria mentioned for their desirable effect on wheat growth under drought stress.

Table 2: Contribution of endophytic bacteria in alleviation of drought stress in wheat plants.

Wheat	Endophytic bacteria	Effects	References
Triticum aestivum	Arthrobacter sp. Curtobacterium flaccumfaciens	Promote growth.	Hone et al., 2021
Triticum aestivum	Bacillus sp.	Increase in root fresh weight, shoot fresh weight, root dry weight, and shoot dry weight and chlorophyll content.	Amjad et al., 2021
Triticum aestivum	Bacillus subtilis	Increase plant growth. Enhance transpiration intensity, root RWC and osmotic potential, proline accumulation. Antioxidant accumulation, depletion of ascorbate (AsA) and glutathione (GSH).	Lastochkina et al., 2020 Lubyanova et al., 2023 Maslennikova and Lastochkina, 2021
Triticum turgidum	Pantoea agglomerans	Increase chlorophyll content and favored K^+ accumulation.	Cherif-Silini et al., 2019
Triticum aestivum	Pantoea alhagi	Accumulation of soluble sugars.	Chen et al., 2017
Triticum aestivum	Pseudomonas sp.	Siderophore production, EPS production, ACC deaminase activity. Increase in plant height, root length, shoot dry weight, root dry weight, chlorophyll, SOD activity and in the concentration of shoot N, P and K.	Zhang et al., 2020b Naderi et al., 2022
Triticum turgidum	Pseudomonas brassicacearum	Improve growth parameters.	Draou et al., 2022
Triticum aestivum	Pseudomonas protegens	Increase the IAA/ABA, improved the water balance, reduce MDA.	Bakaeva et al., 2022
Triticum turgidum	Pseudomonas putida	Improve growth parameters.	Draou et al., 2022

ACC - 1-aminocyclopropane-1-carboxylate; IAA - indole 3-acetic acid; ABA- abscisic acid; RWC – relative water content; EPS – exopolysaccharide; MDA- malondialdehyde; SOD - superoxide dismutase.

Endophytic bacteria are effective in promoting wheat growth under drought. How their effective in stimulating and improving growth is still unclear; a little information on their mechanism of action is available. Even though so many parameters were investigated, such as physiological, morphological, biochemical, and molecular, there's still a need for further exploration, especially their abundance in the host, interference with other endophytes in the host, interactions with host cells, and the potentiality of using them in a wide range. Offering endophyte as a biofertilizer is promising for sustainability.

5. Choice of Candidates

Many microorganisms are mentioned in this review for their abilities in enhancing wheat tolerance to drought. Here, we analyze these microorganisms at the phylum and genus level (supplementary tables) in order to find a correlation between endophytic and rhizospheric bacteria. Thus, it would be helpful in choosing candidates for biofertilizer and further research.

In comparing rhizosperic to endophytic bacteria, the last belong mainly to Actinobacteria, Firmicutes, and the Proteobacteria phylum; Proteobacteria were the dominant, followed by Firmicutes (Fig. 3.B). Similarly, Proteobacteria and Firmicutes were the dominant in the rhizosphere (Fig. 3.A). All endophytic bacterial phylums mentioned in this review overlapped with rhizospheric bacterial phylums; only the Bacteroidota phylum was not observed as endophytic (Fig. 4.A). This confirms that all endophytes were rhizospheric at one time in their life cycle but not the opposite (Hardoim et al., 2008). Not all rhizospheric bacteria are able to penetrate plant cells. In fact, many factors influence this penetration and the composition of the microbiome. Bacillus, Pseudomonas, and Azospirillum were the dominant genera in the rhizosphere (Fig. 3.C). On the other hand, Bacillus, Pseudomonas, and Streptomyces were the dominant endophytic genera (Fig. 3.D). Azospirillum sp. was not spotted as an endophyte, nor was Streptomyces as a rhizospheric. Bacillus and Pseudomonas genera were overlapped as both endophytic and rhizospheric (Fig. 4.B). Thus, a bacterium that could be represented as both rhizospheric and endophytic has potential for use as a biofretlizer. Moreover, this could promote the growth and survival of both bacteria and hosts under different levels of stress. Further investigations and research on Bacillus and Pseudomonas are required for more information, which may be promising in wheat cultivation under drought stress.

The ability of some microorganisms to fluctuate between rhizosphereic and endophytic is considered a hot spot in the selection of plant growth-promoting microorganisms. Here, we noticed the potentiality of Bacillus and Pseudomonas to act as both rhizospheric and endophytic. Thus, more research on the combination of these genera under drought stress is requisite.

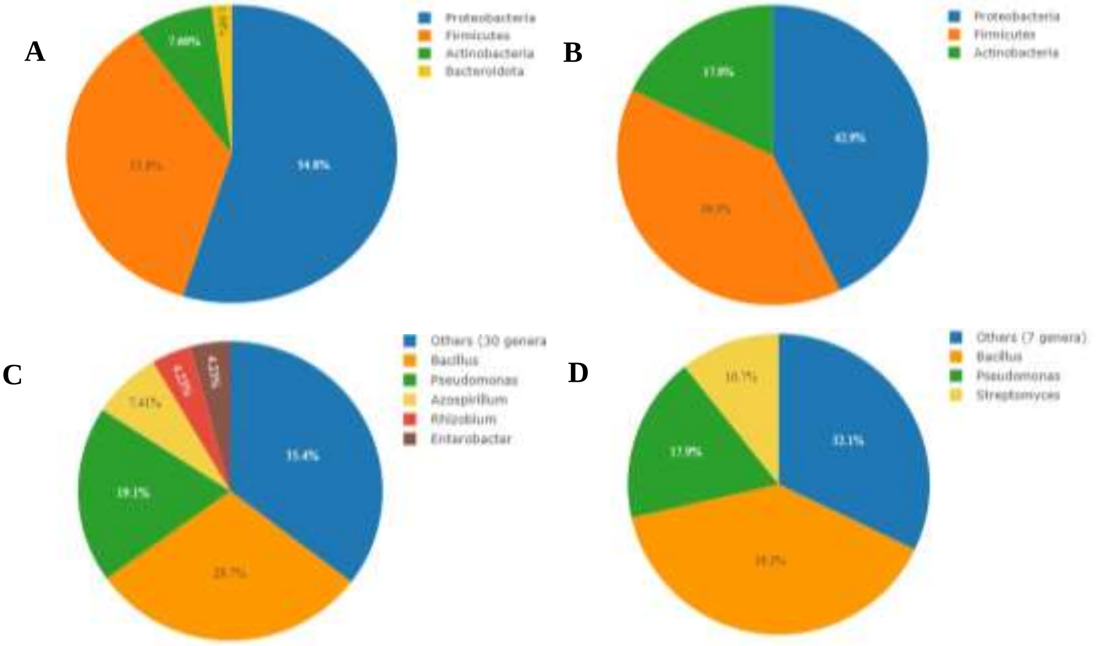

Figure 3: Abundance of wheat microbiomes A) rhizospheric bacteria phylum; B) endophytic bacteria phylum; C) rhizospheric bacteria genera; and D) endophytic bacteria genera, belonging to diverse phylums and genus.

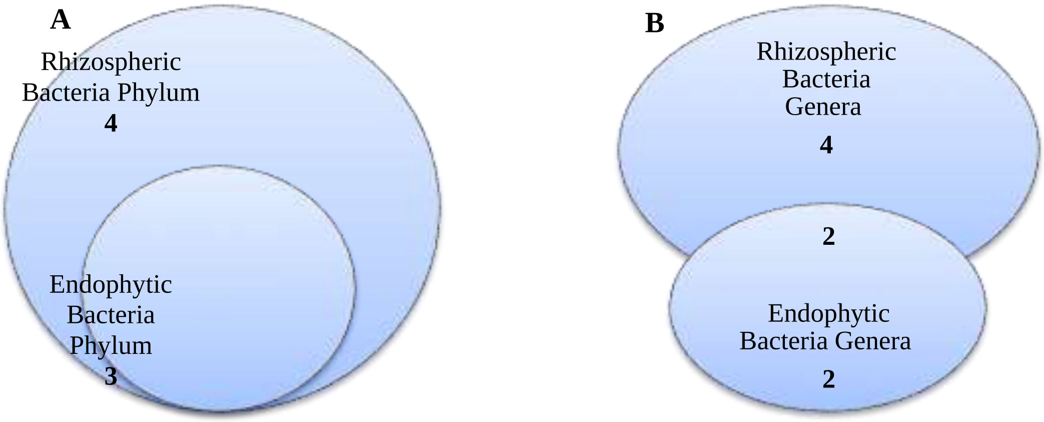

Figure 4: Distribution of bacteria taxa as a A) phylum for rhizosphere and endophytes, B) genera for rhizosphere and endophytes. The Venn diagram shows number of phylum and genera were shared.

6. Conclusion and future direction

The impacts of global warming due to climate change have led to a shortage in water. The drought is continuing to worsen with significant crop damage. Unfortunately, food production is the most affected. Grain crops such as wheat are in confrontation with these challenges. Plant breeders and crop physiologists encounter many difficulties in improving wheat tolerance due to the complexity of genetic traits.

As stated above, many studies on wheat microbiome abilities in mitigating drought stress were offered as sustainable mechanisms for improving growth at many levels. The present review summarizes a tremendous evidence on the use of bacteria as rhizospheric or endophytic plant growth promoters in enhancing wheat performance under drought. The mechanisms by which these microbe strains are able to play a role are mainly achieved by triggering direct or indirect responses. Mostly, biochemically such as phytohormones, osmolytes, enzymatic and non-enzymatic activities, EPS, volatile compounds, ACC deaminase production, and solubilization of minerals. Molecular mechanisms such as the activation of stress genes (APX1, SAMS1, and HSP17.8) and other related genes such as TdDRF1, TaWdreb2, TaBADHb, cAPX, and rbcL. Or by encoding antioxidant enzymes (CAT, APX, and GPX), osmolyte synthesis (P5CS, P5CR, and TPS1), biosynthesis of stress hormone genes (NCED, WZE, SAMS, ACS1, and ACO encoding proteins for the biosynthesis of abscisic acid and ethylene), and calcium transporter (TPC1), and regulation of the ethylene biosynthesis gene and others related. Morphological and physiological effects have been noticed in changes caused by microbes, but many of these mechanisms are still not clear.

Difficulties in linking potential effects with strains are evident, single or several strains. Most studies focus on a combined set of strains rather than a singular microbe. There is a need for more research on the (1) mode of action, (2) influence factors, and (3) interactions between (A) microbes-host, (B) microbes-microbes, and (C) microbes-stress (drought). In this sense, it would be easier to uncover novel effects of a single or several microbes.

High-throughput DNA sequencing has insight into microbial ecology. Even so, research on endophytes in comparison to the rhizosphere is still shy. This shortage is mainly due to (1) the complexity of extraction and cultivation of uncultivatable strains; (2) the adjusting of conditions in the field and labs; (3) the variation in results among fields and labs; and, as we previously mentioned, (4) the linking effects with strain (microbiome core identification), all of which have led to this lack of studies.

Further investigation of both the rhizosphere and endophytes is necessary to fully understand their effects and interactions. Moreover, microbial physiological and ecological studies could be helpful in determining these effects and interactions. Finally, manipulation and the development of an elite microbiome in the future will help to mitigate drought stress in sustainable ways.

Conflicts of Interest: The authors declare no conflict of interest.

Supplementary materials: Contact authours.

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