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Review Article

The role of endophytes and rhizobacteria to combat drought stress in wheat

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Abstract

Wheat production suffers greatly from drought stress, resulting in yield losses. Endophytes and rhizobacteria have been recognized as a valuable source in mitigating of drought stress by improving plant resistance and growth. In this review, we discuss how endophytes and rhizobacteria help wheat cope with drought stress. During drought stress, endophytes have been found to increase plant water usage efficiency and decrease water loss. Endophytes are harmless microorganisms that live inside plant tissues. Rhizobacteria establish colonies in the root system through various procedures, including phytohormones production, modification of root architecture, and activation of stress-inducible genes, thereby promoting plant growth and enhancing stress resistance. Numerous studies have shown how endophytes and rhizobacteria can improve the potential of wheat to withstand drought. For instance, inoculation with endophytes like *Piriformospora indica* and *Bacillus* spp. has been proven to enhance wheat plant yield and drought resistance. Similarly, it has been proven that rhizobacteria like *Pseudomonas* spp. and *Azospirillum brasilense* enhance drought tolerance through a variety of mechanisms. To minimize the consequence of wheat under drought conditions, the efficient method is the use of endophytes and rhizobacteria as biofertilizers, which could ultimately boost yields and sustainability. More research needs to be done so that it can be used most effectively in the field and so that we can better understand how they work. We explained current understanding of the role and mechanisms of endophytes and rhizobacteria in minimizing drought stress effects in wheat. Additionally, we highlighted areas of limited knowledge and suggested directions for future research. This review will provide the new suggestion on the role of endophytes and rhizobacteria in mitigating the drought stress in plants.

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Keywords: drought stress; gene expression; mitigation strategies; molecular markers; PGPR; signaling

Introduction

Wheat, a prehistoric crop, is an important energy source in the human diet worldwide. Its demand has risen due to the availability of affordable end products compared to other cereal crops (Zamaratskaia *et al.*, 2021). According to the FAO, the world's wheat requirement is projected to reach 840 million tons by 2050, excluding animal feed needs (Ratnam *et al.*, 2023). However, achieving this target has either stagnated or slowed down globally. Pakistan is 8th among the 121 countries that grow wheat in terms of both area and output. But when output per unit area is taken into account, it falls to 29th (Islam *et al.*, 2022). Within the agricultural sector, the contribution of wheat amounts to 13.8% of the value added, while it accounts for 3.2% of the GDP. In the agricultural year of 2006-2007, wheat was cultivated on approximately 8.5 thousand hectares, resulting in a production of 23 million tons (Christian *et al.*, 2022).

In addition to its great importance, the development of wheat is being affected by several stress factors such as salinity, water deficit, heat, and metal-induced stresses. Among these stress factors, drought stress has caused a big drop in wheat yields globally. The severity of drought greatly impacts wheat productivity, along with other abiotic stresses (Kong *et al.*, 2016). Drought stress negatively influences crop growth at all stages of germination. When water deficit occurs during the initial stage of wheat germination, it can cause immature seedlings and fewer tillers per hectare. But when droughts happen in the middle of the growth cycle, the amount of dry matter, tillers that work well, and seeds each plant makes goes down. During the final stage of growth, wheat is also hurt badly by drought, which has a negative effect on grain weight, fertility, and feed production. During the maturing stage, wheat needs a temperature between 14 and 15 °C, and temperatures above 25 °C cause the weight of the grain to go down. But for grain filling, the temperature needs to be around 35.4 °C (Si *et al.*, 2023).

Drought stress is a complicated thing that happens when a plant goes for a long time without getting enough water. It is thought to be the most important abiotic stress that hurts plant growth and yield, even in wheat (Baidya *et al.*, 2023). Wheat is affected in many ways by drought stress, including a decrease in photosynthesis and biomass buildup, as well as a decrease in grain output and quality. Also, dry stress can cause oxidative stress, which can damage membranes, proteins, and DNA by upsetting the balance between making reactive oxygen species (ROS) and getting rid of them. So, the lack of water is a big problem for wheat production, and it is important to find ways to fix it (Santibáñez-Andrade *et al.*, 2023) if we want to make sure that everyone has enough food to eat.

Drought stress poses a significant environmental challenge restricting crop yield on a global scale, especially in areas with arid and semi-arid climatic conditions (Wagaw, 2019). Wheat, a fundamental food source relied upon by millions of people in their diets, is considered one of the vital cereal crops globally (Kiran *et al.*, 2022). However, its productivity is severely disturbed by drought stress (Figure 1), leading to significant yield and economic losses (Christian *et al.*, 2022). Therefore, it is crucial to formulate sustainable and efficient approaches that can enhance the drought resistance of wheat and boost its yield under conditions of water scarcity. Drought stress has the potential to impact several mechanisms of plant development and growth, such as water-use efficiency, nutrient uptake, root growth, seed germination, and photosynthesis (Yahaya and Shimelis, 2022).

Stress from drought causes biochemical changes in wheat plants, which raises the amount of ROS and throws off the balance of cells. In the end, this causes oxidative damage to chemicals, which causes the plant to die. Also, dry stress makes wheat plants more likely to be attacked by insects and other pests and to get fungus and bacterial diseases (Azeem *et al.*, 2023; Chaudhry and Sidhu, 2022). So, drought stress is seen as one of the most limiting natural factors for wheat production (Skendžić *et al*., 2023). This is because it makes it harder to get higher outputs and contributes to food shortages and economic loses in impacted areas.

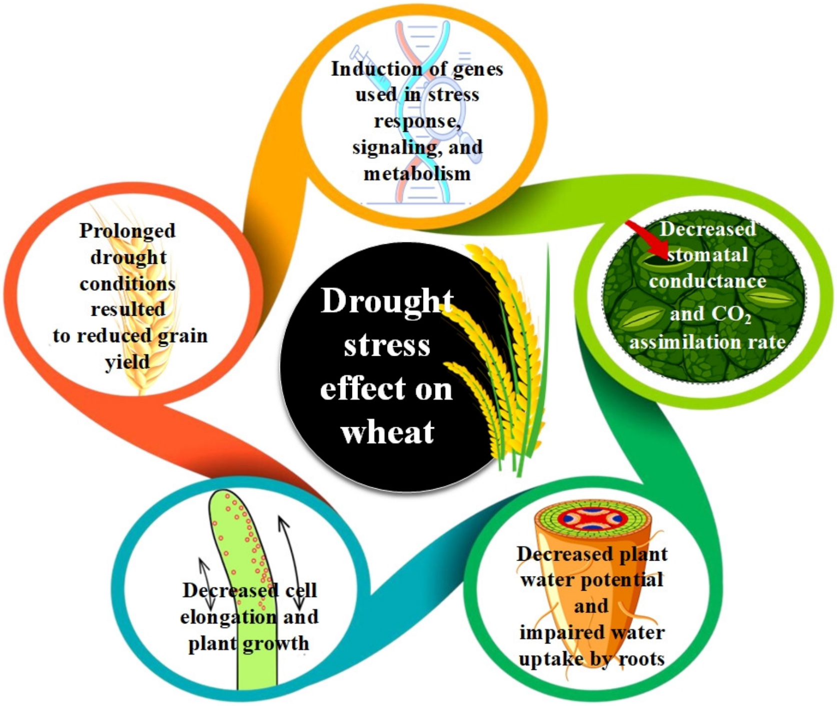

Figure 1. Drought stress-induced alterations in wheat's physiological mechanisms (Wahab *et al*., 2022)

It is imperative to address these limitations in order to enhance wheat production and meet the growing demand (Ahmad *et al*., 2018). Several ideas have been put forward, such as using nanoparticles, crop rotation, conservation farming, water management, genetic changes, and conservation agriculture. However, these strategies can be expensive and labor-intensive (Bernardo *et al*., 2017). Conversely, the utilization of plant growth-promoting rhizobacteria (PGPR) and endophytes is an environmentally friendly approach that also enhances soil fertility. PGPR, being a sustainable and cost-effective approach, have shown effectiveness in mitigating abiotic stress and improving plant productivity (Bishnoi, 2015). The diversity of soil microorganisms is crucial for agricultural productivity, and PGPR have emerged as promising contributors to green farming. They release plant growth regulators and other bioactive substances, modulate phytohormone levels, improve nutrient availability and uptake, alleviate the damaging impacts of plant pathogens, and employ multiple mechanisms to boost plant growth (Gupta *et al*., 2015). By increasing nutrient supply and combating soil-borne diseases, PGPR play a remarkable role in sustaining soil fertility in a commercially viable and environmentally friendly manner (Jan *et al*., 2021). Introducing beneficial microorganisms to plants promotes their growth and enhances their ability to withstand drought in dry regions. PGPR are well-suited to adverse conditions and protect plants from the detrimental impacts of environmental stressors (Kumari and Singh, 2020). Through the activation of physio-chemical changes in plant cells, PGPR provide improved resistance against abiotic stressors, known as induced "systemic tolerance". Certain strains of PGPR, such as *Azospirillum* spp., *Pseudomonas syringae*, P. *fluorescens*, and *Bacillus* spp., have been effective in enhancing wheat's resistance to drought by improving plant development, water levels, membrane integrity, osmolyte absorption, and modulation of stress-induced gene expression. Furthermore, PGPR inoculation facilitates the recovery of drought-affected wheat plants. Therefore, employing PGPR for plant inoculation presents a viable and sustainable solution to alleviate wheat plants drought-induced harms (Sarkar *et al*., 2022).

Endophytes and rhizobacteria are two types of microorganisms that live on plants. Kumari *et al.* (2019) say that these microorganisms help plants grow and deal with stress. Endophytes and rhizobacteria can both make a range of chemicals that help plants grow and make them more resistant to both living and nonliving threats (Basu *et al*., 2021). Endophytes can make a wide range of useful substances, such as plant growth factors, enzymes, antibacterial chemicals, and secondary metabolites (Devi *et al*., 2023). These chemicals are very important to plants because they help them take in more nutrients, grow and develop faster, and stay safe from pests, pathogens, and weather problems like heat, salt, and drought (Patil *et al*., 2023). Notably, endophytes have been shown to help plants respond to drought stress, which is a major natural stressor that affects food yield and quality worldwide (Ali *et al*., 2023). They can help plants deal with dry stress by making it easier for plants to take in and use nutrients, by controlling how much water plants take in, and by affecting plant physiology and biology in many different ways. Endophytic bacteria in plants also make more antioxidant enzymes and compounds, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and endogenous antioxidant molecules like ascorbate (AsA), glutathione (GSH), and carotenoids (Sachdev *et al*., 2023).

In this paper we presented an overview of the current understanding of the role and mechanisms of endophytes and rhizobacteria in reducing drought stress in wheat. Furthermore, this area of research has also identified areas of limited knowledge and outlined future research directions. Additionally, strategies for sustainable agriculture have been emphasized, aiming to ultimately enhance yield and productivity.

Endophytes and Rhizobacteria

The word "endophyte" generally refers to organisms that dwell within the tissues of the plant, but it can also be used to describe organisms that live inside other organisms. Endophytes have the potential to be either advantageous or detrimental to their hosts, contingent upon the species and the circumstances of the interaction (Schulz and Boyle, 2006). Some endophytes are known to provide protection against herbivores or pathogens, while others can cause diseases or reduce the plant fitness. Endophytic bacteria and fungi are of particular interest in agriculture and medicine, as they have been shown to have potential for biocontrol, bioremediation, and drug discovery. Endophytes can colonize different organs of the host and exhibit various forms of symbiotic relationships, ranging from saprophytic to predatory to harmful or even mutualistic. These endophytes can exhibit different relationships with their hosts, such as parasitic, mutualistic, and infectious. Some examples include infectious endophytic bacteria, parasitic endophytic herbs, and mutually beneficial organisms. Additionally, endophytic fungi can exist in latent developmental phases within hosts. While some authors classify the relationships between mycorrhizal fungi and plant roots as endophytic. Endophytes are groups of microorganisms that reside within different parts of a plant, encompassing its roots, stems, leaves, and seeds. These microorganisms do not negatively impact the plant's physiological functions or cause any disease symptoms within the plant tissue, as depicted in Figure 2. Endophytes are critical for the optimal plant growth host as they can regulate secondary metabolites and nutrient absorption, as well as help to shield the plant from infection symptoms caused by pathogens. These microorganisms (bacteria, fungi, or actinomycetes) form a network around the host plant and protect it from bad things in the environment, like weather changes (Stone *et al.*, 2004).

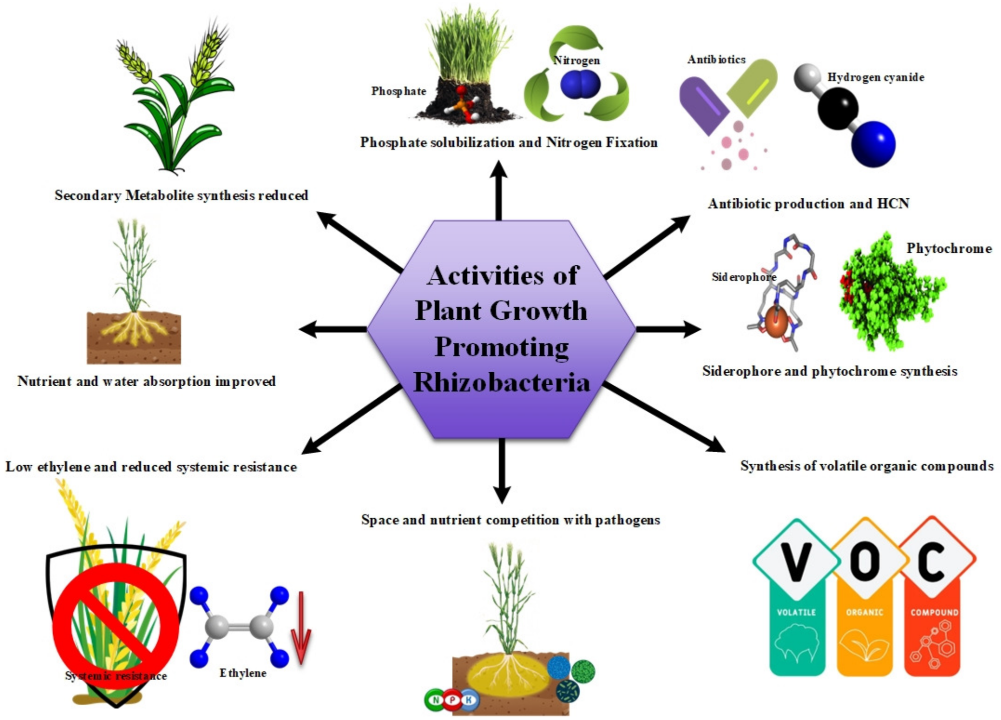

Figure 2. The impact of PGPR on wheat growth across developmental stages (Rizvi *et al*., 2022)

The microbiome is the ecosystem around plant roots in the soil. It is made up of many different kinds of microorganisms, such as bacteria, fungi, protozoa, and algae, but bacteria are the most common. Bacteria are thought to have a big effect on plant health because they are so common in the rhizosphere and because they compete with each other to colonize plant roots (Sharma *et al*., 2015). Microorganisms in the rhizosphere can be put into different groups based on how they affect plants and how they connect with root systems. Rhizobacteria are a type of beneficial microbe that reside in plant roots and exert various positive effects, which can be direct or indirect in nature.

Rhizobacteria possess the ability to enhance plant productivity, mitigate abiotic soil stresses, and regulate plant diseases through the production of molecules and plant hormones, as well as specific structural modifications in roots. The changes brought about by rhizobacteria can improve capability of the plant to deal with unfavorable circumstances by increasing its water potential, improving its nutritional status, and strengthening its defense mechanisms (Deka *et al*., 2019).

Types of endophytes and rhizobacteria

Microorganisms like bacteria, known as endophytes (including actinomycetes or mycoplasma), and fungi have established connections with plant tissues in various ways. There is a link between endophytes and more than 200 bacterial families from 16 phyla, with the majority of species being *Firmicutes*, *Proteobacteria*, and *Actinobacteria* (Vu *et al*., 2020). Figure 3 shows that endophytic bacteria are made up of many different biological groups, such as gram-positive and gram-negative bacteria. In these groups are genera like *Agrobacterium*, *Acinetobacter*, *Achromobacter*, *Bacillus*, *Brevibacterium*, *Xanthomonas*, *Pseudomonas*, *Microbacterium*, and others. They are also known for being able to make a wide variety of beneficial metabolites, such as chemicals that kill germs and fight cancer. Streptomyces is the group that has been reported the most, with 76% of these chemicals being linked to it (Zhang *et al*., 2021).

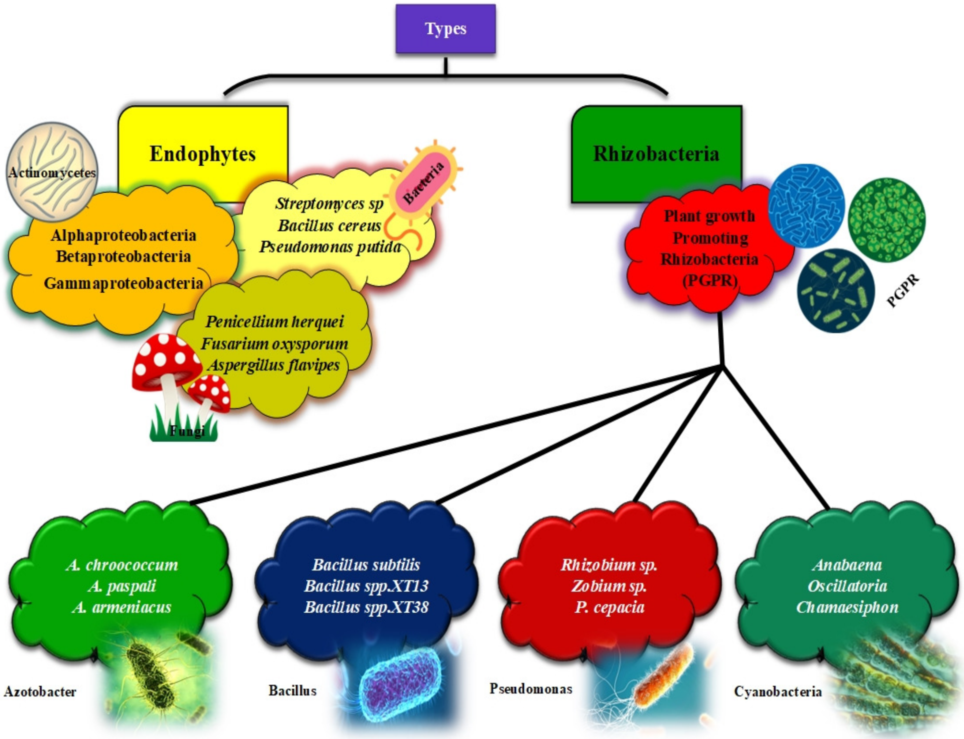

Figure 3. Types of beneficial microbes supporting wheat health and growth under drought stress (Gouda *et al.*, 2016)

Numerous bacterial groups, such as *Azotobacter*, *Alcaligenes*, *Azospirillum*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, and *Pseudomonas* have been found to improve growth of the plant (Subedi *et al.*, 2020). Many available PGPR inoculants appear to boost plant growth through various mechanisms, including suppressing plant diseases (known as Bioprotectants), improving nutrient uptake (known as Biofertilizers), and synthesizing phytohormones (known as Biostimulants). Bacteria such as *Agrobacterium, Bacillus*, *Burkholderia*, *Streptomyces*, and *Pseudomonas* are being investigated and increasingly employed as biological control agents in agriculture (Do Amaral *et al.*, 2016). Among other mechanisms, PGPR have been found to control plant diseases by inducing systemic resistance and producing siderophores or antibiotics. The application of PGPR to the plant triggers a defensive response similar to how it would respond to harmful living beings (Maksimov *et al.*, 2011). Some PGPR produce siderophores that scavenge heavy metal micronutrients, including iron, in the rhizosphere. This deprives pathogenic organisms of these essential nutrients needed for their growth and development. PGPR that generate antibiotics produce chemicals that prevent pathogen growth and colonization, protecting the plant from disease. It should be noted that biofertilizers capable of fixing nitrogen can only provide a limited improvement in crop nitrogen absorption (Subedi *et al.*, 2020).

Endophytes and Rhizobacteria as plant growth promoting agents

Plants receive nitrogen from various bacteria, such as free-living, associative, and endophytic bacteria. Additionally, bacteria like *Herbaspirillum*, *Bacillus*, *Burkholderia*, *Paenibacillus*, and various species perform significant part in fixing nitrogen as PGPR (Mohanty *et al.*, 2021). Nitrogen-fixing bacteria that live on their own can have a strong relationship with plants without taking up residence in their tissues. They can keep a large enough population to keep making nitrogen available for plant growth and development. Phosphorus is one of the most important nutrients for plants. It is needed for photosynthesis, respiration, energy transfer, and signal transmission, among other things (Aloo *et al.*, 2021). PGPR, which are also called phosphate-solubilizing microorganisms (PSMs), can change solid phosphorus into a form that plants can easily absorb, which helps them grow. PSMs are bacteria, fungi, and actinomycetes that live in the rhizosphere, phyllosphere, and endosphere of plants. They use different methods to make phosphorus available for plants to take up (Sharon *et al.*, 2019). Organic acids, Hydroxide ions (OH^-), Carbon dioxide (CO_2), and protons are among the most commonly identified compounds used by microorganisms to solubilize phosphorus. This process has been attributed to various bacteria, including *Pseudomonas*, *Bacillus*, *Burkholderia*, and other taxa. The ability of B. *pumilus* to mitigate stress caused by drought has been observed in *Glycyrrhiza uralensis*, a plant of considerable medicinal relevance (Ubani *et al.*, 2022).

Mousavinik *et al.* (2021) did a study in which they exposed sweet basil plants to drought and gave them three types of bacteria: *B. lentus*, *Pseudomonas* sp., and *A. brasilense*. The results indicated that all three bacterial species exhibited a considerable improvement in chlorophyll concentration and mineral absorption in the plants under drought conditions. In contrast, uninoculated pepper plants were unable to survive for more than 15 days under dry conditions, whereas the inoculated plants were able to endure for a longer period of time, even under stress. Tripathi *et al.* (2022) came to the conclusion that when tomato seedlings were stressed by heat and drought and then given *Septoglomus deserticola* and *S. constrictum*, hey formed a symbiotic relationship with the fungi. This caused oxidative stress and reactive oxygen species to go down. This mutual relationship also made cells work better, stomata work better, and leaves hold more water. Also, mycorrhizal treatment improved the plants' health even more when they were exposed to multiple stresses at the same time.

Mechanisms of water deficit resilience in endophytes and rhizobacteria

Rhizobacteria that help plants grow have unique qualities that allow them to help plants grow. They directly support plant growth by making chemicals like plant growth factors that help cells divide and grow (Nawaz *et al.*, 2022) as shown in Figure 4. Also, PGPR can indirectly help plants grow by stopping plant pathogens from growing in the soil. This lets the plant use more resources to start food seeds (Borah *et al.*, 2022).

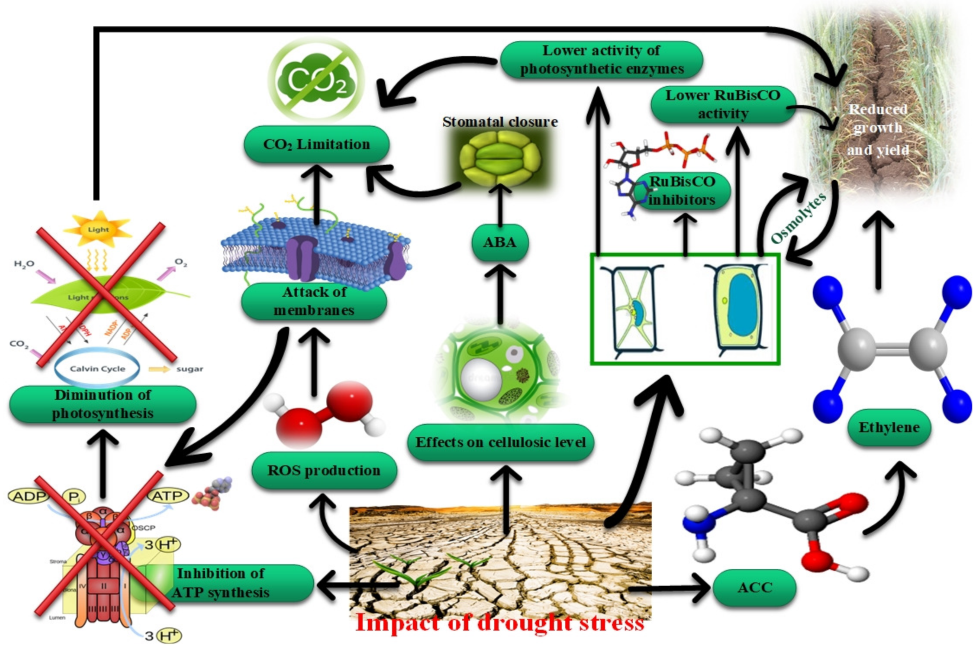

Figure 4. PGPR-mediated mitigation of drought stress in wheat (Camaille *et al.*, 2021)

Multiple investigations have indicated that mycorrhizae can provide significant benefits to plant survival and fitness in dry and drought-prone environments. Fungi belonging to the Arbuscular Mycorrhizal (AM) group, acquired from arid regions, were observed to enhance the water balance of their host plants to a greater extent compared to those obtained from similar genera but from more moist surroundings (Boutasknit *et al.*, 2020). A recent meta-analysis discovered that the presence of both arbuscular and ectomycorrhizal fungi often enhances plant growth during drought conditions (Chandrasekaran, 2022). The reasons for this improvement in drought tolerance or resistance are diverse and may involve enhanced water uptake, increased availability of water in the soil, such as the ability to maintain stomatal conductance under conditions of limited water. The use of PGPR, a type of soil bacteria, is another way to reduce the bad effects of not having enough water and make plants more resistant to dryness. Various mechanisms (Table 1) have been identified through which PGPR adapted to drought can regulate the production of endogenous ethylene in plants, potentially resulting in enhanced plant drought tolerance and productivity (Romero-Munar and Aroca, 2023).

Recent research has demonstrated the close connection between soil microbes and plants, both externally and internally. Microorganisms in the rhizosphere, especially those with growth-promoting activity, have been found to significantly influence plant development. Additionally, some plant growth-promoting microbes (PGPMs) promote growth of the plant by synthesizing hormones and lytic enzymes, indicating their potential use as microbial inoculations. Furthermore, certain bacteria can produce secondary metabolites that aid in carbon immobilization, nitrogen assimilation, and phosphorus activation in the rhizosphere. Soil-borne PGPMs, including fungi, yeasts, and bacteria, have been revealed improve soil health and enhance plant growth (Alzandi and Naguib, 2022).

Table 1. Mode of action of different endophytes and rhizobacteria and their influence on wheat crop

Endophyte/ PGPR	Mechanism of action	Effect on wheat	Reference
Azospirillum sp.	Produces plant hormones and improves water uptake	Increased biomass and yield	(Phour and Sindhu, 2022)
Bacillus subtilis	Produces osmoprotectants and improves water use efficiency	Increased tolerance to drought stress	(Ali *et al.*, 2022)
Enterobacter sp.	Produces phytohormones and improves water uptake	Increased shoot length and biomass	(Ahmed *et al.*, 2021)
Herbaspirillum sp.	Improves water use efficiency and produces phytohormones	Increased biomass and yield	(Zeffa *et al.*, 2019)
Pseudomonas sp.	Improves root growth and water uptake	Increased tolerance to drought stress	(Danish *et al.*, 2020)
Trichoderma sp.	Produces enzymes that degrade cell wall components, facilitating water uptake	Increased root and shoot length	(Szczałba *et al.*, 2019)
Acremonium sp.	Produces phytohormones and improves water use efficiency	Increased biomass and yield	(Byregowda *et al.*, 2022)
Clavibacter sp.	Produces osmoprotectants and improves water use efficiency	Increased root and shoot length	(Mumtaz *et al.*, 2022)

Previous studies have demonstrated their capability to advance nutrient accessibility for plants, modify root architecture, and enhance plant growth and establishment during challenging circumstances such as high levels of potentially toxic elements, salinity, and drought. These PGPMs are known to produce various substances that contribute to plant growth, including phytohormones, enzymes, and secondary metabolites that can solubilize nutrients and sequester carbon in the rhizosphere, as shown in Table 2. Consequently, they have promising potential as bioinoculants for sustainable agriculture (Govta *et al.*, 2022).

Table 2. Bioactive molecules produced by PGPR and their impact on wheat growth

Active biomolecule	Source	Mode of action	Effect on wheat growth	References
Abscisic acid (ABA)	Fungi and organic matter	Inhibits seed germination and water loss, regulates stress response	En Increase stress tolerance and seedling establishment	(Chen *et al.*, 2020)
Cytokinins	Rhizobacteria and fungi	Promotes cell division and differentiation	Increases tillering and grain yield	(Zaheer *et al.*, 2022)
Enzymes (e.g., phosphatases, proteases)	Soil microorganisms	Break down organic matter and release nutrients	Increases nutrient availability and uptake	(El-Sawah *et al.*, 2021)
Indole-3-acetic acid (IAA)	Rhizobacteria, fungi, and organic matter	Promotes root growth, cell division, and elongation	Increases root length, biomass, and nutrient uptake	(Etesami, 2022)
Gibberellic acid (GA)	Fungi and organic matter	Stimulates stem elongation, cell division, and seed germination	Increases stem length and plant height	(Orozco-Mosqueda *et al.*, 2023)
Siderophores	Rhizobacteria	Chelates iron and other nutrients	Improves nutrient uptake and alleviates nutrient deficiency	(Srivastava, 2023)
Phytohormones (e.g., auxins, cytokinins)	Soil organic matter	Stimulates plant growth and development	Improves plant growth and yield	(Orozco-Mosqueda *et al.*, 2023)
Volatile organic compounds (VOCs)	Soil microorganisms	Induce systemic resistance and stimulate plant growth	Enhances plant defense against pathogens and improves growth	(Poulaki and Tjamos, 2023)

Wheat Responses to drought stress

Wheat can grow and be produced even when there isn't much water. But the amount of water wheat needs to grow depends on how far along it is in its growth and on things in the surroundings (Adesina *et al.*, 2020). In hot and dry weather conditions, wheat plants require significant amounts of water and undergo various physiological, biochemical, and morphological changes. To survive the challenges of water deficit conditions, wheat plants employ a range of mechanisms at the cellular level. These processes can be categorized into three drought response strategies: escape, avoidance, and tolerance, which enable wheat plants to thrive in dry situation (Yahaya and Shimelis, 2022). Wheat plants utilize the escape strategy by completing their life cycle during a period when there is sufficient water supply, for example, through early maturation, before the onset of drought stress. Numerous studies have demonstrated that early maturation in wheat can help mitigate water scarcity during later growth stages, resulting in higher crop yields (Soto-Cerda *et al.*, 2022).

Drought avoidance in plants encompasses their ability to optimize water absorption and reduce water loss. In the case of wheat, this involves adopting strategies to enhance water absorption through an extensive root system (Danakumara *et al.*, 2021), while simultaneously minimizing water loss through leaf and stomatal mechanisms, such as reducing transpiration from the leaf surface (Zagoub *et al.*, 2023). Drought resistance is a crucial characteristic that enables wheat plants to endure periods of water scarcity and rapidly recover following rainfall. Dehydration tolerance plays a vital role in this process by allowing wheat plants to sustain metabolic activity for extended periods, even under conditions of low tissue water potential (Ozturk *et al.*, 2021).

Table 3. Effects of drought stress on various morpho-physiological and biochemical characteristics of wheat crops

Morphological	Physiological	Biochemical	References
Dwarfness	Reduced photosynthesis	Production of ROS	(Ors *et al*., 2021; Shemi *et al*., 2021; Wu *et al*., 2022)
Reduction in leaf area	Enhanced water use efficiency	Generation of ABA	(Kong *et al*., 2021; Toscano *et al*., 2019; Ullah *et al*., 2019)
Reduced leaf size	Diminished relative water contents	Production of Proline	(Batool *et al*., 2020; Ghaffari *et al*., 2019; Misra *et al*., 2020)
Less numbers of leaves	Changes in integrity of cell wall	Oxidative damage	(Huang *et al*., 2019; Liao *et al*., 2019; Marthandan *et al*., 2020)
Improved root/shoot ratio	Closing of stomata	Reduction in chlorophyll contents	(Tátrai *et al.*, 2016; Marthandan *et al*., 2020; Qaseem *et al*., 2019)
Reduced shoot length	Reduced growth rates	Reduction in photochemical activity	(Seleiman *et al*., 2021; Shen *et al*., 2020; Zokaee-Khosroshahi *et al*., 2014)

Physiological responses

Investigating the physiological mechanisms of several wheat cultivars in response to drought is a valuable approach for gaining insights into the mechanisms underlying drought resistance (Francesconi *et al*., 2021). Water scarcity causes significant alterations in the physiology of wheat, and different wheat varieties possess a wide range of adaptations (Table 3) that enable them to tolerate the adverse consequences of water deficiency. Research has shown a close link between physiological responses and drought resistance mechanisms in wheat plants, including elevated levels of chlorophyll and relative contents. Sommer *et al.* (2023) concluded that there is a relationship between physiological and yield parameters, indicating that these traits are valuable for drought resistant mechanisms. These findings indicate that the identified characteristics may serve as reliable indicators of wheat's ability to cope with water stress. The drought tolerance mechanisms identified through physiological studies provide valuable awareness regarding responses of plants under drought stress and their ability to maintain growth and yield during challenging conditions (Gambetta *et al*., 2020). Additionally, these traits play a crucial role in breeding programs aimed at screening and selecting genotypes that exhibit enhanced tolerance to drought (Langridge and Reynolds, 2021). According to Ghatak *et al.* (2021) physiological parameters play a critical role in identifying the most promising wheat genotypes that exhibit superior drought resistance in arid regions.

Enhancing crop yields during drought remains one of the most challenging objectives for plant breeders. Classical breeding programs can be utilized to identify and incorporate drought tolerance mechanisms in crops that are suitable for water-limited regions (Han *et al*., 2020). In a study conducted by Emam *et al.* (2022) the consequence of drought and irrigation on productivity and yield-related traits of wheat cultivars was assessed. The findings indicated that wheat genotypes exhibiting favorable characteristics associated with grain production could be selected for both irrigated and water-stressed environments.

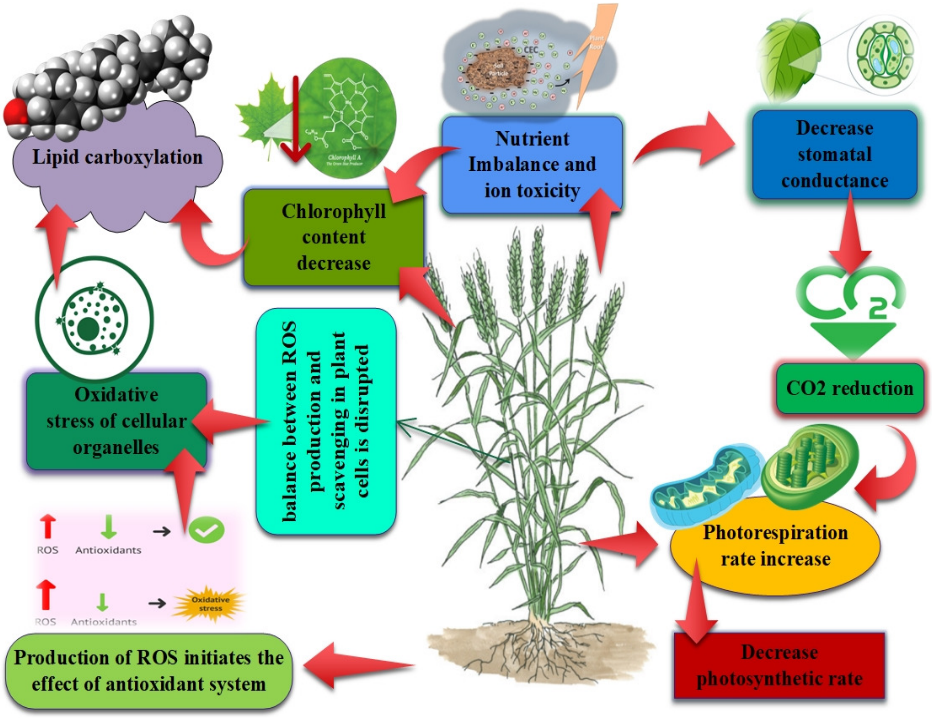

Figure 5. The toxic effects of drought stress on wheat. Drought decreases photosynthesis, increases respiration, ROS production, oxidative damages, cause nutrient imbalance and disturb nutrient balance thus cause reduction in plant growth (Wahab *et al.,* 2022)

Morphological traits

The correlation observed between morphological traits is often used as an indicator for the identification of drought-resistant wheat varieties with the potential to yield higher outputs (Sun *et al*., 2021). Several morphological features are commonly employed to screen drought-tolerant genotypes. In his study Nehe *et al.* (2019) analyzed the positive associations between growth parameters and grain production in wheat. Additionally, the study showed that tolerant genotypes had higher total dry matter at maturity and larger leaf areas (Racz *et al*., 2022).

Photosynthesis and pigment composition

Under extreme drought stress, plant photosynthesis is adversely affected due to alterations in chlorophyll concentration, changes in chlorophyll components, and damage to the photosynthetic system. Water stress conditions are reported to lead to a reduction in the total chlorophyll content. Drought-sensitive genotypes experience a more rapid decline in chlorophyll concentration than drought-tolerant cultivars (Yahaya and Shimelis, 2022). It is believed that increased levels of chlorophyll in leaves of various plant species are a desirable trait for achieving better crop yield during drought (Delfin *et al*., 2021). Several investigations indicate a maximum relationship between leaf chlorophyll concentration and photosynthetic ability. Chlorophyll is a vital constituent of the chloroplasts responsible for photosynthesis, and its concentration directly controls the rate of photosynthesis. During drought, a decrease in chlorophyll content is a common indication of the production of ROS. Plants depend on photosynthetic pigments for absorbing light and producing reducing agents, and both chlorophyll *a* and *b* are affected by drought stress (Munné-Bosch and Villadangos, 2023) (Figure 5). Under water-limited conditions, two cultivars of okra showed enhancement in chlorophyll b concentration while chlorophyll a concentration was not affected, leading to a proper decline in the concentrations of chlorophyll a to b in both cultivars (Hannachi *et al*., 2022). In plants, water stress and other alterations may cause to reduce in tissues levels of chlorophylls and carotenoids, primarily caused by ROS production in the thylakoids (Dmitrieva *et al*., 2020). The results suggest the need for a collaborative approach to either stimulate pigment production or modify pigment biosynthesis pathways in plants in order to enhance their ability to withstand drought (Abdelsattar *et al*., 2023).

Biochemical responses

Reactive oxygen nitrogen species (RONS)

In answer to different abiotic problems, one of the first things that eukaryotic cells do is make more RONS. It is one of the first things plants do when they feel stressed by drought. RONS is a mixture of ions and oxygen free radicals that are made when oxygen is broken down. It is used by cells to send signals. But when plants are stressed by things like drought, the amounts of ROS go up a lot, which causes molecular damage (Bano *et al*., 2021). Water stress induces oxidative imbalance in plants, which is characterized by the increased generation of RONS (Jóźwiak and Politycka, 2019). The occurrence of water deficit leads to an elevation in RONS formation, resulting in an increase in malondialdehyde (MDA) levels. MDA is one of the most reliable indicators of membrane lipid peroxidation and reduction in membrane stability, which is caused by RONS generated under water stress (Xiangyang Li *et al*., 2022).

Antioxidant enzymes

Plants possess an intricate enzymatic defense system that is capable of preventing oxidative damage by active oxygen, ensuring proper cellular function (Sharma *et al*., 2019). The interplay between the function of antioxidative enzymes and the generation of ROS determines whether oxidative signaling and damage take place (Sies *et al*., 2022). Non-enzymatic antioxidants and enzymatic components work collaboratively during oxidative stress to maintain membrane integrity. Enzymatic components can directly eliminate ROS or generate non-enzymatic antioxidants. For effective degradation of oxygen (O_2) and Hydrogen Peroxide (H_2O_2) in plant cells, antioxidants need to work together. SOD is available in chloroplasts, mitochondria, cytoplasm, and peroxisomes, and it converts O_2 into H_2O_2. POD plays a key role in scavenging H_2O_2 produced by O_2 dismutation mediated by SOD. CAT, a crucial enzyme found in mitochondria, also eliminates H_2O_2 (Oldford *et al*., 2019). The ability of antioxidant enzymes produced in plants to minimize the impact of ROS and their detrimental effects may be related to drought tolerance of plant (Iqbal *et al*., 2019).

Signaling channels and gene expression changes in wheat plants during drought stress

The plant's response to drought stress is classified into ABA signaling mechanisms and non-ABA signaling pathways, as ABA plays a significant role in the initial response to drought. The AREB/ABF (Abscisic Acid-Responsive Element-Binding Protein/Abscisic Acid-Binding Factor) regulon is responsible for ABA-dependent signaling, while recent studies have shown that AP2/EREBP (Ethylene-Responsive Element Binding Protein) also participate in ABA-dependent and independent signaling pathways. Although these pathways are distinct, there may be some interaction between them (Bedoui *et al*., 2020). TaERF, a member of the AP2/ERF (Ethylene-Responsive Element Binding Factor) transcription factors (TFs) group, has been found to enhance drought resistance in wheat by increasing the levels of proline and chlorophyll (Sadati *et al*., 2022). The plant-specific Ser/Thr kinases known as sucrose non-fermenting1-related protein kinase 2 (SnRK2) act as positive regulators for ABA signaling (Bhagat *et al*., 2021). In wheat, SnRK2s such as PKABA1 are essential components of ABA signaling. Additionally, SnRK TFs are also part of the ABA-independent pathway (Chang et al., 2019). In wheat, SnRK2s such as PKABA1 are essential components of ABA signaling. Additionally, SnRK TFs are also part of the ABA-independent pathway (Chang *et al*., 2019). However, while ABA-dependent mechanisms in wheat have not been extensively studied, they have been well-researched in rice and *Arabidopsis* (Chang *et al*., 2019). The regulons that are independent of ABA include CBF/DREB (C-

Repeat Binding Factor/Dehydration-Responsive Element-Binding), NAC, and ZF-HD (Zinc Finger Motif-Associated Homeodomain) (Fatima *et al.*, 2022).

Use of molecular markers to identify drought signaling genes

Classical breeding selection relies on plant characteristics that are influenced by the environment, making it challenging to select desirable traits. However, the identification of DNA markers, specifically single nucleotide polymorphisms (SNPs), has facilitated the selection of desirable traits with greater efficiency and reliability within a shorter time frame. These markers are particularly useful in identifying genes associated with stressors such as drought. For example, the utilization of P21F/P21R primers specific to the A genome, as well as the P18F/P18R primer targeting the B genome, through the RAPD (random amplified polymorphic DNA) marker technique, facilitated the localization of the *DREB1* gene to the 3A chromosome (Kumar *et al.*, 2021). In wheat, the identification of DREBs was achieved by tagging them with five SNPs across the A, B, and D genomes. The *DREB1* gene was found to be localized on chromosomes 3A, 3B, and 3D. Two of the SNPs, S646 and S770, were utilized to map DREB-B1, which was found to be located between markers *Xfbb117* and *Xmwg818* on chromosome 3BL (Latif *et al.*, 2020). Additionally, the *1-FEH-A* and *1-FEH-B* signaling genes, which are involved in fructan-1-exohydrolase activity, were found to be connected to yield attributes (Begović *et al.*, 2020). Correlations among morpho-physiological characteristics and SNPs indicate that the identified SNPs play a critical role in the ability to resist drought. The most effective approach for identifying allelic variants is through the High-Resolution Melting (HRM) technique. Discrepancies observed in peptide sequences have been associated with alterations in protein conformation and the identification of cis-elements related to ABA signaling (Ai *et al.*, 2022). The mapping of SNPs has identified two crucial TFs, *DREB1* and *WRKY1*, which provide drought and salt tolerance (Urbanavičiūtė *et al.*, 2021). This approach facilitates the improvement of drought resistance with reduced labor and expenses, ultimately accelerating breeding efforts in the future. Table 4 shows different molecular markers locating the drought signaling genes.

Table 4. Summary of genetic markers and genes associated with chromosomal locations

Chromosome location	signaling gene	Marker type	Primer	References
5A	TaSnRK2.8	SNP	M13	(Miao et al., 2017)
6A	1-FEH-A	SNP	W12	(Latif et al., 2020)
3B	ERA1-B	SNP	ERA1B	(Ai et al., 2022).
3A	DREB1A	SNP	P21	(Ghazy et al., 2021).
--	HKT-1	SNP	HKT-1	(Singh et al., 2019)
3A	DREB1	RAPD	P18F/P18R	(Latif et al., 2020)
3A	DREB1	SNP	P21F/P21R	(Aldory and AL-Assie, 2019)
3D	DREB1	SNP	P22F/PR	(Latif et al., 2020)
--	ERA1-D	SNP	ERA1D	Edae et al., 2013
AF303376.1*	DREB1	SNP	DREB1a	(Sareen et al., 2021)

Endophytes and rhizobacteria to combat drought stress in wheat

Selection criteria for effective endophytes and rhizobacteria for drought stress tolerance

PGPR can perform multiple roles, including nutrient acquisition, hormone production, biocontrol of pathogens and pests, and enhancing soil structure (Sansinenea, 2019). They can also enhance water use efficiency (WUE), photosynthesis, and the ability to overcome stressful conditions. Furthermore, some PGPR can remove or reduce toxic elements found in the soil to make it more suitable for plant growth (Vocciante *et al.*, 2022).

The use of PGPR in the field sector has become more environmentally friendly compared to pesticides and chemical fertilizers (Mekonnen and Kibret, 2021). By stimulating plant growth and strengthening plant immunity, PGPR reduce the need for synthetic inputs, thus reducing environmental pollution and the costs associated with conventional agriculture (Jing *et al*., 2022). PGPR can be applied to soil, seeds, or plant foliage through different methods, and their effectiveness depends on various aspects such as bacterial strain, environmental restrictions, plant species, and integrated management practices (Elnahal *et al*., 2022). In conclusion, PGPR are beneficial microorganisms that perform a significant part in plant development and improving soil texture. Adopting rational agricultural practices that incorporate these microbes can help enhance food security, mitigate climate change, and support ecosystem services (Sekaran *et al*., 2021).

Moreover, PGPR are eco-friendly alternatives to synthetic fertilizers, which can have deleterious impacts on environment as well as human health (Fasusi *et al*., 2021). PGPR are also more sustainable as they promote natural processes of soil fertility and plant growth, rather than relying on external inputs. By enhancing plant growth and productivity, PGPR can contribute to agricultural sustainability and food security, especially in developing countries where resources are limited. In conclusion, PGPR are a diverse bacterial groups that have positive impacts on plants, soil, and the environment (Özdoğan *et al*., 2022). Their potential for improving agricultural productivity, sustainability, and resilience, as well as reducing the reliance on chemical inputs, makes them an attractive option for modern agriculture. However, further investigation is required to establish their intrinsic mechanisms and communications with plants and other microorganisms, and also assess their potential risks and limitations (Vaou *et al*., 2021).

Furthermore, the interaction between PGPR and plants can result in increased nutrient uptake, leading to better plant production and increased yields, as shown in Figure 6. This is due to the capability of PGPR to boost the growth of beneficial root microorganisms and improve nutrient availability. In addition to their benefits for plant growth and performance, PGPR can also have positive impacts on the environment (Oubohssaine *et al*., 2022). By promoting plant health and minimizing the need for chemicals, PGPR can contribute to more environment-friendly and sustainable agricultural practices (Das *et al*., 2022). Overall, PGPR play a significant role in improving plant performance, particularly during challenging environmental situations such as drought stress. As our understanding of these microorganisms continues to grow, we may unlock even more potential benefits for the agricultural sector and the environment (Khatoon *et al*., 2020). Thus, endophytes and rhizobacteria could be an important play to mitigate the toxic effects of drought stress in wheat. However, more research is direly needed for their promising future.

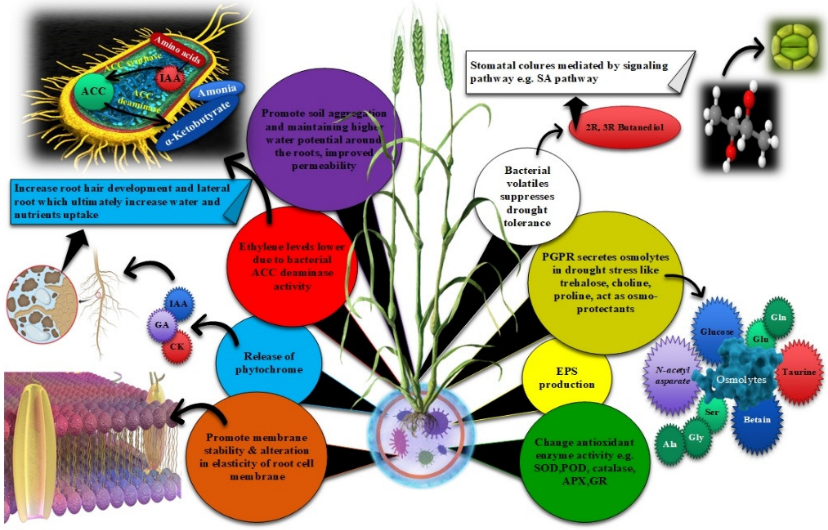

Figure 6. Mechanisms of drought tolerance induced by PGPR in wheat (Vurukonda *et al*., 2016)

The role of endophytic and rhizobacteria in regulating water uptake and maintaining plant water balance

It is important to note that RWC (Relative Water Content) should not be used as the sole indicator of water availability in plants, it can be affected by things like leaf age and tissue type (Ievinsh, 2023). Other indicators, such as leaf potential and stomatal conductivity, should also be taken into consideration. PGPR have demonstrated promising results in enhancing plant water status, particularly under stressful conditions like drought (Notununu *et al.*, 2022).

This has important implications for crop productivity and sustainability, especially as climate change continues to exacerbate water scarcity in many regions. Further research is required to elucidate the mechanisms by which PGPR regulate water and to optimize their application in agriculture. PGPR have been found to have a significant influence on the plants relative water content (El-Mageed *et al.*, 2022). In conclusion, endophytic and rhizobacterial maintain the better root growth that can ensure the better water uptake to counter the toxic effects of drought.

Endophytic and rhizobacterial aspects in regulating osmotic stress and ROS scavenging

Understanding the molecular mechanisms that regulate ROS scavenging and antioxidant defense systems is crucial for improving crop productivity and environmental sustainability. Research has demonstrated that genetic modification or manipulation of key genes involved in antioxidant pathways can enhance stress resistance and increase crop yield (Gómez *et al.*, 2019). Additionally, the use of natural or synthetic antioxidants as supplements or activators can also improve plant responses during stress conditions. In conclusion, the intricate interplay between antioxidant defense systems and ROS synthesis in plants highlights the importance of considering the molecular and responses anatomical of plants to stress. By harnessing the potential of these natural defense mechanisms, we can develop sustainable agricultural practices that promote crop resilience and contribute to environmental conservation (Chattha *et al.*, 2022; Thakur *et al.*, 2023).

The enzymatic system includes glutathione peroxidase (GPX), while the non-enzymatic antioxidants comprise phenolic compounds such as terpenes, carotenoids, alkaloids, tocopherol, glutathione, proline, and ascorbate (Rajput *et al.*, 2021). Additionally, plant growth regulators produce organic acids and enzymes to aid in nutrient acquisition, as well as siderophores to assist in iron uptake. They also facilitate the solubilization of macronutrients from the soil. The presence of PGPR can help withstand water stress by promoting root growth and enhancing water uptake, thereby increasing WUE of plant (Kaur *et al.*, 2021). Moreover, PGPR has the capability to alleviate the detrimental impacts of oxidative stress induced by drought by producing enzymes that detoxify ROS. Thus, *endophyte and rhizobacterial* improves the antioxidant activities that prevent the oxidative damages and ensures the survival of plants under drought stress.

The role of endophytes and rhizobacteria in regulating plant hormone signaling and gene expression

Certain rhizobacterial strains can induce systemic resistance in plants through hormone-mediated mechanisms. For instance, specific rhizobacterial strains can trigger the production of ethylene in crops, thereby activating plant systemic tolerance against pathogenic attacks (Rehman *et al.*, 2020). Conversely, other rhizobacteria can encourage growth and yield of the plant by producing metabolites that mimic the action of plant hormones (auxins or cytokinins) (Keswani *et al.*, 2020). The intricate interplay between rhizobacteria and plant hormones offers valuable insights into the mechanisms of plant-microbe connections in the rhizosphere (Bhatt *et al.*, 2022). Understanding the specific roles of different rhizobacteria in modulating hormone signaling pathways in plants has the potential to drive innovative approaches for enhancing plant growth and improving overall plant health in agricultural and environmental contexts (A. Khan *et al.*, 2019). According to many studies, the proportion of plant PGPR-assisted hormones during stress conditions performs better than a single hormone in plants (Guan *et al.,* 2023; Kumawat *et al.,* 2023). Liu and Wei (2019) found drought exposure affected seedlings GA:ABA and zeatin riboside (ZR):IAA ratios. Dark septate endophytes (DSE) inoculated seedlings had a greater IAA/ABA proportion than non-inoculated seedlings. However, *Acrocalymma vagum* inoculated seedlings had lower GA/ABA, ZR/ABA, and ZR/IAA ratios. This means that A. *vagum* may help keep the balance of host hormones by altering hormonal proportions following symbiotic associations with the host, reducing plant development and growth to prevent it from utilizing unnecessary water, preserving cellular tension typical to maintain water-equilibrium usual, enabling stomatal closure to stop water loss, and raising cell solute concentration to assist plants in consuming more water, which makes them better at dealing with water shortage conditions.

Furthermore, certain rhizobacteria have the ability to control the ABA levels in plants by either increasing or decreasing its synthesis, or by enhancing its catabolism (Oleńska *et al*., 2020). These bacteria can also improve the functionality of ABA receptors and induce the expression of ABA-responsive genes, thereby regulating plant development under various stress conditions. Additionally, rhizobacteria are capable of producing phytohormones (auxins, cytokinins, gibberellins, and ethylene) which can also influence plant development and growth. Beneficial rhizobacteria, for example, can produce auxins and cytokinins, promoting root growth and enhancing nutrient availability (Metin *et al*., 2021). Some rhizobacteria can produce ethylene or inhibit ethylene synthesis, thereby regulating plant growth and development under the influence of different stressors (Khanna *et al*., 2022).

Additionally, beneficial rhizobacteria could produce siderophores, which chelate iron and make it available to crops. This enhances plant growth and development by improving nutrient availability (Srivastava, 2023). These compounds can act as plant growth regulators or assist as signals that fascinate or resist insects or pathogens (Bordoloi *et al*., 2023). In conclusion, rhizobacteria are capable of producing a variety of chemicals that regulate plant growth under different abiotic stresses (Murchie and Ruban, 2020). This study recommends that endophytes may play a role in helping sorghum plants better tolerate and respond to drought conditions. The specific mechanisms by which these endophytes influence gene expression and enhance plant resilience to stress are still not fully understood and require further investigation (Sohrabi *et al*., 2023). However, these findings suggest that endophytic bacteria could potentially be utilized as a tool for sustaining crop productivity and enhancing tolerance to changing environmental challenges (Kamran *et al*., 2022). The endophytes mediated increase in osmolytes and hormones accumulation maintain membrane stability, improves antioxidant activities, nutrient availability and genes expression and resulting in significant increase in drought tolerance.

Future perspectives

Due to agronomic and economic concerns, numerous studies examined PGPR inoculation on wheat drought resistance. Researchers should focus on producing microbial formulations that improve the efficiency of plants during drought stress while minimizing pesticide and chemical fertilizer utilization. Presently, everyone knows that PGPRs can assist wheat plants in growing stronger roots and shoots and even produce more grain in a variety of distinct manners. At this point, we don't know much about the exact mode of action because it involves the synthesis of phytohormones, Exopolysaccharides (EPS), or ACCd (1-Aminocyclopropane-1-Carboxylate Deaminase). The positive physiological influence that is seen on a plant might be the result of multiple PGPRs utilizing one or more of the pathways discussed in the previous sections. It is still challenging to understand which mechanism in a plant is accountable for specific consequences. Uncertainty persists about the functions of various networks, such as the alteration of antioxidants or the amount or functioning of osmolytes. There is rarely an apparent connection between the genetic potential of the strain and the consequences that take place on plants. The published assessments frequently examine biomass, growth, or yield, not the processes involved in the background. Furthermore, different strains often have more than one PGPR trait and experiments using particular knock-out mutants might assist in verifying and assessing the roles of various mechanisms related to drought adaptation. Although IAA is one of the phytohormones that has been studied the most in the relationship between wheat and PGPR, the effects of other hormones like BR (Brassinosteroid) and CK (Cytokinin) are not yet widely recognized. The ability of PGPR to make wheat more resistant to drought is still a hopeful and challenging subject to address, but its exact mechanism is not yet completely understood.

The root system of wheat is critical for water uptake and transport. Developing root systems that can better withstand drought stress could improve wheat survival in drought conditions. Several studies have shown that deep root systems are critical for enhancing drought resistance in wheat. By increasing root length and density, wheat plants can access deeper soil-water and endure longer periods of drought conditions. For instance, the introduction of a root hair-specific promoter from *Arabidopsis* into wheat can enhance its root length and density, leading to improved drought tolerance. Additionally, developing root systems that can effectively maintain water uptake in drought conditions by adjusting the root architecture or by regulating the water transporters could be considered as future perspectives for improving wheat's drought resistance. Improving water-use efficiency is another strategy that could be explored to enhance wheat survival in drought conditions. Developing wheat varieties that use water more efficiently and lose less water through transpiration could help reduce the impact of water stress on wheat crops (Farooq *et al.*, 2019). For example, the development of wheat varieties with minimized stomatal conductivity could lead to reduced water loss through transpiration, resulting in improved water-use efficiency. Similarly, identifying and characterizing water transporters such as aquaporins that can facilitate water-uptake and transport during water deficiency could be explored as future perspectives for improving WUE in wheat.

Conclusions

There is mounting evidence that endophytes and rhizobacteria play a crucial role in helping wheat survive abiotic stress, such as drought. Several studies have shown that drought may alter rhizobacterial communities in a way that lasts for a long time. These alterations can affect the growth and physiology of plants. It has been discovered that endophytes, microorganisms that reside within plants, enhance wheat's ability to withstand drought by improving water usage efficiency, controlling stomatal closure, and triggering the production of osmo-protectants. Endophytes also strengthen plants' antioxidant defense mechanisms, reducing the risk of oxidative damage caused by drought stress. Similarly, rhizobacteria, which are found in the soil near plant roots in the rhizosphere, can enhance wheat's ability to withstand drought by promoting root development and enhancing nutrient uptake. Rhizobacteria can produce plant growth hormones that help plants overcome drought challenges by regulating their physiological processes. The review paper concludes that endophytes and rhizobacteria have the potential to be exploited in agricultural systems and used as biocontrol agents to enhance crop resilience to drought stress. However, further research is still necessary to fully understand the mechanisms by which these microorganisms enhance plant resilience to drought and to optimize their practical implementation in agricultural settings.

Authors' Contributions

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Ethical approval (for researches involving animals or humans)

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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