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Review

Wheat Responses to Abiotic Stresses and Microbiome Dynamics: A Review

Buğdayın Abiyotik Streslere ve Mikrobiyom Dinamiklerine Yanıtları: Bir Derleme

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ABSTRACT

Wheat (*Triticum aestivum*) is renowned as one of the world's most crucial cereal crops. Throughout agricultural production, wheat faces multiple stressors, with numerous researchers investigating both these stress factors and the resultant response mechanisms. The main abiotic stress factors that wheat is exposed to include drought, salinity, and temperature. Drought stress negatively affects plant productivity by reducing photosynthetic capacity and increasing water loss. Salinity stress disrupts ion balance, limiting plant growth and nutrient uptake. Heat stress leads to yield loss through protein denaturation and a decline in photosynthetic activity. The responses of wheat to stress conditions are supported by various physiological and biochemical mechanisms. These include an increase in hormones such as abscisic acid (ABA), stomatal closure, and osmotic adjustment mechanisms. Additionally, microbiome dynamics are among the important factors supporting wheat against these stresses. Researchers have reported that rhizobacteria (PGPR) and mycorrhizal fungi enhance nutrient uptake, thereby improving stress tolerance. In this context, the response mechanisms of wheat to stress conditions and microbiome interactions have played a critical role in agricultural productivity. The use of microbial supplements in agricultural production is believed to have the potential to increase wheat productivity. In our study, the detailed mechanisms of these interactions have been presented and examined from a sustainable perspective.

Keywords: Wheat; Microbiome; Abiotic stress; PGPR

ÖZET

Buğday (*Triticum aestivum*), küresel ölçekte gıda güvenliğinin sağlanmasında temel bir stratejik ürün konumundadır. Tarımsal üretim sürecinde, özellikle kuraklık, tuzluluk ve yüksek sıcaklık gibi abiyotik stres faktörleri bitkinin büyüme ve verim potansiyelini önemli ölçüde sınırlandırmaktadır. Kuraklık stresi, fotosentetik etkinliği azaltarak ve transpirasyon yoluyla su kaybını artırarak bitki verimliliğini düşürürken; tuzluluk stresi iyon homeostazını bozarak kök gelişimi ve besin alımını olumsuz etkiler. Yüksek sıcaklıklar ise protein denatürasyonu ve fotosentez kapasitesinde azalma gibi etkilerle önemli ölçüde ürün kaybına neden olur. Bu stres koşullarına karşı buğday, abiyotik stres toleransını artıran bir dizi fizyolojik ve biyokimyasal savunma mekanizmasını devreye alır. Abscisik asit (ABA) düzeyindeki artış, stomatal düzenleme ve osmotik ayarlama süreçleri bu adaptif tepkilerin başlıca bileşenlerini oluşturur. Bununla birlikte, bitki kök mikrobiyomu da stres toleransının güçlendirilmesinde tamamlayıcı bir rol üstlenmektedir. Bitki gelişimini destekleyen rizobakteriler (PGPR) ve arbusküler mikorizal mantarlar, su ve besin alımını iyileştirerek bitkinin stres koşullarına daha dayanıklı hale gelmesini sağlar. Mikrobiyal etkileşimlerin tarımsal üretim sistemlerine entegre edilmesi, hem kimyasal girdi bağımlılığının azaltılmasına hem de üretim istikrarının artırılmasına katkı sunabilecek önemli bir strateji olarak değerlendirilmektedir. Bu bağlamda, mikrobiyom temelli yaklaşımlar, buğday üretiminde stres toleransını güçlendiren sürdürülebilir uygulamalar için güçlü bir potansiyel taşımaktadır.

Anahtar Kelimeler: Buğday; Mikrobiyom; Abiyotik stres; PGPR

1. INTRODUCTION

Wheat (*Triticum aestivum*) is a critical cereal crop in terms of global food security and agricultural sustainability. Being one of the most extensively cultivated crops globally, wheat is subjected to a range of abiotic stress factors throughout the agricultural production process (Alzahrani et al., 2018). Among these, drought, salinity, and heat stress are the most commonly studied (Farooq et al., 2009; Munns & Tester, 2008; Hasanuzzaman et al., 2013). Drought stress diminishes productivity through enhanced water loss and reduced photosynthetic capacity (Abid et al., 2016). Salinity stress adversely affects nutrient uptake and root development by creating ion imbalances, while heat stress limits plant growth through protein denaturation and reduced photosynthetic efficiency (Munns & Tester, 2008; Hays et al., 2007).

Wheat's responses to stress conditions are supported by physiological and biochemical regulations. Under stress conditions, the increase in abscisic acid (ABA) plays a key role in mechanisms such as stomatal closure and osmotic adjustment (Bashan & de-Bashan, 2010). Additionally, plant–microbiome interactions are also significant contributors to enhanced stress tolerance (Vishwakarma et al., 2020; Fitzpatrick et al., 2020). PGPR and mycorrhizal fungi improve the plant’s resistance to stress by optimizing nutrient uptake and increasing water retention capacity (Vurukonda et al., 2016).

This review examines the physiological and biochemical responses of wheat to various abiotic stress factors, as well as its interactions with microbiome dynamics, based on existing literature. Biotic stress factors such as pathogens and pests are beyond the scope of this study. The potential of microbial inputs to enhance wheat productivity under stress conditions was evaluated, and recommendations were made for sustainable agricultural practices.

2. WHEAT RESPONSES TO STRESS CONDITIONS

In response to abiotic stress factors, wheat has evolved a range of adaptive mechanisms. Environmental stresses such as drought, salinity, and high temperature directly affect the physiological and biochemical processes of wheat, leading to adverse consequences on growth, development, and yield (Büyük et al., 2012; Sharma et al., 2022). Drought stress has been shown to limit photosynthetic capacity by reducing water potential, while salinity stress disrupts nutrient uptake and osmotic balance through ion imbalances (Munns & Tester, 2008). Heat stress, on the other hand, interferes with metabolic processes by causing protein denaturation and impairing enzymatic activities (Hays et al., 2007).

To cope with these stress factors, wheat plants activate various biochemical mechanisms to enhance abiotic stress tolerance, including ABA signaling, antioxidant enzyme activity, and osmoprotectant production (Vurukonda et al., 2016). In addition, the root microbiome and rhizosphere-associated bacteria particularly PGPR play a significant role in enhancing stress tolerance (Bashan & de-Bashan, 2010). The major physiological and biochemical response mechanisms of wheat under drought, salinity, and heat stress are summarized in Table 1.

Table 1. Major physiological and biochemical response mechanisms of wheat to different abiotic stress factors

Abiotic Stress Factor	Physiological Response Mechanisms	Biochemical Responses	Key Molecular Components (Hormones, Enzymes, Genes)	Reference
Drought	Stomatal closure, reduced leaf area, increased root depth, enhanced water use efficiency	Osmotic adjustment, increased antioxidant enzyme activity, accumulation of proline and glycine betaine	ABA, SOD, CAT, POD, DREB, NAC, MYB, WRKY	Abid et al. (2016); Yasmeen et al. (2013); Gill and Tuteja (2010)
Salinity	Reduced stomatal conductance, maintenance of ion homeostasis, regulation of water potential	Regulation of Na^+/K^+ ratio, osmolyte accumulation, detoxification of reactive oxygen species (ROS)	ABA, SOS, HKT, Proline, GB, SOD, CAT, POD	Munns and Tester (2008); Shi et al. (2002); Zhu (2021)
High Temperature	Increased transpiration rate, reduced leaf surface area, synthesis of heat shock proteins	Protein stabilization, maintenance of membrane integrity, ROS scavenging	HSPs, HSFs, ABA, Proline, GB, SOD, CAT	Hays et al. (2007); Kotak et al. (2007); Wahid et al. (2007)

Abbreviations: ABA = abscisic acid; ROS = reactive oxygen species; SOD = superoxide dismutase; CAT = catalase; POD = peroxidase; GB = glycine betaine; DREB, NAC, MYB, WRKY, SOS, HKT, and Hsf indicate stress-responsive genes.

In this context, research aimed at understanding wheat's responses to stress conditions holds critical importance for improving sustainable agricultural production and productivity.

2.1 Drought Stress

Drought is one of the most significant abiotic stress factors causing yield losses in wheat (*Triticum aestivum*) cultivation. Water scarcity adversely affects plant size, grain filling, and overall productivity by reducing photosynthetic capacity and lowering turgor pressure (Sharma et al., 2022). In response to drought stress, wheat develops various adaptation mechanisms at morphological, physiological, biochemical, and molecular levels. To minimize water loss and enhance water retention capacity, wheat exhibits morphological changes such as expanding the root system deeper or wider to access water in the soil (Yasmeen et al., 2013). Root angles also play important roles in improving drought resistance because they influence the depth and distribution of the root system, thereby enhancing water uptake from deeper soil layers (Lynch, 2013; Trachsel et al., 2011; Uga et al., 2013). M. Qiao (2024), in his study on different food crops, emphasized that "reduced leaf area is another adaptation that minimizes water loss through transpiration," highlighting the role of reduced leaf area in limiting transpiration losses.

Under drought conditions, wheat activates stomatal closure mechanisms to maintain turgor pressure and reduce water loss. Stomatal closure minimizes water loss through transpiration by limiting gas exchange; however, it may also reduce photosynthetic rates, thereby negatively affecting yield (Chaves et al., 2009). Additionally, plants accumulate osmolytes such as proline and glycine betaine to maintain osmotic balance and increase water retention capacity (Ashraf & Foolad, 2007).

Wheat responds to drought stress by modulating phytohormone levels. ABA is one of the most critical responses, promoting stomatal closure to minimize water loss (Nakashima & Yamaguchi-Shinozaki, 2013). Furthermore, antioxidant enzymes -such as superoxide dismutase, catalase, and peroxidase- help alleviate oxidative stress by scavenging reactive oxygen species (ROS) (Gill & Tuteja, 2010). Several genes and transcription factors, such as DREB (Dehydration-Responsive Element-Binding), MYB (Myeloblastosis), NAC (NAM, ATAF, and CUC), and WRKY (Tryptophan–Arginine–Lysine–Tyrosine), are activated in wheat under drought stress. These genes regulate the synthesis of protective proteins and facilitate metabolic adaptations to water deficit (Joshi et al., 2016).

Taken together, these responses demonstrate that wheat develops a multifaceted adaptation strategy to minimize water loss and optimize metabolic processes under drought stress conditions.

2.2 Salinity Stress

Soil salinity is a significant abiotic stress factor for sensitive cereal crops such as wheat, negatively affecting plant size, nutrient uptake, and yield by inducing osmotic stress and ion toxicity (Munns & Tester, 2008). Wheat attempts to maintain its viability and productivity under salinity stress by developing a range of physiological, biochemical, and molecular adaptation mechanisms.

Wheat exposed to salt stress develops osmotic adjustment mechanisms to minimize water loss and maintain osmotic pressure (Zhu, 2021). It strives to enhance salinity tolerance by regulating the Na^+/K^+ balance, as high Na^+ accumulation leads to ion toxicity, while K^+ is essential for critical metabolic functions in plants (Hasegawa et al., 2000). Stomatal closure can reduce water loss through transpiration; however, it may also limit photosynthetic efficiency (Chaves et al., 2009).

In the process of adaptation to salinity stress, wheat accumulates osmolytes such as proline, glycine betaine, and sugar alcohols to enhance its physiological resilience (Ashraf & Harris, 2004). Moreover, antioxidant enzymes -including superoxide dismutase, catalase, and peroxidase- play a key role in detoxifying reactive oxygen species (ROS) generated under salinity stress, thereby reducing oxidative damage (Mittova et al., 2004)

Certain genes and transcription factors play crucial roles in plant adaptation to salinity. Ion transport-related genes such as *SOS* (Salt Overly Sensitive) and *HKT* (High-Affinity Potassium Transporter) help maintain ionic balance by regulating Na^+ accumulation (Shi et al., 2002). In addition, transcription factors such as *DREB*, *MYB*, *NAC*, and *WRKY* have been shown to enhance plant stress tolerance by activating protective mechanisms (Yamaguchi-Shinozaki & Shinozaki, 2006).

In light of these findings, wheat utilizes a range of strategies to mitigate salinity stress, aiming to reduce water loss, maintain ion homeostasis, and optimize metabolic processes.

2.3 Heat Stress

Rising temperatures driven by global warming adversely affect the physiological and biochemical processes of plants, leading to significant yield losses. Wheat attempts to maintain its viability and productivity under heat stress by activating a range of adaptive mechanisms. Major effects of heat stress in wheat include protein denaturation, reduced photosynthetic efficiency, and disruption in metabolic processes (Hays et al., 2007). These impacts influence both the grain filling process and the overall biochemical balance of the plant.Elevated temperatures have been reported to impair water balance in wheat by reducing stomatal conductance and increasing transpiration losses (Wahid et al., 2007). Furthermore, temperatures exceeding 40°C adversely affect photosynthetic enzymes, thereby limiting carbon assimilation (Farooq et al., 2011). Under heat stress, wheat plants attempt to reduce water loss by increasing transpiration rates and decreasing leaf surface area.To mitigate the effects of heat stress, wheat synthesizes heat shock proteins (HSPs) that help stabilize protein structures (Vierling, 1991). Osmotolerant compounds such as proline and glycine betaine also play an essential role in maintaining metabolic homeostasis (Sairam & Srivastava, 2001). Key transcription factors are activated in plants under heat stress to regulate gene expression. Heat Shock Factors (HSFs) promote the expression of HSP genes, enhancing the plant’s thermotolerance (Kotak et al., 2007). Similarly, transcription factors such as DREB and MYB are involved in perceiving stress signals and initiating defense responses (Yamaguchi-Shinozaki & Shinozaki, 2006). In conclusion, wheat employs a variety of adaptation mechanisms to cope with heat stress, aiming to minimize damage and maintain physiological and metabolic stability.

3. WHEAT MICROBIOME AND ITS INTERACTION WITH STRESS CONDITIONS

The wheat root microbiome plays a critical role in the plant's adaptation to stress conditions. PGPR and mycorrhizal fungi have been reported to enhance stress tolerance by improving nutrient uptake in plants (Bashan & de-Bashan, 2010). The growth, productivity, and health of agricultural crops such as wheat are closely linked to their interactions with the soil microbiota. The plant root microbiome, through beneficial microorganisms residing in the rhizosphere, contributes to the plant's ability to adapt to stressful environments, thereby supporting agricultural sustainability (Bashan & de-Bashan, 2010).

The wheat root microbiome establishes symbiotic and mutualistic relationships with the plant, optimizing water uptake, enhancing nutrient cycling, and increasing resistance to pathogens (Mendes et al., 2013). Rhizobacteria and mycorrhizal fungi colonize the root zone and play a crucial role in enhancing plant resilience to various abiotic and biotic stresses (Berendsen et al., 2012).

PGPR, which support plant development, enhance wheat's tolerance to stress conditions by increasing nutrient acquisition. PGPRs regulate phytohormone levels and activate mechanisms that mitigate biotic and abiotic stresses, thereby improving the plant's resistance to pathogens (Glick, 2012).

Mycorrhizal fungi form symbiotic associations with plant roots, enabling more efficient uptake of phosphorus and other essential nutrients (Smith & Read, 2008). These fungi significantly enhance the plant's capacity to absorb water and nutrients under abiotic stress conditions such as drought and salinity, thereby greatly improving the survival and performance of wheat (Evelin et al., 2009). The key microbial groups contributing to improved wheat tolerance under abiotic stress conditions are summarized in Table 2.

Table 2. Microbial interactions enhancing wheat tolerance to abiotic stress factors

Microbial Group / Species	Target Stress Type	Mechanism of Action	Physiological / Biochemical Contribution	Reference
Bacillus spp. (PGPR)	Drought	Enhancement of root growth, stomatal regulation, modulation of ABA metabolism	Increased water uptake capacity, reduced transpiration loss, osmolyte accumulation	Sandhya et al. (2010); Marulanda et al. (2009)
Pseudomonas spp. (PGPR)	Salinity	Maintenance of Na^+/K^+ homeostasis, synthesis of osmoprotectants	Reduced ion toxicity, improved salinity tolerance	Egamberdieva et al. (2019); Bharti et al. (2016)

Microbial Group / Species	Target Stress Type	Mechanism of Action	Physiological / Biochemical Contribution	Reference
Azospirillum spp. (PGPR)	Drought and Heat	Increase in ABA levels, regulation of root architecture	Enhanced water use efficiency, maintenance of photosynthetic capacity	Cohen et al. (2008); Ngumbi and Kloepper (2016)
Arbuscular Mycorrhizal Fungi (AMF)	Salinity and Drought	Improved water and nutrient uptake through symbiosis, buffering of ion toxicity	Maintenance of osmotic balance, improved water potential, mitigation of salt stress	Evelin et al. (2009); Smith and Read (2008)
Microbial consortia (PGPR + AMF)	Drought, Salinity, Heat	Multiple mechanisms (root growth promotion, ion homeostasis, osmoregulation, HSP induction, antioxidant activation)	Enhanced multi-stress tolerance, reduced yield losses	Vurukonda et al. (2016); Vishwakarma et al. (2020)

Abbreviations: PGPR = plant growth-promoting rhizobacteria; AMF = arbuscular mycorrhizal fungi; ABA = abscisic acid; HSP = heat shock proteins.

3.1 Drought and the Microbiome

Drought poses a significant threat to plant growth and productivity. PGPR and mycorrhizal fungi have been shown to enhance drought tolerance by increasing the plant’s water retention capacity (Vurukonda et al., 2016).

PGPR can enhance drought resilience by improving root development and water uptake capacity. These bacteria modulate plant hormonal regulation, particularly abscisic acid (ABA) metabolism, thereby influencing stomatal closure responses and reducing water loss (Cohen et al., 2008; Bresson et al., 2013; Ngumbi & Kloepper, 2016). As a result, water loss is minimized, and photosynthetic efficiency is maintained. In drought conditions, stomatal closure limits CO_2 uptake, thereby reducing the rate of photosynthesis (Chaves et al., 2003).

Certain PGPR strains also contribute to drought tolerance by producing osmoregulatory compounds such as proline and glycine betaine, which enhance the plant’s ability to retain water (Sandhya et al., 2010). In particular, species from the genera *Bacillus* and *Pseudomonas* are known to actively secrete these bioactive compounds in the rhizosphere, supporting the plant’s adaptation to drought conditions (Marulanda et al., 2009).

Under drought stress, PGPR also increase the activity of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase, thereby reducing oxidative damage (Sandhya et al., 2010). This mechanism not only helps the plant defend against reactive oxygen species (ROS) but also contributes to the maintenance of photosynthetic performance and prevents growth loss (Kohler et al., 2008).

3.2 Heat Stress and the Microbiome

Cereal crops such as wheat may suffer from reduced photosynthetic efficiency, protein denaturation, and disruption of metabolic homeostasis when exposed to high temperatures (Hays et al., 2007). However, the plant root microbiome can enhance the plant's adaptability to heat stress through various biochemical and physiological mechanisms (Berendsen et al., 2012).

Beneficial microorganisms residing in the plant root rhizosphere employ multiple strategic mechanisms to improve plant tolerance to heat stress. These microbes enhance the plant’s water retention capacity, mitigate oxidative stress, and regulate stress-related gene expression (Coleman-Derr & Tringe, 2014).

PGPR, a diverse group of rhizospheric microorganisms that enhance plant development, have been shown to improve heat stress tolerance by inducing the synthesis of heat shock proteins (HSPs) and activating antioxidant enzymes such as superoxide dismutase and catalase, thereby supporting the maintenance of cellular metabolic homeostasis (Glick, 2012).

Arbuscular Mycorrhizal Fungi (AMF) enhance plant resilience to heat stress through their symbiotic relationship with plant roots. AMF optimize water uptake, reduce water loss, and help sustain agricultural productivity, particularly in arid regions (Smith & Read, 2008).

In response to heat stress, rhizobacteria and mycorrhizal fungi support the plant by promoting the synthesis of osmoprotectants (e.g., proline and glycine betaine), activating antioxidant defense mechanisms, and inducing the production of heat shock proteins (HSPs), thereby improving the plant's ability to tolerate elevated temperatures (Mittler, 2002).

3.3 Salinity and the Microbiome

Salinity stress is a major constraint in agricultural production, adversely affecting plant growth and productivity. Excess salt accumulation in the soil induces osmotic stress and ion toxicity, reduces the plant’s water uptake capacity, and disrupts metabolic functions (Munns & Tester, 2008). However, the plant root microbiome plays a critical role in supporting agricultural sustainability by helping plants adapt to such adverse conditions (Shrivastava & Kumar, 2015).

Beneficial microorganisms in the plant rhizosphere develop a range of biochemical and physiological mechanisms to enhance plant tolerance to salinity stress. These microbes contribute to salinity resistance by producing osmotic balance-regulating compounds, maintaining ion homeostasis, and improving the plant’s water retention capacity (Egamberdieva et al., 2019).

Halophilic bacteria can enhance plant salinity tolerance by synthesizing osmoprotectants such as proline and glycine betaine. These microorganisms help maintain ionic balance by optimizing the Na^+/K^+ ratio and reducing oxidative damage in plants exposed to salt stress (Bharti et al., 2016). PGPR can also regulate levels of ABA and gibberellins (GA), enhancing the plant’s adaptability to salinity (Nguyen et al., 2020).

AMF, through their symbiotic relationship with plant roots, improve plant resilience to salinity stress. AMFs enhance water and nutrient uptake, optimize osmotic pressure, and act as a buffer against ion toxicity (Evelin et al., 2009).

The plant microbiome mitigates the effects of salinity stress by supporting osmoprotectant production, thereby reducing water loss. It also activates antioxidant defense systems that prevent damage caused by reactive oxygen species (ROS) and modulates salt-responsive gene expression to improve stress tolerance (Yamaguchi-Shinozaki & Shinozaki, 2006).

By developing multifaceted adaptation mechanisms against salinity, the plant microbiome contributes significantly to maintaining agricultural productivity. Rhizobacteria and mycorrhizal fungi enhance plant tolerance to salinity stress, thereby playing an essential role in sustainable agricultural practices.

4. CONCLUSION AND RECOMMENDATIONS

Wheat (*Triticum aestivum*) is a major agricultural crop that responds to stress factors such as drought, salinity, and high temperature through various physiological and biochemical mechanisms. Recent studies have demonstrated that the plant microbiome particularly PGPR and arbuscular mycorrhizal fungi (AMF) plays an important role in enhancing wheat’s tolerance to these stress conditions. These microorganisms strengthen the plant by increasing water and nutrient uptake, regulating hormonal balance, reducing oxidative stress, and activating stress-responsive genes.

The integration of microbiome-based practices into sustainable agricultural strategies offers significant potential to reduce reliance on chemical inputs and minimize environmental impacts. To achieve this, it is essential to identify microbial strains capable of withstanding drought, salinity, and heat stress and to incorporate them into biofertilizer formulations.

Combining microbiome-based applications with the use of drought-tolerant varieties, improved irrigation practices, and soil management strategies is expected to generate synergistic benefits. Furthermore, the use of advanced molecular approaches such as metagenomics and transcriptomics will provide deeper insights into plant–microbiome interactions under stress conditions.

Validating these findings through large-scale field trials, rather than relying solely on controlled environments, will increase the reliability and applicability of microbiome-based strategies. Finally, policy support, farmer education, and effective extension programs are crucial for the widespread adoption of these approaches. Altogether, such strategies will enhance wheat's resilience to stress factors, contributing to the development of productive and sustainable agricultural systems that are better adapted to the challenges of climate change.

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