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Review

Exploring the Genotype-Dependent Toolbox of Wheat under Drought Stress

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Abstract: Drought stress imposes substantial constraints on the growth and production of wheat (*Triticum aestivum* L.), a globally important cereal crop essential for food security. To mitigate these adverse effects, researchers are intensifying their efforts to comprehend how different genotypes respond to drought stress, aiding in the development of sustainable breeding and management strategies. This review summarizes past and recent research on genotype-dependent responses of wheat plants to drought stress, encompassing morphological, physiological, biochemical, molecular, genetic, and epigenetic reactions. Screening drought-affected features at early developmental stages can provide valuable insights into the late growth stages that are closely linked to plant productivity. This review underscores the importance of identifying traits associated with drought resistance, and the potential of leveraging wheat diversity to select cultivars with desirable agronomic characteristics. It also highlights recent advancements in investigating Bulgarian wheat genotypes with varying levels of drought tolerance, specifically in detecting essential features contributing to drought tolerance. Cultivating drought-resistant wheat genotypes and understanding stress stability determinants could markedly contribute to enhancing wheat production and ensuring stable yields under changing climate conditions.

Keywords: drought stress; wheat genotypes; drought-resistant cultivars; genotype-dependent responses; wheat diversity

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1. Introduction

The increasing global population and intensifying weather extremes present significant threats to global food security and sustainability. Among the many environmental challenges, water shortage is a major constraint that affects all aspects of plant growth and development and agricultural productivity [1,2]. Drought can occur across all of Europe in any season, irrespective of whether the region experiences high or low rainfall. The impacts of drought become particularly pronounced in areas with limited water resources or inadequate management practices, leading to an imbalance between water demands and water supply. In recent decades, the frequency and severity of drought events have increased, particularly in Central and Southern Europe, including Bulgaria [3–5]. The increase in summer temperatures by up to 2.4 °C in combination with dry spells has led to prolonged drought periods, which worsen the agrometeorological conditions in the initial stages of the development of winter crops, such as wheat [6]. Improving our understanding of the complex mechanisms behind plant drought responses and survival requires extensive research efforts because drought outcomes are affected by various external and internal factors, such as duration and severity of water loss [7], the age and stage of development during drought exposure [8], and the affected organ and cell types [9]. In the coming decade, collaborative efforts among scientists, breeders and farmers will play a pivotal role

in identifying and understanding traits associated with plant drought resistance, as well as in breeding crop cultivars that are resilient to drought [10].

Wheat (*Triticum aestivum* L.) is an extensively cultivated and globally consumed food crop renowned for its high protein content [11]. Wheat has been cultivated for over 10,000 years and currently occupies approximately 220 million hectares of arable land worldwide [12]. This extensive production area spans various climates and regions testifying to wheat adaptability. Such versatility makes wheat a dietary staple for people worldwide and contributes to global food security [13]. Over the past century, there has been a significant rise in wheat production, primarily attributed to the advancements in agricultural technology, innovations in crop breeding methods and the adoption of enhanced farming techniques [14]. High-yielding wheat cultivars have been developed to enhance resistance against pests and diseases, tolerate adverse environmental conditions and maximize resource utilization [12,13,15]. There are more than 25,000 genotypes of *T. aestivum* adapted to different temperate environments [16]. In the span from 2018 to 2021, wheat grain yields ranged between 732.1 and 760.9 million tons per year [11]. The stability of wheat production directly influences prices, impacting the purchasing power of consumers and consequently their access to food [13]. Therefore, any fluctuations in wheat yields or disruptions in production areas can have far-reaching consequences, potentially endangering the food security of vulnerable populations.

The current wheat production capacity is not sufficient to prevent the depletion of global inventories, which are threatened by dry weather spells and other unpredictable climate events that can result in substantial crop losses. Compared to other agricultural commodities like rice and soybean, wheat is more sensitive to disruptions in water supply, resulting in reduced productivity [17]. Water scarcity can affect wheat at all developmental stages: germination, early seedling growth, flowering, and grain filling [18]. Drought can lead to reduced seed germination rates, irregular growth, and ultimately lower yield and quality. Insufficient water during early seedling growth hampers root and shoot development, making plants more susceptible to pests and diseases. In the flowering phase, water scarcity disrupts pollination, resulting in poor pollen production, reduced fertilization and diminished grain formation. Water shortages during grain filling restrict nutrient transfer to developing grains, leading to smaller, less nutritious wheat grains and the potential for premature ripening, further impacting yield and quality [1,2,18]. Wheat plants primarily rely on stored soil moisture [19], which is gradually depleted during extended dry periods and replenished by rainwater [20]. Enhancing water uptake and optimizing water use efficiency (WUE) through dedicated breeding efforts hold the potential to enhance yields and to bolster crop quality [21–23]. The WUE quantifies the relationship between the amount of biomass produced and the water consumed [24,25]. Given the increasing global population and the ongoing climate fluctuations, it is crucial to continue research efforts aimed at improving wheat drought resistance.

This review provides an overview of plant defense mechanisms against drought and explores past and recent research on how wheat plants respond to drought stress, covering a wide range of aspects such as morphology, physiology, biochemistry, molecular biology, genetics and epigenetics. It emphasizes the significance of identifying specific traits linked to drought resistance and the potential of harnessing the diversity within the wheat species to choose cultivars with favorable agronomic traits. Recognizing the complex influence of water scarcity on wheat crops is essential for safeguarding food security and promoting sustainable agricultural practices.

2. Plant Defense Strategies against Drought

Plants have evolved various defense mechanisms to withstand environmental variations, such as stress escape, stress avoidance, and stress tolerance (Figure 1). These mechanisms can operate independently of adverse conditions or be specifically adapted to a particular stressor and facilitate a heritable plastic response [26]. By leveraging the

stress-adaptive strategies, plants can better cope with extreme weather and improve their chances of survival and successful reproduction.

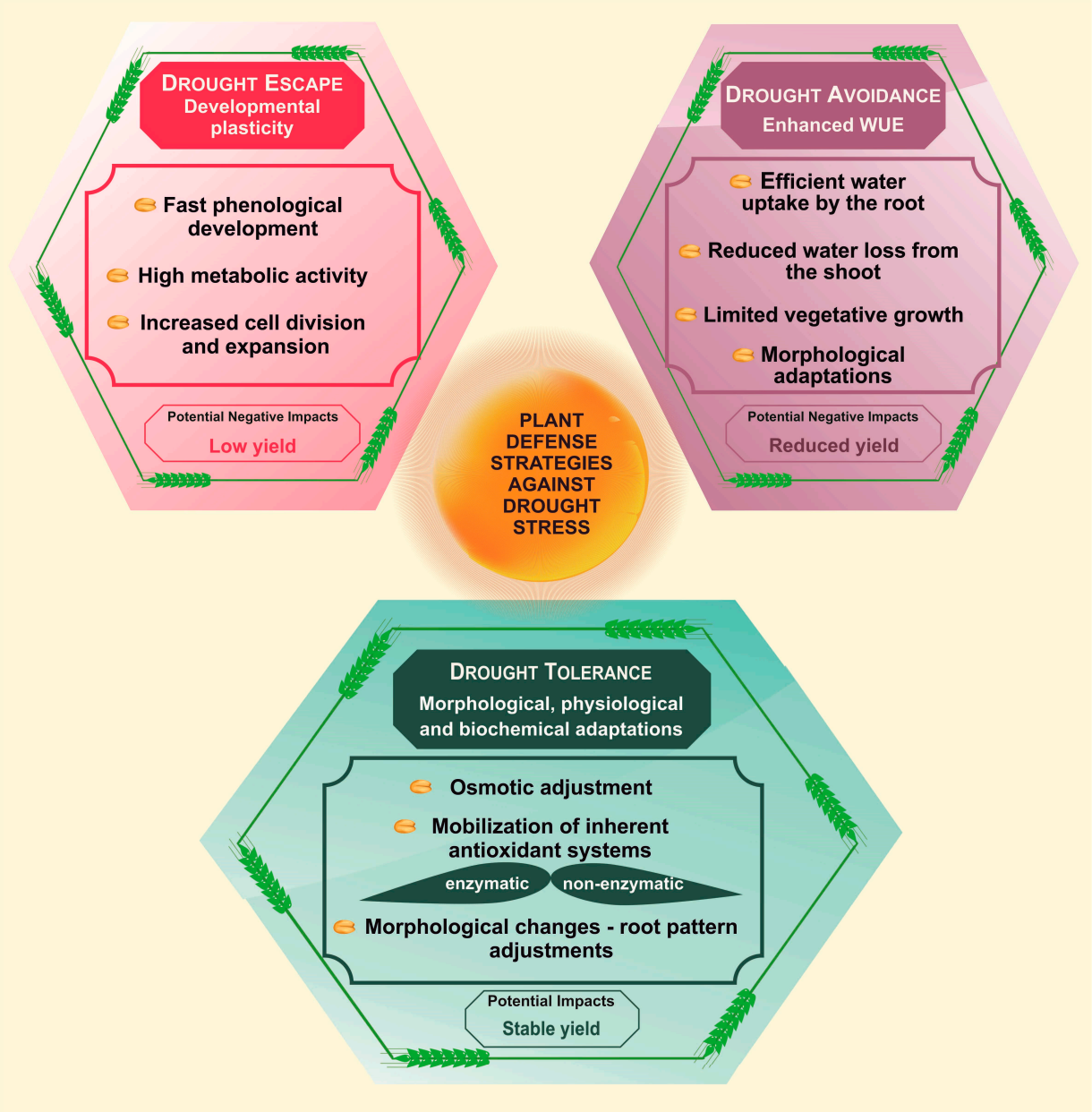


Figure 1. Plant defense mechanisms against drought stress. Abbreviations: WUE, water use efficiency.

2.1. Drought Escape Strategy

Drought escape is a survival mechanism that allows plants to successfully undergo their entire life cycle before experiencing drought-induced stress, entering a state of dormancy during periods of favorable weather conditions [27]. Drought-escaping plants typically do not undergo special morphological, physiological, or biochemical modifications. Instead, developmental plasticity is the key mechanism that enables these plants to escape from drought. Plant plasticity is associated with varying the duration of the transition from vegetative to reproductive stages, and fast phenological development, including early flowering and early maturation [28].

To achieve rapid plant development necessary for drought escape, several variables come into play, such as decreased stomatal conductance, low transpiration, and high photosynthetic carbon gain [29]. These factors promote metabolic activity, and lead to

increased cell division and expansion and the formation of new seeds before the drought-induced end of the plant life cycle [30]. Drought escape strategy is widely employed by natural plants [31] and also by crops like wheat [27], rice [32], and *Brassica rapa* [29]. This strategy can be highly effective in coping with short or recurrent drought periods, but it may not be as efficient under prolonged water shortages [27]. This is because the strategy relies on plants completing their life cycle before the onset of drought stress, which can be challenging during prolonged drought periods.

Early flowering is a critical aspect of drought escape as it shortens the vegetative development phase, but it can potentially decrease crop yield. Therefore, the timing of the crop life cycle, primarily determined by the flowering time, is essential for yield production in water-limited environments. Under normal conditions, a longer crop cycle generally promotes productivity by allowing extended photosynthetic seasons and greater opportunities to harness solar energy [33]. Severe terminal drought can reduce yields due to depleted soil water before the end of the crop cycle [34]. For instance, wheat genotypes selected in Mediterranean environments, where terminal drought stress frequently occurs, show substantially lower production due to the higher risk of water stress during the reproductive or grain filling stages [35].

2.2. Drought Avoidance Strategy

Drought avoidance, also known as the 'succulent strategy', is a plant adaptation that enhances WUE in dry environments. This strategy can be achieved through two main mechanisms: efficient water uptake by the plant root system, and reduced water loss from the shoot parts [28]. Values of WUE may vary depending on plant species and the duration and severity of drought. A higher WUE is generally linked to increased yields under water shortage [36]. A drought avoidance strategy is typically connected with limited vegetative growth and involves specific plant adaptations, such as maintaining low metabolic rates, small or closed stomata to reduce water loss, decreased transpiration and photosynthesis rates, and morphological adjustments, like leaf curling and increased wax deposition on the leaf surface [37].

Plants that use a drought avoidance strategy can be broadly classified into two categories: water savers and water spenders [38]. Water savers limit water loss from the plant canopy by developing thicker cuticles, closing stomata, decreasing transpiration area and radiation absorption, and conserving water in specialized tissues for later use during grain filling and yield formation. In contrast, water spenders achieve a high tissue water status by maintaining water uptake through increased rooting and enhanced hydraulic conductance [39,40].

The drought avoidance strategy is evident not only in natural herbaceous populations [31] but also in cultivated crops [41,42]. Certain wheat cultivars possess specific attributes, such as thicker cuticles, reduced stomatal density, and deep root systems that allow them to minimize water loss through transpiration and survive in drought conditions [43,44]. Nevertheless, the effectiveness of this strategy depends on the interplay between plant adaptations, soil moisture conditions, and environmental variables. Although drought avoidance could be effective in conserving water, it is essential to bear in mind that it may potentially lead to limited vegetative growth, which could, in turn, reduce crop productivity.

2.3. Drought Tolerance Strategy

Drought tolerance is a complex phenomenon that enables plants to survive drought exposure by employing various physiological, biochemical, or morphological adaptations, which prevent or mitigate the harmful effects of dehydration [45]. This defense strategy involves drought-induced responses, encompassing physiological mechanisms that plants employ to contend with water scarcity across multiple tiers, spanning from the molecular to the whole-plant level. These mechanisms include the intricate regulation of gene expression, dynamic protein turnover, DNA or protein repair, the maintenance of tissue turgor through

osmotic adjustment, alterations in cell wall extensibility, the reinforcement of protoplasmic drought resistance, the preservation of redox homeostasis, and the maintenance of tissue turgor. The latter involves osmotic adjustment, which entails the accumulation of soluble molecules to maintain cell turgor pressure [34,46]. These soluble compounds, commonly referred to as osmoprotectants, comprise substances like proline, polyamines, ammonium compounds, soluble sugars and various ions, all of which work to mitigate cell dehydration [47]. The accumulation of osmoprotectants results in a decrease in the inner osmotic potential of the cells, thereby enhancing water retention and maintaining homeostasis. These events ensure the proper functioning of plants under drought stress [48].

Water scarcity induces oxidative stress in plants due to the excessive generation of reactive oxygen species (ROS), which are byproducts resulting from the aerobic metabolism of plants. ROS can often trigger irreversible DNA damage and cell death, but they can also function as signaling molecules that regulate normal plant growth and stress responses [49,50]. To cope with challenging conditions, plants have developed mechanisms for drought tolerance, primarily relying on the mobilization of their endogenous antioxidant systems, which can alleviate the damaging effects [51]. These defense systems include enzymatic components, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX) and glutathione reductase (GR), as well as nonenzymatic antioxidants like flavonoids, ascorbic acid, α-tocopherol, reduced glutathione and β-carotene [52]. Among enzymatic components, SOD efficiently converts ·OH into H_2O_2, and subsequently, the produced H_2O_2 is transformed into water and dioxygen by POX and CAT [53]. Non-enzymatic systems primarily rely on low-molecular-weight antioxidants such as glutathione, ascorbic acid and flavonoids, which eliminate hydroxyl radicals and singlet oxygen [54]. When cellular ROS levels exceed the capacity of these scavenging systems, cells enter an oxidative state, leading to oxidative modifications and potential cell damage, even culminating in cell death. Low ROS levels may act as second messengers in processes like stem cell maintenance, cell division, differentiation, organogenesis and responses to environmental factors [49,50]. Modulation of the antioxidant defense systems represents a major strategy for enhancing drought tolerance. Plant species resistant to dehydration generally contain higher concentrations of osmoprotectants and possess a more robust antioxidant system [51,55].

Drought-tolerant wheat cultivars have the capacity to sustain productivity even in water-limited conditions by employing various mechanisms, such as increased root growth, osmotic adjustment, and improved WUE to achieve drought tolerance [25,34,56–59], ensuring stable crop yield despite water scarcity. Selecting drought-tolerant wheat genotypes is not only economically viable but also a sustainable approach to supporting wheat production in drought-affected regions [58]. To facilitate the selection of such genotypes, it is essential to identify relevant plant features that confer advantages under drought stress. Screening for such traits, particularly during the early stages of wheat development, can provide valuable hints for the subsequent growth stages linked to plant productivity. Hence, wheat plants can employ a combination of drought escape, drought avoidance, and drought tolerance strategies. The choice of the most suitable strategy relies on the specific genetic makeup of the wheat cultivar and the prevailing environmental conditions.

In addition, the categorization of plants into drought-escape or drought-avoidance types is not entirely precise in practice because they occur at different times. Drought escape happens prior to a drought event, while drought avoidance occurs during or after a drought period. Researchers and breeders should actively pursue the development of wheat cultivars with a combination of strategies to increase their resilience to drought stress in changing environments.

3. Genotype-Dependent Morphological Responses

Figure 2 presents the genotype-specific effects of drought stress on the root and shoot morphology of wheat plants.

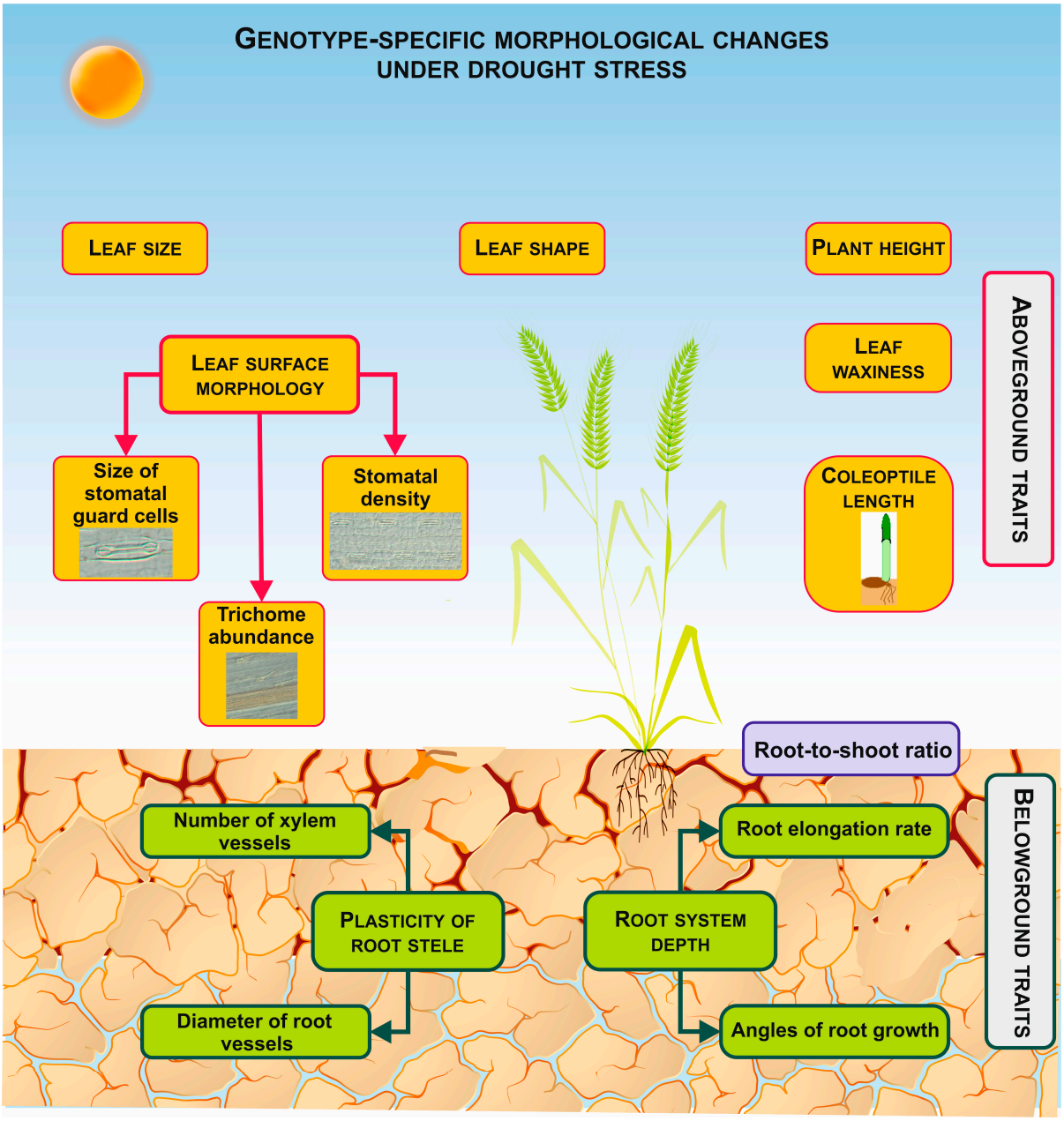


Figure 2. Genotype-dependent morphological changes in the root and shoot of wheat plants under drought stress.

3.1. Root System Traits

The ability of plants to thrive in arid environments depends on root system traits (Figure 2), vital to absorption of soil water and nutrients under favorable and extreme conditions [60]. Monocots, such as wheat, possess a complex root system that comprises seminal roots originating from the embryo of germinating seeds, nodal roots developing from the base of the tiller, and fine roots, like lateral roots and root hairs that further enhance the root absorption capability [61,62]. Seminal roots possess the ability to grow and absorb water from deeper soil layers, providing an advantage in terms of water absorption [63]. A greater root density and deeper root distribution can enhance water acquisition from lower soil layers [64–66], and lead to increased grain yield even under the conditions of terminal drought stress [67]. Comparative analysis of two wheat genotypes with differing root depths has shown that the genotype with an extensive root system generally provides

higher yields in drought-prone environments, possibly due to improved water supply during the grain filling stage [68].

A deeper root system is often related to a higher rate of root elongation [57,67] and/or narrower root angles [69,70]. Narrow root growth angles facilitate vertical growth, allowing roots to penetrate deeper into the soil and access water and nutrients during drought periods [71]. In support of this, Fang et al. [72] observed that the recently developed cultivar CH1 exhibits accelerated root growth, enabling improved water uptake from subsoil layers after anthesis, which substantially contributes to achieving high grain yield under drought conditions. A cluster analysis of 29 wheat cultivars based on their seminal root traits revealed that cultivars better adapted to drought conditions tend to have a narrower angle of seminal axes resulting in higher yields, which is attributed to the enhanced plant ability to access soil water [68]. On the other hand, after evaluating six genotypes with a varying drought susceptibility index, Grzesiak et al. [73] showed that a more downward orientation of root growth can be beneficial, but not mandatory for mitigating drought impacts on tolerant cultivars. McDonald [74] did not find a direct correlation between root angles and higher yield. Nevertheless, wheat genotypes with narrower root angles demonstrate a tendency to produce slightly higher yield.

Xylem vessel diameter [75] and root-to-shoot ratio [72] are other genotype-dependent traits related to wheat aridity resistance and productivity. Drought-adapted wheat cultivars utilize the plasticity of wheat root stele and xylem number/diameter features to improve WUE [76]. Narrower xylem vessels have been successfully employed in breeding programs for enhancing wheat drought tolerance and developing advanced wheat lines [77]. These lines have a decreased size and higher number of metaxylem vessels at the root–shoot junction, and the opposite pattern near the root tips. Such a configuration facilitates the efficient utilization of soil water resources.

Adaptive phenotypic plasticity of the root system, changing the root-to-shoot ratio can mitigate the negative impacts of drought stress [78]. In water-limited environments, the growth of shoot plant parts is constrained, resulting in a shift in the root-to-shoot ratio. This shift reduces the evaporation area of shoots compared to the absorptive area of roots, thus improving WUE [79]. However, some researchers argue that having a larger root biomass may not necessarily be advantageous for drought adaptation, as it can increase the risk of depleting available soil water before completing grain filling [67].

Although the relationship between belowground characteristics and the drought response is complex, the root system undeniably plays a critical role in the plant's capacity to absorb soil water and nutrients, thereby influencing crop productivity and adaptation to harsh environmental conditions. Further research exploring the specific mechanisms by which root traits of various wheat genotypes impact drought resistance could provide valuable insights for optimizing agricultural practices and enhancing plant resilience.

3.2. Aboveground Traits

Under drought stress, wheat plants notably change their aboveground traits (Figure 2), encompassing plant height, coleoptile length, leaf size, shape and perimeter, leaf surface morphology and waxiness, and various anatomical adjustments [80–83]. These variations are contingent upon the drought susceptibility of the genotypes, the duration and severity of drought events, as well as the growth stage of the plants [18,73,84,85].

Typically, drought stress causes a reduction in leaf area, which can subsequently decrease the photosynthetic capacity of the leaves [86]. Modern semi-dwarf wheat varieties maintain better water balance even under severe drought as compared to older tall bread wheat varieties. These variations can be partly ascribed to a smaller leaf size and more rounded leaf shape, which contribute to enhanced drought tolerance by reducing evaporation and preserving the integrity of cell membranes [82]. In contrast, when comparing two wheat genotypes with differing levels of drought resistance under moderate dehydration, the drought-tolerant cultivar accumulates higher shoot dry biomass, has a larger flag leaf size and water content, and a higher harvest index and WUE, compared to the susceptible

genotype [87]. Micromorphological features of leaves, such as stomatal and trichome density and size, as well as leaf waxiness, are also considered important traits related to drought tolerance and adaptation [82,88]. Screening five wheat cultivars, David et al. [89] revealed substantial variations in the number of trichomes and stomata among the cultivars. Interestingly, the two genotypes with higher drought tolerance exhibited a greater abundance of trichomes on both the upper (adaxial) and lower (abaxial) leaf surfaces, and a lower number of stomata. During drought exposure at anthesis and early kernel development, Jäger et al. [90] identified two drought-tolerant wheat cultivars using yield parameters, RWC in flag leaves, and leaf micromorphological features. The tolerant cultivars displayed a reduced occurrence of stomata on the flag leaf surfaces along with larger stomatal guard cells and high membrane integrity. In contrast, the drought-susceptible cultivars exhibited lower membrane integrity and a higher number of stomata on both leaf surfaces.

Additionally, under dehydration, the length of coleoptiles has notable variations among wheat cultivars [81] with longer coleoptiles that enhance the frequency of seedling emergence during desiccation, and potentially resulting in higher yields [91,92]. Conversely, shorter coleoptiles can negatively impact plant growth and productivity under dry conditions [81,93].

Utilizing these simple belowground and aboveground traits as selection criteria for drought tolerance holds promise for supporting breeding efforts aimed at developing drought-resistant wheat genotypes [56,81–83,90]. By focusing on these traits, breeders can effectively identify and select genotypes that are more likely to withstand water scarcity; however, to achieve optimal results, it is important to conduct comprehensive research that considers not only the individual traits but also their interactions with one another.

4. Genotype-Dependent Physiological and Biochemical Responses

Drought stress commonly triggers various physiological and biochemical responses in wheat plants (Figure 3), such as changes in relative water content (RWC), leaf gas exchange rates, production of ROS, oxidative stress, membrane integrity, accumulation of osmolytes, and induction of leaf senescence [94,95]. Certain cultivars can sustain their biological functions under conditions of limited water supply and rapidly recover upon restoration of normal watering [59,96–98]. Relative water content serves as a vital indicator of plant water status and susceptibility to drought, since it closely correlates with moisture levels in the soil and atmosphere. The extent of drought-induced reduction in RWC typically depends on the stress tolerance level of a specific wheat genotype [97,98]. Under severe water stress, drought-sensitive Bulgarian wheat cultivars experience a more significant decline in leaf water potential, while the drought-tolerant Katya cultivar sustains a higher water potential [59]. After the rewatering phase, Katya water potential returns to its original control values as early as the first day, whereas the drought-sensitive cultivars take until the third day of recovery to approach similar values. Furthermore, Katya exhibits nearly complete recovery in leaf gas exchange and photosynthetic activity, which could be attributed to its more dynamic stomatal responses.

Several parameters have been proposed for the selection of drought-tolerant wheat germplasm, such as stomatal conductance [99], water retention capability [100], leaf chlorophyll content, fluorescence induction parameters in leaves at grain filling stage [101,102], and leaf organelle ultrastructure [103]. Drought stress greatly impacts water dynamics, hampering the inherent ability of plants to retain water effectively, primarily through stomatal and cuticular transpiration, which regulate water loss via leaves [104,105]. Drought-tolerant plants have evolved mechanisms to balance stomatal and cuticular transpiration, allowing them to conserve water and mitigate the negative impacts of water scarcity. Cultivation of three elite wheat cultivars in a dry environment has revealed that the tolerant cultivar has lower stomatal conductance, reduced intercellular CO_2 concentration, transpiration and photosynthetic rates, but higher WUE, compared to the other two genotypes [106]. The tolerant cultivar has also exhibited significantly greater grain yield, emphasizing the important role of leaf gas exchange characteristics in wheat productivity.

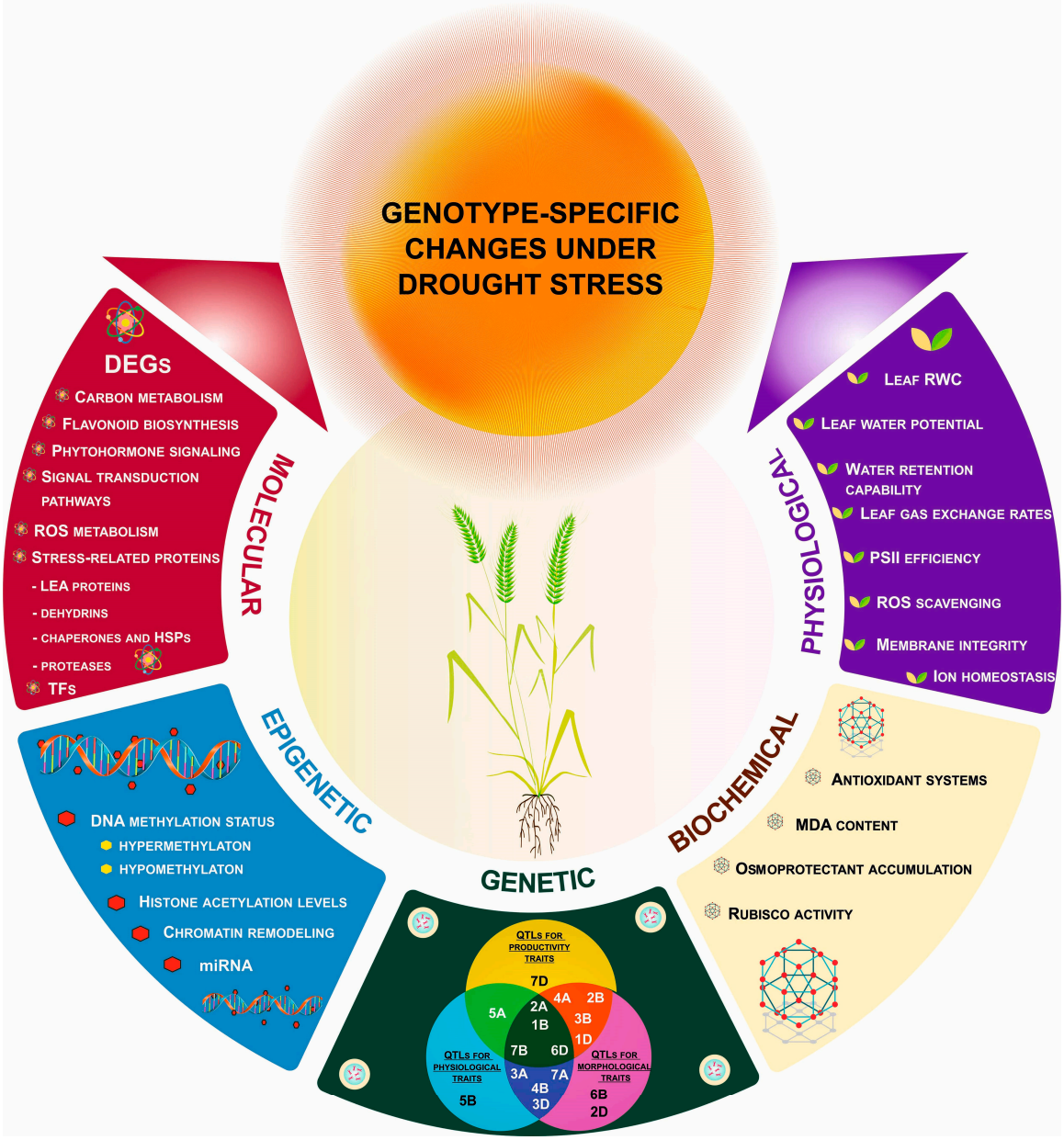


Figure 3. Genotype-dependent physiological, biochemical, molecular, genetic and epigenetic changes in wheat plants under drought stress. Abbreviations: DEGs, differentially expressed genes; LEA proteins, late embryogenesis abundant proteins; MDA, malondialdehyde; miRNAs, microRNAs; PSII, Photosystem II; QTLs, quantitative trait loci; ROS, reactive oxygen species; Rubisco, Ribulose-1,5-bisphosphate carboxylase/oxygenase; RWC, relative water content; TFs, transcription factors. The uppercase letters in the field for genetic changes represent the three wheat genomes (A, B and D), and the Arabic numerals (1–7) correspond to chromosome numbers.

Another potential drought-induced limitation to photosynthesis could be attributed to alterations in Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase) activity, the enzyme responsible for CO_2 assimilation during photosynthesis, as well as in Rubisco activase, a molecular chaperone essential for the light activation of Rubisco. In field studies, relatively stable or elevated levels of Rubisco large subunit, Rubisco small subunit, and Rubisco activase are associated with drought tolerance and higher productivity. Drought-tolerant cultivars have the ability to achieve greater yields even under severe drought conditions [97,107,108].

Water shortage often leads to an increase in the production of ROS through the transfer of photosynthetic electrons towards molecular O_2 [96], which subsequently increases lipid peroxidation [109]. The relationship between leaf gas exchange parameters, RWC, malondialdehyde (MDA) content, and drought tolerance displays genotype-dependent changes among six winter wheat cultivars. However, internal CO_2 concentration and MDA content did not consistently correlate with drought tolerance across the genotypes [110]. In general, MDA, a byproduct of lipid peroxidation, is used as an indicator of membrane damage and wheat drought tolerance [111]. While some studies did not find a clear correlation between drought tolerance and MDA accumulation in wheat cultivars [110,112], others reported that genotypes with lower MDA content under dehydration are more drought-resistant [96,113].

As aforementioned, plants have developed enzymatic and non-enzymatic mechanisms to protect themselves from stress-induced ROS accumulation [114]. The activities of antioxidant enzymes, such as SOD and CAT, have been suggested as selection criteria for drought resistance and productivity in wheat varieties [115]. A drought-tolerant genotype with high activity of POX and CAT, as well as with high levels of ascorbic acid, exhibit lower accumulation of hydrogen peroxide and lipid peroxidation compared to a sensitive genotype [116]. Fan et al. [117] categorized the drought adaptation strategies of old and modern wheat varieties into different defense phases, based on drought severity. The second and third phases are connected with increased levels of ROS and greater activity of antioxidant enzymes, resulting in membrane lipid peroxidation. Modern wheat varieties possess a greater capacity to resist drought than the old varieties, which is partially related to different antioxidant capacities. Genotype-dependent differences in the activities of APX and GR, as well as non-enzymatic protection responses such as the accumulation of reducing sugars and sucrose, have been identified in two winter wheat cultivars with contrasting productivity [112].

Wheat plants employ a range of osmoprotectants as a means of defense to bolster their resistance against drought [48,118,119]. Proline and soluble sugars are the primary molecules that contribute to enhancing wheat drought tolerance [120]. In a study assessing 25 bread wheat genotypes, four showed improved growth under dehydration due to the accumulation of free proline and soluble phenolics, which improves tissue water status and photosynthetic capacity [121]. Drought-tolerant genotypes accumulate higher levels of proline in the leaves, which partially mitigates the detrimental drought effects [122]. While glycine betaine does not directly scavenge ROS [123], its excessive accumulation can activate the antioxidant defense system in transgenic wheat plants [124]. Moreover, under drought stress, tolerant cultivars typically deposit more soluble sugars like sucrose than susceptible cultivars [118,125,126]. Khoshro et al. [127] also reported that drought sensitive wheat cultivars accumulate significantly lower levels of soluble sugars, proline, glycine betaine, and potassium compared to tolerant cultivars. Additionally, dehydration tolerance in wheat is linked to a higher proportion of raffinose, which serves as a protective molecule, aiding in the stabilization of cellular structures and preventing damages caused by dehydration [128].

Hence, the extensive array of physiological, biochemical, and metabolite responses during dehydration demonstrates the existence of diverse mechanisms employed by various wheat genotypes to endure drought conditions. As dehydration tolerance is a multifaceted adaptation that is controlled at various levels of plant organization and varies depending on the developmental stage of the plant, the identification of a comprehensive set of independent and interrelated physiological and biochemical traits can serve as direct and indirect selection criteria for wheat drought tolerance.

5. Genotype-Dependent Molecular Responses

Understanding the intricate molecular mechanisms that underlie wheat responses to dry environments is essential for developing wheat genotypes with enhanced drought resistance [129,130]. Comparative transcriptomic analysis of drought-induced gene expression

in wheat cultivars with varying stress tolerance revealed that differentially expressed genes (DEGs) are mainly linked to carbon metabolism, flavonoid biosynthesis, and phytohormone signaling (Figure 3) [129,131,132]. Drought-tolerant winter wheat cultivar exposed to water stress during various growth stages has shown that DEGs are associated with floral development, photosynthetic activity, and stomatal movement [133]. Study of root transcriptomes in two wheat genotypes with contrasting root growth under drought stress reveals the downregulation of hormone pathway genes in both genotypes. However, the tolerant genotype demonstrates the upregulation of genes related to ROS metabolism, chaperones, transcription factors, and cell-wall synthesis, enabling more effective drought adaptation [134].

Another transcriptome profiling during the early seedling stage of wheat under water deficit showed that a drought-susceptible genotype has numerous genotype-dependent DEGs with predominantly upregulated metabolism-related genes, such as those involved in carbohydrate, lipid, amino acid, and terpenoid pathways. This implies the presence of an energy-intensive adaptation strategy to cope with water deficit [135]. Conversely, in the tolerant genotype, a notable downregulation of metabolism-related genes, including those implicated in secondary metabolite synthesis, indicates an energy-saving response to the stress. The same authors identified genes that are exclusively upregulated in the tolerant genotype, with seven genes involved in flavonoid biosynthesis, six in phenylpropanoid biosynthesis pathways, and seven associated with plant signal transduction pathways. Two of these genes encode SAUR (Small Auxin Upregulated RNA) proteins responsible for cell enlargement, and plant growth and adaptation.

In two pairs of near-isogenic lines (NILs), DEGs linked to drought tolerance are involved in protein phosphorylation, oxidation-reduction, and transcription regulation [136]. The DEGs primarily function in protein and ATP binding, protein kinase activity, and DNA binding. The tolerant wheat genotype rapidly upregulates homologous genes connected with phospholipase C, components of the mitogen-activated protein kinase (MAPK) cascade, as well as the ethylene and abscisic acid (ABA) signaling pathways under drought stress [132]. Moreover, through gene enrichment analysis, elite wheat cultivars demonstrate distinct drought response strategies, with the tolerant cultivar featuring genes related to intracellular signal transduction, the MAP kinase pathway, and cellular response to abiotic stress, granting it better drought adaptability compared to the sensitive cultivar [129]. Other molecular components related to genotype-dependent variation in wheat drought responses and adaptation are chloroplast genes encoding photosystem II core proteins [137], heat shock protein [138] and dehydrin [139] genes, as well as genes encoding late embryogenesis abundant (LEA) proteins, proteases, protease inhibitors [140], and the transcription factors AP2/EREBP, bZIP, MYB/MYC, NAC, and WRKY [141]. The overexpression of a gene called *MORE ROOT* (*TaMOR-D*), which encodes a wheat auxin responsive transcription factor from the LBD family, increases root growth and enhance grain yield in rice [142]. Additionally, *ASYMMETRIC LEAVES2/LATERAL ORGAN BOUNDARIES DOMAIN* (*AS2/LOB*) wheat genes have led to the identification of a specific transcription factor that plays a role in optimizing root architecture, thereby aiding in drought adaptation [143].

Overall, these findings emphasize the complexity of wheat response to drought and the involvement of distinct molecular mechanisms in drought adaptation across different wheat cultivars, which suggest potential targets for improving drought resistance through genetic engineering.

6. Genotype-Dependent Genetic Basis of Drought Tolerance

Wheat drought tolerance is a complex trait governed by multiple genetic loci known as quantitative trait loci (QTLs), as well as by environmental factors and their interactions. The study of wheat drought tolerance genetics entails examining both phenotypic (observable characteristics) and genotypic (genetic makeup) data to pinpoint chromosomal regions that harbor the pertinent loci (Figure 3). However, the identification of QTLs for drought tolerance is challenging due to the large size of the wheat genome, the numer-

ous genes affecting drought resistance, epistatic QTL interactions, and the instability of certain QTLs [144–147]. To address these challenges, researchers have adopted diverse approaches, encompassing studies conducted under various environmental conditions to identify loci connected with drought stress tolerance in wheat [148,149], the utilization of different types of bi-parental populations [150–152], and the implementation of a wide array of DNA molecular markers [150,153]. To reveal genomic regions governing wheat drought tolerance, various methodologies have been applied encompassing genome-wide association studies (GWAS) and QTL mapping. In addition, association mapping has been used to assess genetic diversity among wheat genotypes from different geographic regions [154,155]. Recent research using simple sequence repeat (SSR) markers has revealed the genetic diversity among a population of 117 modern wheat varieties (*T. aestivum*) from Bulgaria and several Western, Central and Eastern European countries. In this study, several drought-tolerant Bulgarian cultivars are grouped together, forming a branch within one of the sub-clusters linked with drought stress tolerance, thus highlighting their unique genetic makeup in relation to drought tolerance [156]. Furthermore, genomic regions related to drought tolerance-related traits have been successfully detected through QTL mapping [157]. Most mapping studies in wheat have primarily focused on identifying QTLs responsible for the final yield components under drought stress conditions. These studies have successfully pinpointed major genomic regions on chromosomes 1B, 2B, 3B, 7B, 4A, 5A, 1D, and 7D that control various productivity traits, such as grain yield, kernel number per spike, thousand-kernel weight, heading time, among others. The genomic regions have also shown associations with QTLs related to drought-adaptive traits, which suggest their importance in conferring wheat drought tolerance [158–160]. It is noteworthy that some QTLs may have pleiotropic effects, meaning they can simultaneously influence multiple agronomic traits in either a synergistic or antagonistic manner. Additionally, the same QTLs can exhibit neutral effects on these traits in different environmental conditions. QTLs with pleiotropic effects on agronomic traits have been identified on chromosomes 1B, 4B, 5A, 4A, 7A, 2D, 3D, 5D, and 6D [161–165]. Later, the identification of QTLs associated with morphological and physiological traits linked to wheat drought tolerance has become a priority area of research. This shift in focus is driven by the belief that indirect selection based on these traits can be more efficient than direct selection for higher yield and provides a better understanding of the drought impacts at different growth stages [18]. Using microsatellite markers, Malik et al. [166] effectively mapped QTLs related to photosynthesis, cell membrane stability, and RWC on chromosome 2A, reporting their connection with the plant developmental stage. During the early stages (earing), marker–trait associations have been detected on chromosomes 1B, 4B, 5B, and 7A, while in the later stages (maturing), they have been observed on chromosomes 1B, 2A, 3D, 4B, 5B, and 6D. Another study confirmed the critical role of chromosome 2A in conferring drought-tolerant status to wheat plants. The researchers identified candidate genes associated with hormonal signaling pathways mediated by gibberellic, jasmonic, abscisic, salicylic acids and ethylene [167]. Moreover, ABA responsiveness at the seedling stage has been reported on chromosomes 1B, 2A, 3A, 5A, 6D, and 7B [168,169].

The seedling stage plays a key role in drought tolerance, as it greatly impacts all subsequent growth stages and, ultimately, the grain yield. Several studies have been dedicated to exploring genetic variations during the seedling stage, leading to the identification of numerous QTLs with varying effects on seedling traits. These QTLs have been mapped to specific chromosomes, namely 1B, 1D, 2B, 3A, 3B, 3D, 4A, 6A, 6B, 6D, 7A, and 7B [170]. Further analysis of these QTLs has shed light on a specific region on chromosome 7B, which is linked to drought susceptibility. Gene annotation analysis by Ahmed et al. [170] revealed the presence of gene clusters within this region that encode for ubiquitin-associated (UBA)-like superfamily proteins, which act as negative regulators of drought stress responses. In addition to the above findings, several other studies have identified QTLs related to shoot dry weight, the number of culms, plant height, root dry weight, root volume, root length, root surface area, and the number of root forks and tips.

Kocheva et al. [171] observed improved adaptation to drought stress in wheat seedlings carrying *Rht-B1* alleles. Further analysis has revealed that one of the QTLs on chromosome 4B corresponds to the *Rht-B1* locus, which substantially influences shoot and root traits [172]. Recently, Schierenbeck et al. [173] conducted an association analysis to identify quantitative trait nucleotides (QTNs) influencing drought tolerance traits during the seedling stage. They discovered 70 stable QTNs across 17 chromosomes, with eight of them specifically located on chromosomes 1B, 2A, 2B, 2D, 4B, 7A, and 7B, all related to multiple seedling growth-related traits.

To reiterate, wheat drought resistance is a multifaceted phenomenon governed by numerous genetic factors and strongly influenced by environmental conditions. Recent research has made significant progress in mapping QTLs linked to various drought-related traits; however, only a limited number of these QTLs have consistent effects across different environments and populations [174]. Leveraging genomic information for predicting the performance of individuals holds great potential in enhancing breeding efforts aimed at developing drought-resistant varieties. Additionally, the discovery and utilization of epistatic QTLs (QTL interactions) can further improve breeding strategies for drought resistance [146].

7. Genotype-Dependent Epigenetic Responses

Epigenetic modifications, which alter gene expression patterns without changing the underlying DNA sequence, have also emerged as principal regulators of wheat responses to drought stress (Figure 3).

Water deficit exerts a profound impact on the DNA methylation status of plants, shaping gene expression and plant drought stress tolerance. Dynamic DNA methylation and demethylation events target specific genetic loci, and result in intricate patterns of plant methylation [175]. Mounting evidence indicates that different wheat genotypes exhibit distinct DNA methylation patterns under drought stress, suggesting a potential correlation between methylation status and drought tolerance [176]. DNA methylation emerges as the primary mechanism activated in wheat that actively shapes the plant's ability to cope with the adverse conditions, while demethylation events play a complementary and supportive role [177]. It has been observed that hypermethylation is mainly associated with increased vulnerability to drought, whereas hypomethylation is indicative of enhanced resilience and tolerance to arid conditions [176,178]. Furthermore, the impact of drought stress extends to organ-specific alterations in the methylation levels of the wheat genome, as elucidated through studies comparing the methylation patterns of two contrasting genotypes: the drought-tolerant genotype C306 and the drought-sensitive genotype HUW468. Interestingly, while some similarities in DNA methylation patterns are observed between the leaves and roots of these genotypes, notable differences in methylation and demethylation events are still apparent [176]. The drought-tolerant genotype C306 displays a higher frequency of demethylation events, whereas the drought-sensitive genotype HUW468 exhibits a higher occurrence of methylation events. Moreover, under drought stress, wheat leaves display a higher content of 5-methyl cytosine and greater overall methylation levels compared to root tissues [177,179].

Alterations in histone acetylation levels represent another crucial mechanism that affects the expression of stress-responsive genes. In general, wheat tissues that grow faster show higher expression levels of histone acetyltransferase (*HAT*) genes. This suggests that the way *TaHATs* are expressed varies among tissues and is connected to the plant growth [180]. In the drought-resistant wheat variety BN207, the levels of *HAT* genes, including *TaHAG2*, *TaHAG3*, *TaHAC2* and *TaHDT1*, have been upregulated compared to the levels observed in the drought-sensitive varieties BN64 and ZM16 [181]. The dynamic regulation of *HATs* and histone deacetylases (*HDACs*) controls multiple signaling pathways involved in drought responses, such as those involving ABA, acetic and jasmonic acids [182,183]. A comprehensive analysis of the wheat genome has identified a total of 166 SET (Su(var)3–9, Enhancer-of-zeste and Trithorax) domain genes (SDGs). Among these

genes, 30 were downregulated, and six exhibited upregulation in different plant organs during the seedling stage. Under drought conditions, only *TaSDG23b-1BI* was upregulated, emphasizing its role as an epigenetic mark involved in the methylation of H3K9 [184]. The expression of *TaSDG1a-7A* and *TaSDG20-3D* genes, responsible for the methylation of H3K9 and H3K27, respectively, is also induced by drought stress. Importantly, the methylation of histones mediated by these genes ultimately leads to the downregulation of specific target genes, which is associated with enhanced stress tolerance of wheat plants.

Chromatin remodeling processes involve the dynamic change in histone–DNA interactions, leading to the unfolding of compact DNA structures and facilitating the access of transcription factors [185]. These processes can be achieved through two distinct mechanisms: the action of chromatin-remodeling factors (e.g., SWI/SNF, ISWI, INO80, and CHD) or specialized enzymes [186]. The involvement of these factors in chromatin remodeling has already been demonstrated in *Arabidopsis* [187,188]. The first indication of transcription factor-mediated recruitment for chromatin remodeling in wheat was provided by Wang et al. [189]. They found that the wheat CHD-type chromatin remodeling factor, known as TaCHR729, interacts with the promoter regions of wheat 3-KETOACYL-CoA SYNTHASE (TaKCS6). This enzyme plays a pivotal role in wheat cuticular wax biosynthesis. Additionally, TaKPAB1, a bHLH type transcription factor, has also been associated with the *TaKCS6* promoter in conjunction with *TaCHR729*. Wang et al. [189] further revealed that the silencing of *TaCHR729* regulates the interplay between wheat and powdery mildew by modulating histone methylation and finely adjusting the biosynthesis of cuticular wax.

Small interfering RNAs (siRNAs) are a predominant class of small RNAs (sRNAs) in plants [190,191]. Alongside microRNAs (miRNAs), they play vital roles in epigenetic regulatory pathways and modulate the expression of genes associated with development and stress tolerance [192,193]. Using deep sequencing technology, Ma et al. [194] analyzed two wheat genotypes with contrasting stress tolerance and identified 367 differentially expressed miRNAs in leaves under drought stress. Among these, 13 miRNAs are downregulated in the drought-tolerant cultivar Hanxuan10, but upregulated in the drought-susceptible cultivar Zhengyin1. Moreover, a comparative transcriptome analysis of the roots in modern durum wheat and its wild relatives (*Triticum turgidum* ssp. durum variety Kızıltan and two *Triticum turgidum* ssp. dicoccoides genotypes TR39477 and TTD-22) displays genotype- and/or stress-specific associations of miRNAs under drought conditions [195]. The levels of miRNA expression vary between stress-tolerant and stress-sensitive genotypes based on the type of stress, genotype and time point. Through transcriptome sequencing, DEGs associated with hormone homeostasis, photosynthesis and signaling are discovered [196]. Furthermore, miRNA regulation in durum wheat controls physiological parameters, yield performance, and grain quality traits in the subsequent generations following drought stress [197]. Li et al. [198] focused on noncoding RNAs (lncRNAs and miRNAs) and their role in regulating gene expression during drought stress using two wheat genotypes with different drought tolerance. Analyzing the relationships and expression patterns of lncRNAs, miRNAs, and DEGs, they identified 10 regulatory modules responsible for wheat response to drought stress.

In summary, epigenetic modifications are important regulatory mechanisms that fine-tune gene expression and ultimately contribute to the plant capacity to withstand and adapt to drought challenges. The exploration of these epigenetic processes holds great promise for unraveling novel strategies to enhance drought resilience in wheat and other essential crops. Moreover, studies on the transgenerational effects of drought stress have provided valuable insights into the long-term impact of epigenetic modifications on phenotypic traits, highlighting the significance of the epigenetic marks on crop performance and quality. Understanding the specific epigenetic modifications unique to each genotype offers valuable insights into the molecular mechanisms governing plant responses to water scarcity, thereby paving the way for targeted approaches to enhance drought resilience in agricultural systems.

8. Exploring the Drought Resistance of Bulgarian Wheat Genotypes

Maximizing the assessment and characterization of wheat genotypes in various repositories is instrumental in optimizing the utilization of these invaluable resources. Bulgaria, known for its rich history in wheat cultivation, has been curating collections of wheat genotypes, primarily in the breeding centers of Dobrudzha Agricultural Institute in General Toshevo and the Institute of Plant Genetic Resources in Sadovo [199–201]. These collections represent vital repositories for exploring and identifying cultivars with improved traits, particularly in relation to their ability to withstand drought conditions.

Previous investigations have extensively investigated the performance of Bulgarian wheat genotypes under varying degrees of water scarcity and subsequent recovery phases. Through detailed analysis, these studies have successfully identified several traits associated with enhanced wheat drought tolerance [59,97,107,202–204]. Generous funding provided by the National Science Fund of Bulgaria for the project titled 'Study on adaptive mechanisms to drought in Bulgarian winter wheat varieties' has enabled these studies to progress seamlessly and encompass an assessment of a wide range of agronomic, physiological, molecular, and genetic traits of genotypes with different stress tolerance levels. Examination of the genetic and phenotypic diversity among multiple wheat cultivars has provided valuable insights into plant adaptability to diverse agro-climatic regions. The prevalence of specific SSR alleles in sub-populations indicates that different cultivars have developed specific genetic traits to thrive in their respective environments [156]. Genotype-dependent impacts of drought and subsequent rewatering have been noticed in various aspects, including leaf water deficit and transcriptional changes in DNA methyltransferase coding genes [205], leaf morphology (trichome density, stomatal frequency, and guard cell length), alterations in phytohormone levels and their derivatives, mobilization of antioxidant defense components, and modifications in the functioning of the photosynthetic apparatus, evident through changes in the mRNA content of chloroplast-encoded photosynthetic genes *psbA* and *rbcL*. Through GC-MS analysis, cultivar-dependent drought adaptation strategies were found, with noticeable changes in primary and secondary metabolites. Furthermore, the activation and suppression of protease isoenzymes showing cultivar-dependent variations, particularly in root proteases. Dehydration also triggered the mobilization of different components of the antioxidant defense system, displaying organ- and genotype-specific responses. Cultivars displaying higher tolerance to water deficit exhibited greater total antioxidant activity and ROS scavenging potential. Additionally, dehydration induced primary DNA damage, including single- and double-stranded breaks in all wheat cultivars, with more pronounced effects observed in sensitive genotypes (unpublished data).

Overall, the comprehensive assessment and characterization of Bulgarian wheat genotypes highlight their diversity and offer potential markers for distinguishing between resistant and sensitive cultivars. This knowledge can facilitate the development and selection of local wheat cultivars with enhanced drought tolerance.

9. Conclusions

While understanding the responses of different wheat genotypes to drought stress represents a crucial step towards developing drought-resistant wheat cultivars and optimizing agricultural practices in water-scarce regions, it is important to recognize that our current knowledge in this field is insufficient and can be considerably improved. By delving deeper into the intricate mechanisms governing drought tolerance, researchers can identify specific genes and regulatory pathways that hold the key to enhancing resilience in wheat cultivars. This newfound knowledge could serve as a solid foundation for developing drought-tolerant wheat cultivars. Traditional breeding techniques can be informed and accelerated by the identification of these key genetic elements, whereas cutting-edge biotechnological methods like gene editing offer promising avenues for more precise and rapid cultivar development. The synergy between these approaches holds great potential for ensuring a more sustainable and secure food supply in the face of escalating

climate uncertainties. In addition, the data gathered from these studies not only aid in the creation of improved wheat cultivars but also provide valuable insights for devising effective agronomic strategies. By implementing appropriate management practices informed by this research, farmers can minimize the adverse effects of drought on wheat production, which in turn can contribute to the ultimate goal of food security, helping communities adapt to the challenges of an ever-changing climate. In essence, the journey toward drought-resistant wheat and sustainable agriculture is ongoing and evolving, with each step forward bringing us closer to a more resilient and food-secure future.

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