

Review

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Review

A Review of CiteSpace-Based Studies Regarding the Effects of Drought Stress on the Physiological Characteristics of Wheat (*Triticum aestivum* L.)

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Abstract: Drought is one of the most significant agrometeorological hazards which limit wheat production and yield. Wheat exhibits a variety of morphological, physiological, biochemical and molecular responses to drought stress. In this study, we simulated the effects of drought stress in wheat by using the CiteSpace visualization tool, summarized climate impact and adaptation to drought stress of wheat production, drought tolerance in wheat, progress and technologies on breeding wheat for drought tolerance, and drought stress impact on vigour, plant traits and yield. Under drought stress, plant height, water content, leaf area index, chlorophyll content and chlorophyll fluorescence parameters of wheat showed different degrees of decline, and water stress significantly increased the content of osmoregulatory substances (proline, free amino acid, total soluble sugar) in wheat. Drought tolerance is a complex trait controlled by multiple genes, and its expression is influenced by various environmental factors. Research on the evolutionary trend of dry matter accumulation in different ploidies of wheat during the process of hybridization and domestication is necessary, and molecular-level studies on the drought tolerance mechanism in wheat should be conducted to provide a basis for wheat breeding. Wheat breeding with new traits is a climate change adaptation option, however its effect will vary among different regions and limited under soil conditions and local environmental conditions. This review paper focused on water limitation and its effects on morphological, physiological, biochemical and molecular responses of wheat leaves and possible losses due to drought stress.

Keywords: wheat; growth period; leaf water potential; chlorophyll fluorescence; molecular mechanisms; photosynthesis

1. Introduction

Since the 1970s, global climatic droughts have been intensifying due to increasing warming and changes in atmospheric circulation patterns [1]. Droughts are characterized by high frequencies, long durations, and wide coverage, and they continue to pose a major threat to food security in today's environment, characterized by rising temperatures and decreasing rainfall [2]. The Sixth Assessment Report of the IPCC (IPCC, 2023) states that the negative impacts of highly regional and complex drought hazards on grain yields have continued to intensify, and the contradiction between the increasing demand for wheat and decreasing yields is becoming increasingly prominent. Wheat (*Triticum aestivum* L., $2n = 6x = 42$, AABBDD) is a major food crop globally, and individuals who consume wheat as a staple food account for approximately 35–40% of the world's population [3]. As one of the three major food crops in China, wheat is grown and consumed in huge quantities throughout the country. Global wheat production in the major production regions is being threatened by recurrent drought that is predicted to increase with climate change [4]. Drought is one of the most common environmental stresses that affect growth and development of crops. In the context of the expanding arid and semi-arid areas, confined and regional drought disasters occur frequently [5,6].

South Africa has a semi-arid climate and faces significant drought challenges, with prolonged drought leading to water scarcity, which affects both rain-fed and irrigated agriculture [7]. In India and Pakistan, temperature increases and erratic monsoon patterns have been reported to be collectively linked to decreased wheat and rice yields, highlighting the vulnerability of these staple crops to climate variability [8]. Australia is one of the largest world grains exporting countries, where agriculture is dominated by rainfed cropping in arid and semi-arid regions, experiencing frequent severe droughts in recent decades [9–12]. The droughts caused significant reductions and failures in crop yields across the primary grain-producing areas of south-eastern Australia, particularly in 2019 [13]. They pose a serious threat to China's food security and ecological safety and are important factors affecting China's sustainable socioeconomic development [4,5].

Models based on the Coupled Model Intercomparison Project Phase 6 (CMIP6) project increased drought frequency and severity in Australia under greenhouse warming scenarios [16, 17], indicated that how the rainfed crop yield responds to different drought conditions across regions is essential to develop effective adaptation options to manage the risk of future droughts. Tolerance to water stress is a complicated parameter in which crops' performance can be influenced by several characteristics [18]. Standardized Precipitation Evapotranspiration Index (SPEI) and the Palmer Drought Severity Index (PDSI) were developed to assess different drought metrics such as duration, frequency, and severity [19], whose advantages are easily calculated using readily available meteorological and hydrological data. SPEI set up to above and /or below certain thresholds [20]. In recent years, statistical analysis and crop simulation modeling have emerged as prevalent methodologies for evaluating the impact of climate change on crop production [21–24]. Moreover, Lobell et al. (2015) used a modified APSIM (Agricultural Production Systems Simulator) model to quantify the influence of drought and heat stresses on crop production in northeast Australia. By leveraging such approach, researchers can enhance our understanding and prediction of agro-climatic effects on agricultural systems, thereby aiding in strategies. Additionally, the deterministic nature of empirical and biophysical models [25] makes them accessible for direct use and easy to understand. However, these methods need to be equipped with sufficient input data. In some cases, input data may not be available with detailed measurements at a large scale.

Tolerance can be divided into two parts including drought avoidance and dehydration tolerance [26]. Drought avoidance includes root depth, appropriate use of available water by plants, and changes in plants' lifestyle to use rainfall [27]. Adaptation of plants to drought stress is an important point to develop new improved approaches for increasing stress tolerant plants [28]. Many factors can affect plants' responses to drought stress such as plant genotype, growth stage, severity and duration of stress, physiological process of growth [29], different patterns of genes expression [30], different patterns of the activity of respiration [31], activity of photosynthesis machinery [32], and environmental factors [28,33]. Wheat has a certain degree of drought tolerance and can implement complex physiological and biochemical responses under drought in order to ensure optimal growth and development under such adverse conditions [34]. The leaf is one of the most sensitive organs to drought stress, which inhibits wheat's growth and development, reduces the leaf water potential, affects the photosynthetic mechanism and organic matter synthesis, and, in severe cases, affects the leaf morphology and causes irreversible damage to the leaf. As the main site for photosynthesis, the physiological state of the leaf has a critical impact on the yield of wheat.

Many factors can affect plants' responses to drought stress such as plant genotype, growth stage, severity and duration of stress, physiological process of growth [35], different patterns of genes expression [36], different patterns of the activity of respiration [37], activity of photosynthesis machinery [38], and environmental factors [39]. Drought stress can also influence plants in terms of protein changes, antioxidant production, osmotic adjustment, hormone composition, root depth and extension, opening and closing of stomata, cuticle thickness, inhibition of photosynthesis, decrease in chlorophyll content, reduction in transpiration, and growth inhibition [40–43] to stand with some osmotic changes in their organs. The role of genes can be distinguished by expression of a gene to high resistance levels among varieties [44]. In many drought studies, the role of reactive oxygen

species (ROS) has been identified. Increase in ROS can be caused by drought stress in which oxidative balance of the cell is changed [45,46]. A rise in the generation of ROS prompts to the generation of ABA (abscisic acid) which is a general signal under drought [47–50] and can consequently regulate the antioxidant genes expressions by producing superoxide dismutase (SOD) and catalase (CAT) [51]. Drought can also cause pollen sterility, grain loss, accumulation of abscisic acid in spikes of drought-susceptible wheat genotypes, and abscisic acid synthesis genes in the anthers [45].

Physiological responses include closure of stomata, decrease in the activity of photosynthesis, development of oxidative stress, alteration in the integrity of cell wall, production of metabolites which are toxic and cause plants' death [52], signal recognition of roots, turgor loss and adjustment of osmosis, reduction in water potential of leaf, decrease in stomata conductance to CO₂, reduction of internal CO₂ concentration, and reduction of growth rates. For measuring drought tolerance, various scientists considered maintenance of membrane integrity and its role under water stress [33,34]. K. Wiśniewski and B. Zagdańska [53] also observed that the role of cysteine was improved, but its role was negatively related to the degree of drought tolerance of ten lines of spring wheat. Transpiration efficiency (TE) can be influenced by cultivar and drought [54,55].

Studying the effects of different water stresses on the photosynthesis, growth, yield, water use efficiency (WUE) and irrigation water productivity (IWP) of water wheat will provide data for the development of scientific irrigation strategies for water-saving agricultural methods. The seasonal changes in photosynthetic parameters, such as net photosynthetic rate (P_n), intercellular carbon concentration (C_i), stomatal conductance (G_s) and transpiration (E), significantly decreased under moderate and severe stress. As a result, the height, biomass and grain size of winter wheat decreased significantly, which led to low WUE and IWP. The P_n of the mild stress group only slightly decreased compared to that of the well-watered group, and was actually higher during the flowering and grain-filling stages, resulting in increases in dry biomass and 1000 grain weight of 2.07% and 1.95%, respectively. Higher WUE and IWP were attributed to higher yields and less water use. Thus, mild stress (60-80% field water capacity) resulted in the optimal use of water resources without a significant reduction in yield in the North China Plain (NCP). Therefore, mild stress can be considered a suitable environment for winter wheat growth in arid areas [56]. The stress of water deficit prompted a marked reduction in agronomic parameters while biochemical attributes were increased under conditions of water stress except for total soluble proteins. Si application improves plant biochemical attributes, absorbs nutrients and shows higher growth rate which ultimately helps the plant mitigate the drought-stressing effects. At the anthesis stage, foliar spray was stronger while at the tillering stage, fertigation produced good results [57]. Salicylic acid (SA) is a promising compound to increase plant tolerance to drought stress, and it can affect many aspects of physiological and biochemical processes. Membrane electrolyte leakage, and lipid peroxidation of all ecotypes, were obviously increased under drought stress conditions. Drought stress decreased leaf chlorophyll content, photosynthetic rate, stomatal conductance, carboxylation efficiency, and transpiration rate [58].

The study aims to visualize the intellectual background, current research status and state-of-the-art knowledge structure of drought stress in wheat related literature using CiteSpace based scientometric investigation. The drought stress in wheat related original articles, published from 2013 to 2023, were retrieved from the Web of Science core collection (WOS) and China National Knowledge Infrastructure (CNKI). The most prolific publications, countries and journals involved in the flourishing of wheat drought stress research were identified. Moreover, visualization methods were employed to determine the highly productive articles, keywords, hotspots, and research frontiers in the wheat drought stress domain. Furthermore, the classification of wheat drought stress knowledge was performed in the form of clusters and knowledge structure to achieve five distinct sub-domains [59–61]. The study can help the researchers to spot the new research frontiers and distinguish among the most drought in wheat based knowledge. The research papers were retrieved from the China National Knowledge Infrastructure (CNKI) and Web of Science core collection (WOSCC) databases

and the bibliometric investigation was conducted using CiteSpace software to answer the following questions:

- (a) What is the aspects of growth of published articles on drought stress in wheat research?
- (b) What are the recent and emerging research frontiers in drought stress in wheat research?
- (c) What is the knowledge structure of drought stress in wheat research based the different key words co-occurrence network?

In this study, we analyze the literature related to wheat and drought through CiteSpace visualization on China National Knowledge Infrastructure (CNKI) and Web of Science (WOS) databases, covering a 10-year range, and we explore and summarize the vast research content. The main work can be summarized as follows:

- (1) Comprehensive Analysis: This study provides a comprehensive analysis of research of drought stress in wheat by testing various topics, such as publication trends, journal distributions, author networks, institutional networks, national networks, and keyword co-occurrences, as well as undertaking timeline analysis and emergent word analysis. This comprehensive approach offers a holistic understanding of the research landscape in research of drought stress in wheat;
- (2) Identification of research themes: Through the analysis of keywords and clustering, this study identifies key research themes in research of drought stress in wheat. It highlights the dominant areas of research, including spring wheat fertility in response to drought stress, leaf water potential in response to drought stress, chlorophyll content in response to drought stress, photosynthesis in response to drought stress, chlorophyll fluorescence parameters in response to drought stress, drought stress in wheat at the molecular level. This identification of research themes helps to delineate the major focus areas in the field;
- (3) Visualization of research patterns: The use of visualization techniques, such as network diagrams and timeline analysis, helps to visualize and understand the evolution of research hotspots over time. It allows researchers to observe the dynamics of research themes, emerging trends, and the interconnections between different topics [62–64].

In summary, this review explores the changes in the physiological properties of wheat leaves under drought, so as to provide a theoretical basis for the cultivation and breeding of drought-resistant wheat.

2. Materials and Methods

2.1. Data Sources

In this study, we conduct a statistical analysis through bibliometrics, analyze and summarize the keywords in the literature, and explore their structural characteristics and internal laws in order to obtain a comprehensive and objective understanding of the field. The literature data were obtained from the China National Knowledge Infrastructure (CNKI) databases (<https://www.cnki.net>) and Web of Science core collection (WOS) core collection databases (<https://webofscience.clarivate.cn/wos/author/search>). The Chinese database was searched and screened, spanning the period from 2013 to 2023, with the themes of “spring wheat”, “drought stress”, “leaf”, and “photosynthesis physiology”. The screened literature was exported in the RefWorks format as a sample for data analysis. The English database was searched with “spring wheat drought”, “spring wheat leaf”, and “crop yield” as the themes to achieve an advanced search, and the documents were exported as plain text files in the form of “Full Record with Cited References” as a sample for data analysis.

2.2. Data Processing

2.2.1. Literature Selection Criteria

Advanced searches were conducted on CNKI and WOS using keywords, and the results were organized to exclude documents such as dissertations, conferences, newspapers, book reviews, patents, and almanacs [65,66]. The main proceeds are as follows:

- (1) Inclusion Criteria: The literature chosen for this study focused on research of drought stress in wheat, encompassing topics such as spring wheat fertility in response to drought stress, leaf water potential in response to drought stress, chlorophyll content in response to drought stress, photosynthesis in response to drought stress, chlorophyll fluorescence parameters in response to drought stress, drought stress in wheat at the molecular level.
- (2) Exclusion Criteria: Articles unrelated to the topic, such as achievements, conference papers, patents, advertisements, popular science articles, etc.; Non-original research, such as systematic reviews, meta-analyses, and reviews of wildfire prediction research; Articles with incomplete information, such as author, year, keywords, etc.; Duplicate or withdrawn publications [64,67].
- After applying the screening criteria, a total of 11557 literatures were included as the sample data for this study.

2.2.2. Data Processing Software

CiteSpace, a citation visualization analysis software package, was utilized in this study to analyze the potential knowledge included in the scientific literature. CiteSpace is specifically designed for scientific metrics and data visualization, aiming to uncover dynamic development patterns within disciplines and identify research frontiers. The version used in this study was CiteSpace 6.2.R2 (64-bit), Advanced, developed by Dr. Chaomei Chen and their team [68,69]. CiteSpace 6.2.R2 software was used to generate intuitive knowledge graphs from the analyzed samples of data obtained from CNKI and WOS. In the software, according to the node type, the screened literature was visualized and analyzed by “keyword”, the time frame was set as 2013-2023, and the time slice was 1. A keyword network diagram was constructed so that we could determine the current research hotspots and development trends.

3. Results

3.1. Spring Wheat Fertility in Response to Drought Stress

The fertility period of spring wheat is an important indicator reflecting the growth and development process of this crop, which is affected not only by its genetic characteristics but also by the climatic conditions of the planting area. The alignment between the fertility period and water and heat resources is an important factor affecting the physiological and biochemical characteristics of the crop.

Based on the growth and development characteristics of spring wheat at each stage, the fertility period can be divided into seedling, triticle, tillering, nodulation, gestation, tasseling, flowering, milky, and maturity. Among these, the seedling to tasseling stage constitutes the nutritive growth period, and the flowering to maturity stage constitutes the reproductive growth period [70]. Figure 1 shows the keyword visualization knowledge map for research on spring wheat's fertility in response to drought stress. From the figure, it can be seen that the research on this topic is extensive. In addition to the most common keywords, the current yield, semi-arid zone, post-flowering drought, growth and development, fertility, and photosynthetic characteristics are the main focal points of the research in this field. It can be seen that the semi-arid zone and post-flowering drought represent hotspots in the research on drought stress, and the yield, growth and development, fertility, and photosynthetic characteristics are considered in relation to the effects of drought stress on spring wheat during the fertility period.

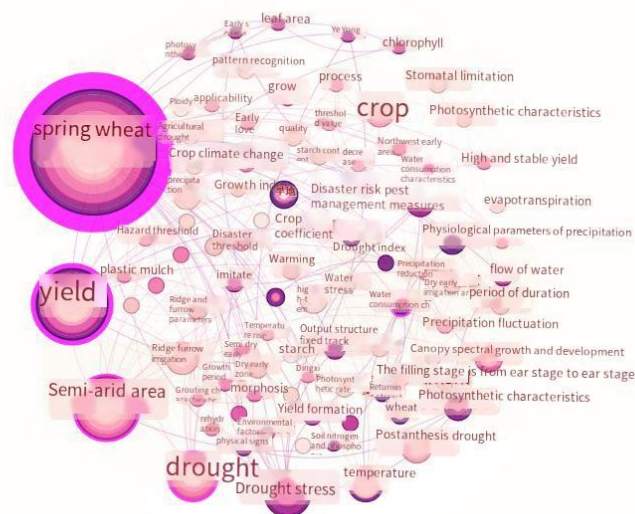


Figure 1. Keyword co-occurrence network mapping for the study of spring wheat fertility response to drought stress.

The effects of drought stress on wheat plants during different fertility periods are directly related to the wheat yield. From the perspective of the whole fertility period, delayed sowing under high temperatures and drought causes an increase in the number of days constituting the nutritional growth stage, leading to a gradual decrease in the duration of postponement. There is also a decrease in the number of days constituting the reproductive growth stage, which shows an advancing trend on average. Moreover, the postponement of sowing and the advancement of maturity are the main factors associated with the shortening of the fertility period in spring wheat [71]. It has also been found that, with a delay in the sowing period, the wheat yield fluctuates, exhibiting a unimodal curve. Thus, coordinating the allocation of water and heat resources with the wheat sowing period is important to realize high wheat yields [72,73]. Er Y. H. et al. found that the length of spring wheat's fertility period is negatively correlated with the early and late sowing period, and the effective cumulative temperature decreases accordingly due to drought and the late sowing in the early fertility period [74]. Mei L. et al. found that, with a delayed sowing period, the wheat fertility period is shortened, while the seedling emergence period is extended [75]. Zhang K. et al. found that the later the sowing date, the slower the nutrient growth, the higher the peak leaf area index, and the slower the leaf senescence [76]. Cui Y. Z. et al. found that the wheat yield increased and then decreased with delayed sowing [77]. Zhang Z. Z. et al. found that delayed sowing reduced the number of days constituting the entire reproductive period in wheat, resulting in the insufficient accumulation of nutrients and a decrease in the wheat yield [78].

When plants were subjected to drought stress, dry matter was redistributed between the above- and belowground parts of the plant. This was typically characterized by an increase in the biomass of the belowground part and a decrease in the leaf area index (LAI) and stem partitioning ratio (SPR). Leaf photosynthesis was inhibited, the light compensation point and light saturation point decreased significantly, and the apparent quantum rate decreased continuously with the increase in the stress intensity. Nutrient deficiencies promoted protein catabolism, and plant senescence was significantly accelerated, causing a reduction in the yield and grain quality in spring wheat [79,80]. During different fertility stages, it was found that the physiological and biochemical characteristics of wheat leaves under drought stress decreased to a certain extent. Drought stress during seed germination affects the wheat germination rate and germination potential; it also significantly reduces the wheat seedling biomass, dry matter conversion, and soluble sugar content. Moreover, biomass is preferentially allocated to the root system, disrupting the coordination of the root–crown ratio and

reducing the efficiency of resource utilization [81]. Drought stress at the tiller stage causes leaf tiller degeneration and death, resulting in a lower leaf area index and reduced water consumption in wheat [82]. The destruction of the chlorophyll structure in flag leaf cells and the reduction in protective enzyme activity allow excess reactive oxygen radicals to damage the membrane system, consequently accelerating leaf senescence [83,84]. The period from nodulation to the tassel stage exhibits vigorous growth, and the growth status of spring wheat shifts from nutrient growth to reproductive growth. The plant is able to resist drought stress by reducing the biomass of the aboveground part and increasing that of the belowground part, as well as increasing the density of the root length to promote the absorption of water and accelerating the metabolism of the chloroplasts to replenish the nutrients required for reproductive fruiting. Moreover, the leaf area is reduced to the minimum in the tasseling stage [85,86]. Under the same degree of drought stress, the magnitude of the decrease in each photosynthetic index and the chlorophyll fluorescence parameter was found to be greater at the filling stage than at the flowering stage. Post-flowering drought caused a decrease in the soluble protein content of each functional leaf in spring wheat, and the trend consisted of a gradual decrease from the physiological upper level to the physiological lower level [87]. In this crop, under warming or water deficit conditions, the yield and fertile grain size decreased with increasing stress, posing a serious threat to the yield and grain quality [88,89].

Table 1. Yield losses at vegetative growth stages under drought in wheat.

Vegetative stage	Yield loss (%)	Reference
Early season stress	22	[90]
Midseason stress	58	[90]
Booting stage	20.74	[91]
Tillering stage	46.85	[91]
1000-grain weight (vegetative stage)	38.67	[92]
Earlier stages	79.70	[93,94]
Spike length (vegetative stage)	16.90	[92]
Number of spikelets per spike (vegetative stage)	28.63	[92]
Grains number (vegetative stage)	72.51	[92]
Grains number (vegetative stage)	61.38	[92]

Table 2. Yield losses at reproductive growth stages under drought in wheat.

High grain protein content, fewer days to physiological maturity, smaller kernel weight and diameter, less grain yield	Not applicable	[95]
Less grain yield (drought-tolerant variety)	43	[96]
Less grain yield (drought-sensitive variety)	26	[96]
1000-grain weight	18.29	[18]
	5	[27]

1000-grain weight (anthesis stage)	38.67	[92]
Biological yield	10	[18]
Maximum grain yield	22	[18]
Decreased seed number	64	[27]
Grain formation stage	101.23	[91]
Grain formation stage	65.5	[93,94]
Number of spikes	19.85	[92]
Number of spikes (anthesis stage)	15.79	[92]
Spike length (anthesis stage)	16.90	[92]
Number of spikelets per spike (anthesis stage)	26.20	[92]
Grain number (anthesis stage)	72.51	[92]
Grain yield (anthesis stage)	64.46	[92]

Growth is sensitive to drought and can be affected by reduction in turgor pressure, whose reason is low turgor pressure, water stress quenches cell expansion and growth. However, when turgor pressure bigger than the cell wall yield, cell expansion can occur [97,98]. Osmotic adjustment is a remarkable part of plants’ physiology by which they respond to water deficits [29,99–103]. Yield losses at vegetative growth and reproductive stages under drought in wheat are provided in Tables 1 and 2.

3.2. Leaf Water Potential in Response to Drought Stress in Spring Wheat

The water potential is an important indicator of the plant’s water status or the degree of water deficit. In particular, the leaf water potential is the most sensitive physiological indicator, reflecting the plant’s water surplus or deficit; thus, it directly reflects the water status of the plant body. Studies have shown that maintaining the stability of the leaf water potential is important to enhance the drought resistance of rice [104,105]. It has also been pointed out that the daily variation in the leaf water potential in spring wheat shows that it tends to increase and then decrease, reaching its highest in the early morning and decreasing to its lowest level in the late afternoon [106]. The early morning leaf water potential reflects the recovery of the plant from a water deficit, and the midday leaf water potential reflects the maximum water deficit in the plant [107]. With decreased soil moisture content and increased evapotranspiration under mild drought stress, the plant establishes a larger water potential difference in the soil–plant–atmosphere continuum (SPAC) by lowering the leaf water potential. This causes water to be transported upward through the water conductance pathway to reach the leaves [108]. In the soil–plant pathway, the soil water potential is positively correlated with the leaf water potential. The leaf water conductance pathway consists of the xylem pathway and extra-xylem pathway. Under severe drought stress, when the leaf water potential decreases beyond a certain threshold, the low-resistance xylem pathway forms an embolism. The resistance to the water supply in the aboveground part increases, and the lack of water reduces the number of chloroplasts, causing the senescence and death of the leaves [109]. Drought tolerance in wheat drives it to attenuate this suppression through different water supply or self-protection mechanisms. In a study, it was found that, with increasing drought stress, the transpiration water consumption of the plant was negative at night, which suggests the existence of water backsorption from the atmosphere to the plant in the plant–atmosphere pathway. This serves to maintain the leaf water potential and ensure a normal xylem water supply to the plant when seedlings are subjected to severe drought stress [110].

An analysis of the covariate mapping shown in Figure 2 indicates that most of the previous studies on the leaf water potential in wheat have focused on the stomatal conductance and

photosynthetic characteristics. It can be seen from the inter-nodal connecting lines that, in wheat, the photosynthetic characteristics are closely linked to the yield and leaf senescence, and stomatal conductance is mainly limited by water stress. The leaf net photosynthetic rate is closely related to the leaf water potential. It was found that when the stress was mild, the leaf net photosynthetic rate appeared to be low near noon, which might indicate that the plant undergoes a period of respite. Moreover, the net photosynthetic rate was lower than that in the blank control group, even reaching half of this value throughout the day when the stress was severe. Mild drought stress rehydration has a promotional effect on plant root and leaf growth, and plants show compensatory effects, where the leaf water potential and photosynthetic capacity are improved. However, severe drought stress can seriously impair water transport in the roots, stems, and leaves and irreversibly obstruct the physiological and biochemical activities of the plant, causing leaf shriveling, premature senescence, and even plant death [111–113]. In a study, it was found that a reduction in the leaf water potential under severe drought stress caused the destruction of the chloroplast structure, the blockage of chlorophyll synthesis, a reduction in protective enzyme activity, damage to the membrane system caused by the accumulation of reactive oxygen species in the organism, and a sharp decrease in photosynthesis, which was manifested in yellowing and senescence of the leaves [114]. Nitrogen application has a compensatory effect on plant water deficits, facilitates the recovery of the nocturnal water potential, enhances the antioxidant properties, and protects the photosynthetic mechanisms [115]. Drought increases the soluble sugar content within leaf cells, altering the osmotic potential and significantly increasing the vein density of the plant in order to increase the water transport channels and the contact area for water exchange with the leaf pulp; thus, the safety of water transport within the leaf is ensured [116–118]. Plant transpiration is linearly related to stomatal conductance, and the attenuation of transpiration under drought stress is mainly regulated by the stomatal length and width. Meanwhile, increasing the stomatal density of the lower epidermal leaves to ensure the CO₂ supply improves wheat's photosynthesis and increases the plant's stress tolerance [119,120].

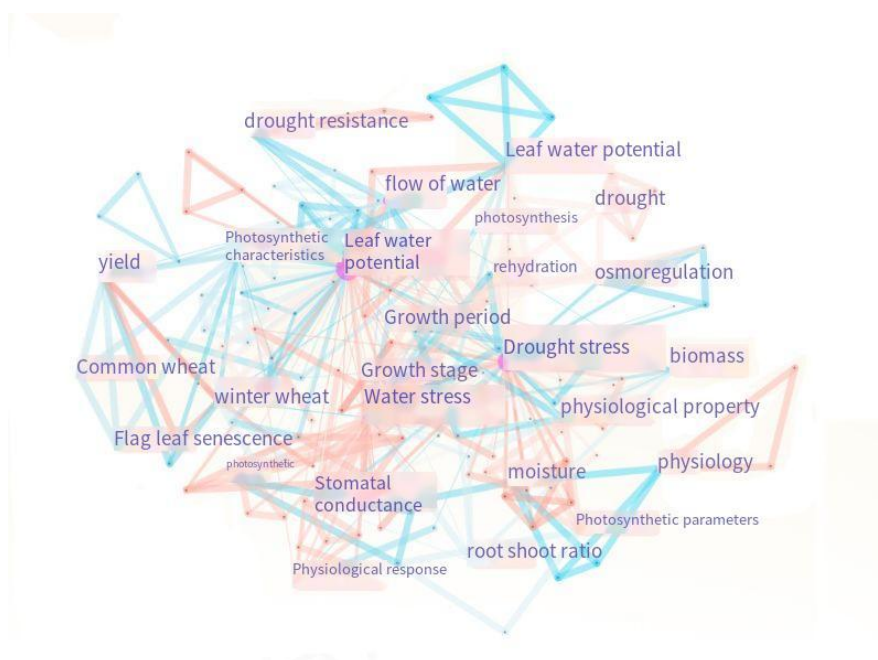


Figure 2. Keyword covariance network mapping for the study of leaf water potential in response to drought stress in spring wheat.

Some researchers studied crop water stress index (CWSI) and midday flag leaf water potential (Ψ_1) on wheat (*Triticum aestivum* L. Adana 99) under the three different supplemental and conventional irrigation strategies using spinkler line-source system during 2014 and 2015 in Adana, Turkey. They found that CI_{100} is recommended when there is no water shortage; however, under

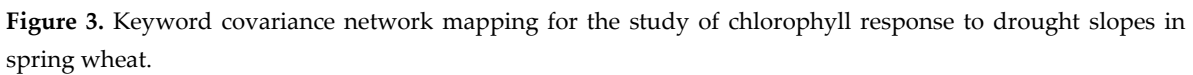
water scarcity conditions CI_{75} , $SIFG_{100}$ and $SIFG_{75}$, with higher WUE and relatively higher yields, are recommended [121]. A technique for studying variation in the accumulation of abscisic acid (ABA) in response to drought stress is decreased. The results was that there was considerable genotypic variation in the rate at which water potential decreased, partly explained by variation in plant size [122]. Identification and understanding of the mechanism of drought tolerance in wheat (*Triticum aestivum* L.) cultivars has long been a major goal of plant breeders. A test was conducted to illustrate Whether leaf water potential, osmotic potential, yield, and yield components could be used to differentiate apparent drought tolerance among the cultivars or not. It found that stress applied at either tillering or heading gave similar results but effects were more pronounced when stress was applied at heading. It was not possible to determine if osmotic adjustment contributed to the differences between cultivars in response to water stress [123].

Currently, the leaf water potential is the best indicator of a plant's water status and it has been extensively investigated, but few studies have comprehensively examined the changes in water circulation and storage in various tissue types under drought. Changes in the leaf water potential, as affected by the soil moisture status and atmospheric water and air pressure deficits, have been addressed in several studies, but most have investigated one of these aspects individually. There is a lack of research that links the two through the SPAC system to explore the similarities and differences in the patterns of response and bias regarding the changes in the leaf water potential.

3.3. Chlorophyll Content in Response to Drought Stress

Chloroplasts are the main sites for photosynthesis in plants, and photosynthetic pigments increase the energy available for photosynthetic carbon assimilation through the absorption, transfer, and conversion of light energy. This indirectly affects wheat's growth and development and yield through effects on photosynthesis, responding to the rate of leaf photosynthesis and the leaf senescence process. This can be used, to a certain extent, to measure the plant's resilience and strength [124]. A reduction in efficiency of photochemical, reduced Rubisco efficiency, gathering of stress metabolites (glutathione, MDHA, glybet, and polyamines), antioxidative enzymes (superoxide dismutase (SOD)), peroxidase(POD), catalase (CAT), ascorbate peroxidase(APX), glutathione reductase (GR), glutathione-S-transferase (GST), glutathione peroxidase (GP)), monodehydroascorbate reductase (MDHAR), and reduced ROS accumulation are biochemical responses of plants to drought stress. Tolerance to drought correlates with a positive response of plants' antioxidant system [125].

As shown in Figure 3, the top ten keywords identified were drought stress, physiological characteristics, photosynthetic characteristics, antioxidant enzymes, chlorophyll, yield, photosynthesis, physiological indexes, drought resistance, seed germination, microstructure, and nitrogen metabolism. Overall, the chlorophyll content in spring wheat under drought stress can be studied from two perspectives: one involves the study of the chlorophyll content and chloroplast structure, and the other involves the study of the plant's photosynthetic characteristics.



Drought stress at different growth stages significantly alters growth, yield, and quality traits of wheat, however, great variability exists among genotypes regarding their response to drought stress. Therefore, determining the impacts of drought stress on yield and quality traits would help to select the superior genotypes. Bin Wang et al. investigated the impact of seasonal droughts on yield variation in different subregions of the wheat belt. They identified significant positive correlations between wheat yields and SPEI (Standardized Precipitation Evapotranspiration Index). They

observed that lower yield corresponded with lower SPEI values, vice versa. This indicates that there was a close correlation between wheat yields and SPEI, confirming that SPEI is an effective drought index. The results are consistent with those from prior studies [138]. These correlations could play an important role in assessing the impacts of drought on wheat productivity.

Carbon and nitrogen substances are the main components associated with the wheat yield and nutritional quality. The carbon and nitrogen substances in the kernel originate from two sources: the re-transportation of substances stored in the nutrient organs prior to flowering and the direct input of photosynthesis products synthesized by wheat leaves during the plumping period. Different varieties rely on both sources to different extents [139]. Terminal drought reduces the leaf area index of wheat and its ability to synthesize photosynthesis products, which severely reduces the accumulation of photosynthesis products in the grain and the amount and rate of translocation of pre-flowering storage material in the plant's organs, resulting in poor yield traits and ultimately leading to yield reductions [140].

3.4. *Photosynthesis in Response to Drought Stress*

Photosynthesis is the most important physiological and biochemical process in spring wheat, and balanced photosynthesis is essential for improved plant survival and agricultural benefits in terms of biomass and yield. However, drought stress (DS) strongly perturbs photosynthetic efficiency due to biochemical and diffusive limitations that reduce key photosynthetic components and close stomata. While stomatal closure, disrupted photosynthetic systems, over-reduced electron transport rates (ETR), partial hindrance of the Calvin cycle, and reduced pigment contents strongly affect the repertoire of photosynthetic processes under DS, chloroplast retrograde signalling also has a plausible role in preserving photosynthetic capacity. Progress in agronomic, genetic engineering approaches and isoprene regulation would help to rescue photosynthetic apparatus under DS [141–143]. The stabilization of the photosynthetic efficiency under drought stress is the goal during the response to this type of stress. According to Figure 4, the most important keyword is “drought stress”, which encompasses the three aspects of photosynthetic characteristics, photosynthesis, and photosynthetic parameters. In a study of the related literature, it was found that the net photosynthetic rate, light saturation point, and dark respiration rate of spring wheat under drought stress showed a decreasing trend with the increase in the drought duration, and the magnitude of this decrease was proportional to the intensity of the stress [144–146]. Research on photosynthesis under drought stress has focused on stomatal limitations, chlorophyll, and the photosynthetic systems. Drought affects photosynthesis through a combination of stomatal and non-stomatal factors [147]. The mentioned study concluded that the reduction in the photosynthetic rate was mainly due to stomatal factors. Moisture stress decreases the stomatal conductance in spring wheat to reduce water loss; stomatal closure hinders CO₂ uptake by the leaves, while a reduction in the dark respiration rate, light compensation point, and light saturation point reduces the photosynthetic carbon loss, enabling the plant to adapt to the lower net photosynthetic rate. Moreover, normal photosynthetic carbon cycling is inhibited, and the photosynthetic pigment content decreases, as well as the net photosynthesis [148]. However, it has also been suggested that the leaves respond to mild drought by closing the stomata to reduce transpiration, and the reduction in the intracellular CO₂ content decreases the net photosynthetic rate. At this time, stomatal factors dominate; when the water stress exceeds a certain threshold, the water deficit leads to the destruction of the leaf's photosynthetic apparatus, and the changes in the net photosynthetic rate and stomatal conductance are no longer linearly related, at which time non-stomatal factors dominate [149,150]. The decrease in the photosynthetic rate caused by stomatal factors can be quickly recovered via rehydration, and the plant shows compensatory effects, enhancing its photosynthetic capacity and improving its stress tolerance. Meanwhile, the decrease in the net photosynthetic rate caused by non-stomatal factors is irreversible, as the photosynthetic system is impaired and the leaves are curled and deformed, which can lead to the death of the plant in severe cases [151–153]. The leaf photosynthetic rate was found to be positively correlated with the soil moisture, which affected the photosynthetic rate by influencing

the photosynthetically active area. Moreover, the effect of lower soil drought on the photosynthetic rate was greater than that of upper soil drought [154,155]. At the same time, a reduction in the water use efficiency reduces the basic efficiency of organic matter accumulation, and, in spring wheat, the upper leaves are the first to be affected; this is manifested by the curling and deformation of the flag leaf and the yellowing of the tip [156,157].

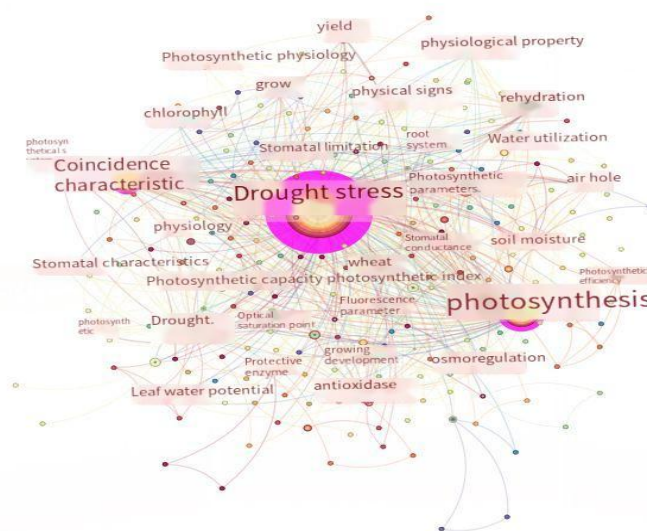


Figure 4. Research keyword covariance network mapping of the effect of drought stress on photosynthesis in spring wheat leaves.

3.5. Chlorophyll Fluorescence Parameters in Response to Drought Stress

Leaf photosynthesis involves adaptive and protective mechanisms, and the photosynthetic system stabilizes the photosynthetic performance by increasing the rate of electron transfer in the non-Calvin cycle, converting excess light energy into heat, eliminating excess light energy, and avoiding damage to photosynthetic structures such as PSII and the electron transport chain, as evidenced by an increase in the non-photochemical quenching coefficient (NPQ) [160]. In a study, the qP and NPQ showed contrasting patterns of change, and the degree of change increased with the degree of drought stress. It was found that, under the action of antioxidant enzymes, PSII was able to mitigate the damage caused by photo-oxidative stress and stabilize the photosynthetic efficiency under photo-oxidative conditions by increasing the rate of electron transfer, enhancing the conversion of light energy, ensuring smooth electron transfer, and dissipating excess light energy. However, excessive drought stress leads to the extreme photoinhibition of PSII receptors, where electrons are unable to function properly, causing severe damage to the photosystem, from which it is difficult to recover. This will attenuate or disrupt the plant's photochemistry, thereby causing premature plant failure [161,162]. At the same time, the leaf stomata are closed, and the insufficiency of the intracellular CO₂ content limits the fixation of carbon via the Calvin cycle. The excessive electron transfer to O₂ and the reduced activity of leaf superoxide dismutase (SOD) and catalase (CAT) lead to the accumulation of excess reactive oxygen species in the cell, and the cellular metabolism becomes dysfunctional, causing photo-oxidative damage [163].

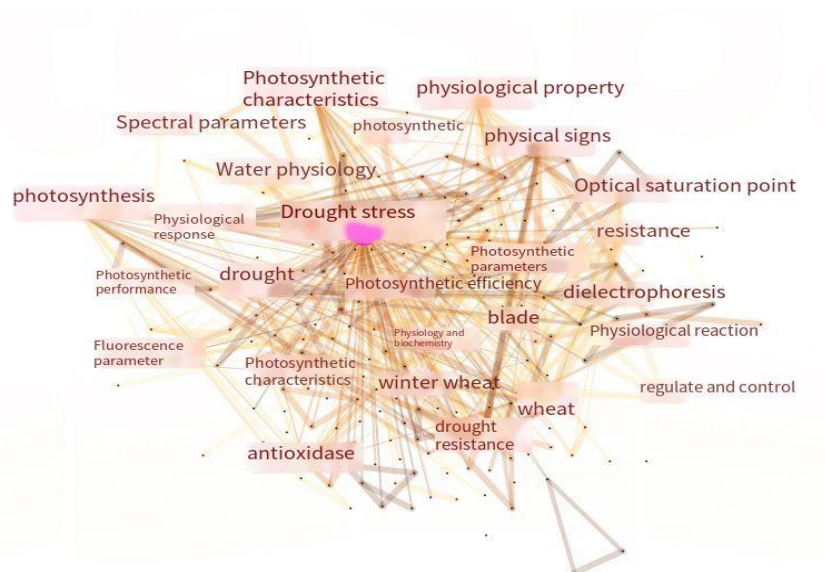


Figure 5. Study of changes in chlorophyll fluorescence parameters of leaves under drought stress Keywords covariance network mapping.

Leaf photosynthesis involves adaptive and protective mechanisms, and the photosynthetic system stabilizes the photosynthetic performance by increasing the rate of electron transfer in the non-Calvin cycle, converting excess light energy into heat, eliminating excess light energy, and avoiding damage to photosynthetic structures such as PSII and the electron transport chain, as evidenced by an increase in the non-photochemical quenching coefficient (NPQ) [160]. In a study, the qP and NPQ showed contrasting patterns of change, and the degree of change increased with the degree of drought stress. It was found that, under the action of antioxidant enzymes, PSII was able to mitigate the damage caused by photo-oxidative stress and stabilize the photosynthetic efficiency under photo-oxidative conditions by increasing the rate of electron transfer, enhancing the conversion of light energy, ensuring smooth electron transfer, and dissipating excess light energy. However, excessive drought stress leads to the extreme photoinhibition of PSII receptors, where electrons are unable to function properly, causing severe damage to the photosystem, from which it is difficult to recover. This will attenuate or disrupt the plant's photochemistry, thereby causing premature plant failure [161,162]. At the same time, the leaf stomata are closed, and the insufficiency of the intracellular CO₂ content limits the fixation of carbon via the Calvin cycle. The excessive electron transfer to O₂ and the reduced activity of leaf superoxide dismutase (SOD) and catalase (CAT) lead to the accumulation of excess reactive oxygen species in the cell, and the cellular metabolism becomes dysfunctional, causing photo-oxidative damage [163].

As the raw material for photosynthesis, water supplies primary electrons and plays an important role in photochemical reactions. The inhibitory effects of water deficits on the photosynthetic electron transfer rate (ETR) and reaction center complex hinder photosynthesis, and the photosynthetic fluorescence parameters will show different degrees of fluctuation. In a study, it was found that the initial fluorescence (F_0) increased under drought stress, the maximum fluorescence (F_m) and photochemical quenching coefficient (qP) values decreased significantly, and the maximum photochemical rate (F_v/F_m) values changed from maintaining dynamic stabilization to a gradual decrease, where the decrease was positively correlated with the stress level [164–166]. F_0 denotes the intensity of chlorophyll fluorescence emission when the photosystem II (PSII) reaction center is fully open, and the degree of change is negatively correlated with the plant's stress tolerance. An increase in F_0 under drought stress indicates that the chlorophyll structure is damaged, which affects the efficiency of PSII in capturing excitation energy and the primary response of photosynthesis [167]. The primary photochemical reaction is the initiation of light energy conversion, which is operated by both PSII and PSI. The light energy absorbed by the plant undergoes the PSII reaction, and the

released electrons are directed along the electron carrier in the thylakoid membrane to PSI, driving the formation of the reducing substance NADPH [168]. The reduction in qP under the combined effect of drought and high temperatures indicates that both the light energy transfer efficiency and photosynthetic phosphorylation in PSII are impeded, severely curtailing the process of electron flow from the oxidizing side of PSII to the reaction centers in PSII, and the capacity for photosynthesis is weakened [169].

3.6. Drought Stress and Wheat at the Molecular Level

The selection, breeding, and identification of drought-tolerant varieties have, to a great extent, relied on the observation of physiological traits. Based on previous research, it has been concluded that drought-tolerant wheat has a higher root–crown ratio and chlorophyll content and lower stomatal conductance and leaf water potential [170,171]. Some genes are known to be influenced and produced different types of drought stress related proteins and enzymes including dehydrins [172], vacuolar acid invertase [173], glutathione S-transferase (GST) [174], and late embryo abundant (LEA) protein [175]; expression of ABA genes and production of proteins like RAB, rubisco, helicase, proline, and carbohydrates are molecular basis of drought tolerance. In wheat seedling stage, a lot of research are conducted in gene expression, but the most sensitive stage is the junction stage which is susceptible to drought. Junction stage is an important linkage point between the vegetative and flowering growth stage, which is vital for development and reproduction [176]. For example, Sivamani et al. [94] indicated that *HVA1* gene assists to increase wheat growth under drought stress. Proline is a important protein in water stress tolerance, which can be produced from pyrroline-5-carboxylate synthetase or P5CR, and the responsible gene for this enzyme has been distinguished in some crops [177–179]. In photosystem II (PS II) reaction center, psbR has an indispensable task in oxidation of water [180], and in Calvin cycle, Rubisco is the key enzyme under drought stress [181]. Some plant proteins can be over-expressed including late embryogenesis abundant (LEA) that are saved in vegetative tissues during desiccation of seeds under drought stress. LEA proteins are shaped by drought stress and their size in wheat studies reach 200 kDa (Wcs 200) [182–184]. Researchers cost a lot of time to engineer LEA producing genes for promoting crop drought stress resistance. PMA1959 and PMA80 improved water deficit resistance in rice [185]. In wheat, the *Em* gene of wheat which encodes LEA protein first group has been vastly researched [186–188]. In durum wheat, *Td27e*, *Td29b*, and *Td16*, gene transcripts were saved late in embryogenesis and throughout seed development [189]. In seeds, transcripts of *Td11* gene were presented whereas no transcripts of *Td25a* gene were detected. Wheat V-PPase genes, TaVP3, TaVP2, and TaVP1 were investigated by Wang et al. [190]. TaRZF70 as a RING-H2 zinc finger gene presented various responsible genes in wheat for drought stress upregulated in leaf and downregulated in root [191]. Another genes expressed in wheat root were TaRZF38 and TaRZF70. However, TaRZF74 and TaRZF59 were mainly expressed in embryo and endosperm. TACCGACAT, the 9-bp consensus sequence, was first distinguished in the promoter of Arabidopsis *rd29A/lti78* and presented to be vital for drought induction in abscisic acid absence [192]. The function and express about DRE-binding (DREB) proteins have detected by some researchers [193,194]. Lucas et al. Used a sequence of putative DREB labelled DREB3A from wheat (TaDREB3A, Gen bank ID: AY781349) to seclude a DREB from wild wheat (*T. turgidum* ssp. *dicoccoides*) and to detect its function in higher drought resistance. The results found that DREB proteins are numerous and vastly upregulated in reaction to drought in root tissue rather than leaf [194]. Additionally RD gene (responsive to desiccation) are also involved in drought stress [195,196]. RD gene comprise two parts: one is expression of regulatory gene and signal direction during the crops' reaction to stress, the other is proteins which directly protect cells from stresses [197]. There are about 265 genes detected at the junction stage and 146 genes distinguished at the seedling stage in response to drought stress in wheat.

The limited success of the physiological and molecular breeding approaches now suggests that a careful rethink is needed of our strategies in order to understand better and breed for drought tolerance. Genomics technologies were seen as a path to understand the genetic and environmental

complexity of drought stress. To be relevant to breeding programs, genomic studies must consider the nature of drought stress in the target environment and use plant material and phenotyping techniques that relate to field conditions [198, 199]. Breeding for drought and heat stress tolerance was initiated by the International Wheat Improvement Network (IWIN) led by the International Maize and Wheat Improvement Centre (CIMMYT) established in 1966 in Mexico and the International Center for Agricultural Research in the Dry Areas (ICARDA)/Lebanon established in 1977 and partnered with Egypt in 1979. Both centres adopted complementary breeding technologies involving conventional and molecular breeding approaches to develop high-yielding germplasm with tolerance to heat and drought stress, diseases and insect pests with acceptable end-use qualities [200,201]. The major limiting factor for breeding progress and genetic gains is the reduced genetic diversity [205]. Some assessments revealed inconsistency contributed by different plant breeding methods perceived to reduce genetic gains [203]. The use of genetic resources such as landraces, obsolete lines and modern pure or breeding lines have potential to contribute to increased genetic gains [204]. A research programme for increasing drought tolerance of wheat should tackle the problem in a multi-disciplinary approach, considering interaction between multiple stresses and plant phenology, and integrating the physiological dissection of drought-tolerance traits and the genetic and genomics tools, such as quantitative trait loci (QTL), microarrays, and transgenic crops [205].

The rapid improvements in modern biomolecular technology have facilitated research on the relationship between abiotic stress and wheat at the molecular level, providing a basis for improvements in the drought tolerance of wheat and for the selection and breeding of resistant wheat varieties. The current research is aimed at addressing the changes in wheat's physiological traits by identifying and utilizing drought-tolerance-related genes. Such genes protect plants against drought by encoding functional proteins that act both directly and indirectly as transcription factors. Proteins are the direct functional molecules of organisms, and functional proteins mainly include antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT); enzymes involved in the synthesis of osmoregulatory substances, such as glutamate synthetase; and proteins that protect the cellular structure, such as thermokinins and proteases [206,207]. In a study, it was found that heat stress reduced the total protein content and caused the most severe damage to the photosynthetic proteins and enzymes involved in metabolism. In contrast, heat-stimulated proteins were rapidly synthesized to repair the damaged cytoskeleton through phosphorylation reactions, and the level of peroxidase was increased to combat oxidative senescence in wheat cells [208,209]. The amino acid sequence of HSP70 depolymerizes proteins and attenuates organismal damage. TaAQP genes are involved in the stress response under the high expression of water channel proteins, which selectively control the flow of water and ionic molecules inside and outside of the cell membrane system; this is closely related to the leaf water potential [210]. Transcription factors regulate gene-specific transcription through binding to promoters. Changbiao Wang et al. found that, as the primary transcription factors, B-type ARR transcription factors regulate plants' hormone responses, as well as regulating cell growth and development in response to drought [211]. Du P. P. et al. found that the TaNF-YB4 gene, which regulates downstream gene transcription in the nuclear factor Y (NF-Y) transcription factor, resists adverse conditions by maintaining the dynamic balance of sugar and nitrogen accumulation [212]. Genes can also improve plants' drought tolerance by directly or indirectly inducing hormone synthesis [213,214]. With the continued, in-depth exploration of wheat, new genes are constantly being discovered and characterized.

4. Conclusions

Climate change is projected to decrease global wheat production by - 1.9% by mid-century. Top wheat-producing countries such as India, Russia, Australia and Pakistan are projected to have declining wheat yields. Wheat breeding with new traits is a climate change adaptation option, however its effect will vary among different regions and limited under soil conditions (i. e., intercropping, mulching, and crop rotation) and local environmental conditions (e. g., rainfall,

temperature and soil nutrients) where water and N stress limit benefits of traits for high-temperature tolerance, early vigor, and delayed flowering adaptations. Therefore, future research should target improving prevailing stresses concurrently, to achieve improved grain yield and quality of wheat under water limited conditions.

Strategies such as breeding high-yielding cultivars, high-throughput phenotyping, and improving irrigation and water use efficiency are extremely important. Understanding the environmental variables and agronomic factors that determine wheat's response to drought and yield is critical. The exploitation of genetic resources such as landraces, synthetic lines and wild relatives will help to identify the wealth of important alleles that can be used in breeding and improvement programs. Progress in molecular markers and marker technologies such as QTL analysis and detection could speed up genetic selections for prominent breeding traits thus reducing the breeding cycle. Therefore, elucidation of gene loci for important breeding traits that promote adaptation and drought tolerance in wheat and their expression patterns in response to drought stress will provide a solid foundation for gene-based breeding approaches and strategies to improve germplasm for adaptation to multiple and specific environments. Although plant breeding provides strategies to develop drought-resistant cereal species reducing yield losses under unpredictable climate change, integration into the local climatic context should also be a key consideration in the application of technological innovations.

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