



Review

Elucidating the Drought Responsiveness in Wheat Genotypes

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Abstract: Drought is one of the major abiotic constraints on wheat yields and also for sustainability of production levels around the world. In the near future, the occurrence likelihood of droughts is predicted to become more common, due to changing climatic conditions, thereby posing a serious threat to the food security system. Heterogeneity, in its time of occurrence and severity levels, is likely to further augment the complexity of drought conditions. Although wheat crop growth has progressively risen to good levels, as evident by notable increases in both area and production, the expected wheat demand for the ever-growing population is quite high. Besides crop yield volatility in the era of climate change and dwindling resources, "trait-based" breeding programs are required, so as to develop high yielding, climate resilient and stable genotypes, at a faster pace. For this to happen, a broad genetic base and wider adaptability to suit varied agro-ecologies would provide enough scope for their quicker spread. The current review places emphasis on making distinct categories of the wheat cultivars/advanced breeding lines, as tolerant, moderately tolerant or susceptible to drought stresses, duly supported by an extensive up-to-date literature base and will be useful for wheat researchers, in order to choose the best potential donors as parents, coupled with the associated traits for the development of drought-tolerant wheat varieties, and also to facilitate molecular studies.

Keywords: wheat improvement; drought; trait-based breeding; physiological traits; biochemical traits; molecular traits



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1. Introduction

Wheat (*Triticum aestivum* L.) is one of the vital staple crops worldwide, by virtue of its significant contribution to food and nutritional security across regions and countries. The global wheat production was estimated to be 772.64 million tons during 2020 [1]. In India, wheat was cultivated across 31.76 million hectares, with a production of 109.5 million tons, which constituted about 14% and 13.64% of global wheat area and production, respectively, during 2020. Keeping the cultivation area constant, the average wheat yield needs to be increased from the present productivity of 3.3 tons/ha to 4.7 tons/ha by the year 2050, to meet the global wheat demand [1,2]. However, the overlapping cycles of different environmental stresses resulted in the stagnation of the wheat yield and also a reduction in harvest grain quality [2,3]. It is likely that, several cropping zones may face rather frequent heat waves and severe droughts due to the increasing average ambient temperature and CO₂ concentration in the atmosphere. The global wheat production may be reduced by around 29% by the year 2050, due to environmental stresses resulting from climate change. In contrast, wheat demand is expected to increase by 60% [1]. Also, droughts induced due to receding water tables is also pernicious to wheat production.

The micro- and macro-environmental variations are anticipated to be more severe in the coming years, which are further made complex by the declining arable land and

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irrigation water [4]. Water stress is the continuing limiting factor and the foremost natural threat to wheat productivity, particularly in the semi-arid and arid regions. Moisture deficiency can cause stress at any stage of the wheat crop, starting from seedling up to maturity, which leads to significant yield losses [5]. In recent years, about one-third of the area under wheat cultivation has been estimated as a drought-affected region in India. Due to its agro-climatic diversity, India is more prone to weather vagaries and the intensity of drought has been increasing continuously in many parts of the Indian sub-continental basins [6]. From the year 1891 to 2009, India has experienced about 23 large-scale droughts and the relative occurrence of dry events is increasing year after year [7]. Drought stress continues to be an important area of concern to agricultural researchers and, more so, to plant breeders, as they are continuously trying to enhance wheat adaptation to stress-prone environments, with multiple approaches. The main challenge under the existing circumstances is to enhance the agricultural productivity to meet the increasing population, by using the available gene pool and diminishing natural resources [8].

Efforts are being made all over the world to mitigate droughts through the development of drought-tolerant cultivars. However, the progress has been delayed due to the complexity of the drought-tolerance trait, as the trait is controlled by many genes, with significant environmental influence. It is difficult to predict the severity of droughts because no single attribute has a direct association with grain yield under stress. Development of a new variety is a cumbersome and time-consuming process and all the efforts to accelerate crop improvement programs rely on meticulous screening of the wheat germplasm, along with newly developed progenies for stress tolerance and high yield potential. The gene banks of 90 countries from Europe, Asia, Africa, America, and Oceania have more than 850,000 accessions of wheat germplasm, stored in 229 collections. Among these, CIMMYT, ICGR, NSGC, NBPGR, ICARDA, and NIAS are the top six germplasm collection centers [9,10]. Russia, China, the United States, India, Japan and Italy have the most remarkable national wheat collections, along with CIMMYT in Mexico and ICARDA in Syria. In Saudi Arabia, the Gene Banks of King Abdulaziz City for Science and Technology (KACST-BGB) and Ministry of Environment, Water and Agriculture have 61 and 126 accessions of wheat germplasms conserved, respectively [10].

The researchers need to select the desired parent type from the available gene pool for their breeding programs; however, sometimes breeders get mislead due to lack of understanding of the actual tolerance mechanism of the genotypes. Several traits known for drought tolerance are governed by additive gene action, with high heritability, and display incessant variation, which suggests that there is substantial room for improvement in drought tolerance [11]. The inconsistency among the experimental results of different studies of the same genotype further deepens this complexity. To fix the inconsistency, an analysis of the global wheat genotypic pool is required to identify the research gaps and potential for collaboration across different wheat-producing countries. A piece of accumulated information is essential for speeding up abiotic (drought stress) research investigations in wheat, minimizing duplication, and maximizing the worldwide impact on wheat production systems. Hence, an effort has been made to classify the wheat genotypes, based on different adaptive mechanisms, and to classify them as tolerant/susceptible genotypes, based on a comparative analysis of genotypic behavior under drought stress. This is the first compilation of its kind to consider in depth about genotype classifications for traits, by including exhaustive research papers on drought stress in Indian and global wheat genotypes. Compiling the information on all drought studies is important for the classification of genotypes as tolerant or susceptible, and also for the associated traits for the development of new varieties, with improved drought tolerance.

2. Plant's Adaptive Crosstalk to Face Drought

Drought stress primarily signifies the unavailability of soil moisture to the plant roots, beyond the threshold level defined for normal plant growth and development [12]. Besides being sessile, plants possess the capability to sustain, by an array of morphological,

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biochemical, physiological, and molecular responses, against environmental stresses [13]. Empirically, under a moisture deficit regime, the priority of the plant is only survival, as almost all the plant's metabolic activities get disturbed due to tissue dehydration [14,15]. In wheat, the negative effects of drought stress are innumerable. The severity of impact is significantly correlated with the plant growth stage and intensity of occurrence of drought events [16]. Drought tolerance is based on plant's capability to bear dehydration to some degree and regain its growth after moisture availability. Basic mechanisms to alleviate the impacts of droughts include drought tolerance, avoidance, and escape. While, drought avoidance comprises efficient use of available moisture by plants, deeper root depth and required phenological alterations are the adaptive mechanisms in drought tolerance. The escape mechanism involves the completion of the plant's lifecycle before facing the drought event. However, other factors, such as genetic behavior, photo-respiratory patterns, growth, and phenological stages interact differently under different degrees of drought stress.

During a drought, oxidative stress commences various types of physiological responses, such as stomatal closure, altered stomatal conductance, reduced photosynthetic activity, changes in the cell wall integrity, loss of turgor and osmotic adjustment, reduction in water potential, production of toxic metabolites, recognition of death signal by roots, and eventually, reduction in overall growth rates [17]. The significant relationship between different physiological responses and their tolerance functions under drought have been identified [18,19]. The membrane thermo-stability is considered as the most significant trait for measuring drought tolerance under water stress [20,21]. During the early grain filling stage, drought stress diminishes the plant's metabolic activities, resulting in a reduced number of endosperm cells, and decreased sink strength [14,22,23]. Low turgor pressure due to drought sensitivity restricts cell division, expansion, and differentiation and, hence, the overall plant growth [24]. Under such circumstances, osmotic adjustment is a decisive trait of plant physiology, by which they respond to water deficit. Osmotic adjustment (OA) helps plants to maintain turgor pressure and cell volume in water deficit conditions, to maintain their metabolic functions, as well as assisting in the recovery of metabolic activities after relief from drought stress [25]. The OA has expressed more in drought-susceptible genotypes that maintain lower shoot water potential, as compared to tolerant genotypes maintaining higher shoot water potential under stress conditions [26]. High transpiration efficiency is also considered an indispensable phenomenon in plants under drought [21].

Drought stress induces a cascade of reactions, in terms of biochemical regulation, i.e., antioxidant production, protein transformations, reduced chlorophyll content, root deepening, and improved cuticle thickness, to withstand the changes in various plant organs [20,21,27]. The importance of antioxidant production to scavenge reactive oxygen species (ROS) has also been recognized in many biochemical studies. Dat et al. [28] highlighted that the oxidative balance of the cell has changed under increased ROS concentration caused by drought stress. Different sub-cellular organelles, such as chloroplast, mitochondrion, and peroxisome, are the most common sites for ROS production. The photosynthesis and respiration processes are inhibited due to oxidative stress and, thereby, plant growth is hindered. By means of decreased CO₂ diffusion to chloroplast and metabolic constraints, photosynthesis plays a key role in plant performance under drought conditions. Thus, the potential to sustain photosynthetic ability under drought stress has crucial importance for drought tolerance. In response to water stress, the plant rapidly closes stomata to avoid additional loss of water via transpiration. Many in-vivo studies revealed that drought stress results in damage to the oxygen evolving complex of the PS-I and PS-II reaction centers, which are associated with the degradation of D1 protein [29]. The study of the balance between light capture and energy use is of great importance, to assess the responsiveness of the photosynthetic machinery under drought conditions. Photo-oxidative damage may occur when the light excitation energy is in excess after decreased photosynthetic activity. The excess energy in PS-II inhibits photosynthetic functions and increases ROS accumulation, thereby leading to oxidative stress. More generation of ROS-enhanced abscisic acid (ABA) content, a general signal of drought stress, can enhance the expression of antioxidant genes, Sustainability **2022**, 14, 3957 4 of 20

by producing numerous enzymatic and non-enzymatic antioxidative defense compounds. Drought can also affect the reproductive health of the plant by reducing grain number due to pollen sterility. Under low moisture availability accumulation of ABA in spikes and expression of ABA synthesis genes in anthers also occurred in drought-susceptible wheat genotypes [30].

Wheat germplasm is rated as the most enriched, with huge genetic variation for drought-related traits, because of its high yielding and elite genotypes [31,32]. Significant improvement has been made in genome sequencing, annotation, and functional characterization of important wheat genes [33]. A large number of quantitative trait loci (QTLs) have been identified for various morpho-physiological traits in wheat, to facilitate a deeper understanding of the genetic makeup of wheat against drought [34]. Moreover, several transcription factor families, such as DREB (dehydration responsive element binding), ERF (ethylene response factors), ZFP (zinc finger proteins), etc., were also scrutinized, to understand the molecular mechanism of drought tolerance in wheat [35]. Substantial research has been conducted to produce high-yielding varieties, but the impacts of drought stress are diminishing the overall production rate. Therefore, it is a prerequisite to understand the factors triggering various plant processes and the stimulated plant defense mechanisms under droughts simultaneously. This type of interactive study not only helps to categorize the genotypes as per their tolerance potential, but also supports their utmost use in environment-specific research.

3. Trait-Based Classification of Wheat Genotypes

3.1. Indian Wheat Genotypes

3.1.1. Classification of Genotypes Based on Physiological Traits

In the era of "trait-based" breeding for abiotic stress studies, the introgression of physiological traits in breeding programs, for attaining desired gain, is more decisive. Stress-related studies placed greater emphasis on crop cultivation practices, but the current climatic scenario is emphasizing the identification and validation of climate-resilient genotypes. In the current section, we are highlighting the different methods that have been used to evaluate the genotypes for drought tolerance, mainly based on physiological traits. Most of the researchers emphasized root architectural traits, RWC (Relative Water Content), CHL (total chlorophyll), carotenoids, MSI (membrane stability index) or CMS (cell membrane stability), OP (osmotic potential), CFL (chlorophyll fluorescence), higher photosynthetic activity and stress indices, to prove the potential of candidate genotypes against drought. A few morphological traits, such as plant height, leaf area, number of productive tillers, spike length, spikelets per spike, seeds per spike, thousand-grain weight, and yield per plant were highlighted to differentiate the wheat genotypes, under normal and drought conditions.

Based on the hypothesis that, under water limiting conditions, root biomass contributes towards higher yields, a pot experiment was conducted, with a set of 34 genotypes, under three moisture levels. The genotype HD2932 was reported as the most stable and consistent performer, in both normal and drought environments for root dry matter and root volume. The genotypes HD2987, DBW17, HD3086, HD3016, HD3043, HD2932, and GW366 showed STI values (stress tolerance index) of 0.8–0.95, and these high values of STI indicated greater tolerance to moisture stress, along with high root dry biomass in these study genotypes [36]. Further, to explore and characterize the role of root traits during the reproductive stage, Tomar et al. [37] worked with a set of 158 wheat genotypes and shortlisted 31 genotypes, comprising 28 hexaploid (*Triticum aestivum* L.) and 3tetraploid (*T. durum*), after screening in PVC (polyvinyl chloride) pipes. Root architecture traits of drought-tolerant (C306, HD2888, HW2004, and NI5439) and sensitive (HD2877, HD2851, HD2012, and MACS2496) genotypes were critically observed. The root imaging (WinRhizo), at the reproductive stage of HW2004, indicated a deeper and dense root system, while the root of HD2877 exhibited more horizontal spread and less depth.

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To study the effect of moisture in above-ground plant growth and yield, eight wheat genotypes were grown in pots under 70% field capacity [38]. Water unavailability resulted in a reduction in RWC, CHL, carotenoids, MSI, biomass, leaf area, and grain yield, in all study genotypes. The genotype C306 showed a higher grain yield than HD2733 and PBW343. Parameters, such as plant height, spike length, spikelets per spike, and 1000-grain weight, were found to be drastically decreased by increasing water stress. Wheat genotypes C306, HD2967, HD3016, NI5439, which maintained relatively higher values and a lower percentage decline in RWC, MSI, CHL content, leaf area per plant under water deficit stress, also had higher grain yield than HD2733, PBW343, PBW373. A growth-stage-specific water-withholding pot experiment, with four wheat genotypes, C306, AKAW3717, HD2687, and PBW343, was conducted by Sheoran et al. [39]. Drought was imposed at tillering (T), anthesis (A), and 15 days after anthesis (15DAA) stages, at 75% and 45% of field capacity. At tillering, except AKAW3717, all three genotypes showed considerable reduction in grain yield/plant and thousand grain weight (TGW) under severe stress. At anthesis, under medium and severe stress, C306 performed significantly better than AKAW3717, HD2687, and PBW343, for grain yield, compared to the control. Under severe water stress, the highest DSI (drought susceptibility index) was recorded in PBW343 (1.5) and the lowest in AKAW3717 (0.46) at the tillering stage. However, over the three stages, C306 constantly showed low DSI, while HD2687 showed comparatively high DSI value, both under medium and severe drought stress.

To understand the impact of drought stress under field conditions, an experiment was designed, with 30 wheat genotypes at different plant growth stages [40]. The experiment was replicated in three sets; one set under well-irrigated conditions and two sets under drought stress, for two years. In one set (withholding irrigation at 30 days after sowing), drought stress was induced around anthesis and in the second set (withholding irrigation at 70 days after sowing), during the maturity stage, respectively. The third set (full irrigation at both anthesis and maturity) was conducted under the normal package and practice of irrigation. Wheat genotypes C306, Kharchia65, Lok1, Lok1(U), WH157, HW2001, VL421, WH147, WH147(U), WH331, WH533, WL410, W1562, PBW65, HPW(DL)30, HPW65, HD2329, HD2329(U), CPAN1992, CPAN3004 and Kundan were taken for the study. Data were recorded for DH (days to heading), excised-leaf water loss, leaf membrane stability, RWC, and grain yield under drought stress. The genotypes WH147(U), Kharchia65, C306, WL1562, VL421, and HPW42, showed significantly higher water retention and lower loss of water under drought conditions. The genotypes WH147 and WH147(U) showed higher drought tolerance because of high water retention capability and also produced high yield. Kharchia65, C306, and Hindi62, were recorded with a lower membrane injury, along with better water retention in the leaves and higher Drought Response Index (DRI) values. Among all, C306 and Kharchia65 were identified as the most stress-tolerant genotypes, based on DRI values [41]. Hence, the authors recommended the use of C306, Kharchia65, WH147(U), and WH147, in the drought breeding program. In another study, 28 diverse wheat genotypes were evaluated for drought stress-related traits, such as RWC, OP, CMS, and CFL, both under normal and water stress conditions for two years [42]. Based on the data, WH1127 and NW1014 were found to be tolerant to drought. However, PBW175, WH1181, PBW644, UP2425, NW1014, Raj3765, and WH1098, also performed better due to the accumulation of solutes (sugars, sugar alcohols, amino acids, glycine betaines, and proline) and membrane stability under drought. Early heading in WH1182, WH1142, HW2004, NIAW34, and WH1098 indicated that these genotypes have an escape mechanism to counter drought stress, while higher yields and stable heading dates of WH1181, WH1127, and WH1126 were comparatively more influenced by drought avoidance/tolerance mechanisms. Along with C306, WH1142, HW2004, WH1181, PBW175, WH1098, and NIAW34 showed higher values of DRI and DSI. Under both the conditions Lok1, PBW175, HD2858, PBW343 showed early heading, while NIAW34, HW2004, WH1182, and WH1098 fasten their growth under drought to indicate the genotypic plasticity. In a similar study, ten wheat genotypes of diverse genetic backgrounds, with popular Indian cultivars, were screened

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for different morpho-physiological characters under drought conditions and traits, such as plant height, number of productive tillers, days of maturity, length of spikelet, spikelet per spike, seeds per spike, thousand-grain weight and yield per plant, were measured [43]. Along with these, CHL, RWC were also recorded to categorize the genotypes. Based on the studied traits, Raj1555, PBW226, DBW17, PDW291 (durum), VL421, and WH1021 were recognized as better performers for drought conditions.

Pot and open field conditions have their own limitations, such as maintaining drought conditions in a pot is very difficult manually, and also lacks sufficient genotype x environment (GxE) interaction effects, whereas in the field, we have no hold over rain and other indirect water sources, such as dew. In such cases, the screening of genotypes in a controlled environment (such as greenhouse/ROS/lab) is a feasible and reliable strategy. Keeping these obligations in view, a greenhouse experiment was conducted on six wheat genotypes (HD2329, Sonalika, Kundan, IWP72, C306, and Narmada112) to observe the effects of pre-anthesis water deficits on photosynthesis, growth, and yield. On the basis of the recorded traits (photosynthetic data, RWC, and grain yield), it was identified that pre-anthesis stress is more harmful to the main shoot. The genotypes C306 and Kundan compensated the main shoot yield loss by their tillers and grain yield under low water availability [44]. In another study, C306, along with HD2428, were evaluated by Sairam [45], to identify the mechanism of their drought tolerance. It was observed that C306 maintained higher RWC, membrane stability, chlorophyll stability and higher photosynthetic activity, under a low-moisture regime, while HD2428 had reduced metabolic activities under water deficit. Further, C306 showed better reviving capacity when rewatered, which makes it a stable candidate for improving drought stress tolerance. In another study, Singh et al. [46] treated 10 wheat genotypes with polyethylene glycol (PEG) to characterize wheat genotypes under drought stress and recorded LA (leaf area), PT (productive tillers per plant), DM (days to maturity), SS (seeds per spike), LS (length of spike), and YP (yield per plant). He found V110 as the best performer among all others (HD2133, HUW825, R54, K9533, V110, V70, HUW213, V23, VWTH-08-07, and HUW37) for drought. In an indices-based study, WH1021, NI5439 and HD2733 were reported as high yielders and stress tolerant under normal and restricted irrigation [47].

In most of the studies associated with physiological and morphological traits (Table 1), it was found that C306 was highlighted invariably as drought-tolerant genotypes, due to higher RWC, photosynthetic activity, membrane stability, chlorophyll stability, and yield under drought, and also showed better reviving capacity upon rewatering. Based on the DRI values, C306 was found to be the top ranker, followed by Kharchia65. HW2004 was recognized as an early flowering genotype, with a deeper and denser root system, demonstrating its tolerance to neutralize drought stress impact. Another genotype, DBW17, maintained higher values of CHL, RWC, and root dry weight, along with higher STI (0.8–0.95), which signifies its tolerance to moisture stress. The results of indices-based studies should be used effectively in drought-based investigations, as they demonstrate comparative responses of genotypes under stressed and non-stressed situations. Evaluation of genotypes at hot-spot target environments is another option towards identifying tolerant genotypes through stress phenotyping. ICAR-Indian Institute of Wheat and Barley Research, Karnal, India, as a nodal agency for releasing wheat varieties, screened advanced varieties and promising entries, based on data supplemented with DSI, under drought stress hot-spot locations in India, and identified drought tolerant wheat genotypes under the All India Coordinated Wheat and Barley program. Some genotypes, such as Raj3765, MP3288, K1317, and DBW110, have been utilized as a check in drought-related coordination program, and they were consistent in their drought tolerance. Apart from these, few genetic stocks (RW5, DT-RIL-110, M516, WH1235) have been registered for superiority over drought stress testing, based on multi-location multi-year data.

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3.1.2. Classification of Genotypes Based on Biochemical Traits

Exposure to water deficit primarily causes oxidative damage to plant cells due to the formation of ROS. These ROS influence the normal cell functioning and damage lipid synthesis, enzyme production, and protein structure. To face the oxidative stress effectively, plants developed their own antioxidant machinery, comprising numerous enzymatic and non-enzymatic components, such as SOD (Superoxide dismutase), POX (Peroxidase), CAT (Catalase), APX (Ascorbate peroxidise), GR (Glutathion reductase), carotenoids, proline, etc., which accumulate during water stress conditions [18,24,48,49]. Higher nitrate reductase activity (NR) and chlorophyll content (CHL) were also reported as biochemical indicators during stress [50]. According to Moller et al. [51], an increased level of malondialdehyde (MDA) has been accounted as a reliable biochemical marker for drought-stimulated oxidative damage. Therefore, the production and maintenance of the required levels of the antioxidant components can be an excellent approach to counteract the harmful effects of ROS. Intensive research has been conducted on understanding the biochemical basis of drought tolerance in the released Indian wheat cultivars, to prove their efficacy as a practical screening tool under drought stress (Table 1).

The impact of drought stress on biochemical traits, at tillering, anthesis, and 15DAA, was studied in four wheat genotypes (AKAW3717, HD2687, PBW343, C306), under medium and severe stress in pots by Sheoran et al. [39]. The results highlighted increased SOD and POX activity in C306 and AKAW3717, while CAT level decreased under the same set of conditions. The lipid peroxidation (MDA) level was low at the initial stage but increased under severe stress in AKAW3717 and C306. In another study, significantly higher induction of CAT, GR and POX in shoots, CAT in roots and APX in endosperms, was observed under drought conditions and correlated with genotypic tolerance to water deficit conditions. Under rainfed conditions, four wheat genotypes, namely NI5439, PBW175, PBW299, and PBW396, showed >50% increase in CAT activity in roots and maximum APX activity in shoots, followed by roots and endosperms in the control and stressed seedlings. Low APX in shoots could be one of the indicators for drought tolerance capability and PBW343 had low APX activity in shoots. In the endosperms of water deficit stressed seedlings, the genotypes C306, PBW175 and PBW299 showed more than 40% induction of APX activity compared to control seedlings. Under both normal and stressed conditions, GR activity was considerably higher in the shoots and roots, compared to the endosperms of wheat seedlings. However, the three drought-tolerant genotypes (C306, NI5439, and PBW175) showed 30% less GR activity in the endosperms of control seedlings, as compared to the sensitive genotypes. About 40% up-regulation in GR activity was observed in the shoots of all drought-tolerant genotypes. Finally, it was concluded that genotypes showing a reduction in APX and GR activities and improvement in POX activity in shoots, along with a low shoot: root ratio of GR in non-stressed seedlings, could be considered as tolerant. Further, elevated levels of POX and GR in shoots, CAT in roots and shoots, APX in endosperms can be used as indirect traits for the selection of drought-tolerant genotypes [52].

In osmotic stress (using three different concentrations of PEG), studies withC306, PBW175, NI5439, PBW343, and DBW17 at the seedling stage showed in increase in the activities of SOD and CAT, observed in C306 and PBW175, along with better root growth, in comparison to NI5439, PBW343, and DBW17 [53]. In another seedling stage experiment, 22 wheat genotypes, comprising both T. aestivum (Lok1, HW2004, GW173, GW273, GW366, GW322, and GW496) and T. durum accessions, were evaluated for drought tolerance and for which stress was artificially induced, with 0, 5%, and 10% PEG treatment [54]. Data on germination percentage, shoot root length, and seedling vigor index, were recorded and based on the statistical analysis, and HW2004, Lok1 were found to be highly tolerant, while GW273, GW366 were found to be highly susceptible to drought. However, GW173, GW322, and GW-496 were found to be moderately susceptible to drought. Activity of APX, GR, CAT, SOD, and POX were analyzed in another water stress experiment anda significant increase in their expression was observed in UP2752 and PBW343, as compared

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to the other tested varieties. These two varieties showed comparatively better antioxidant defense mechanisms under severe stress for a longer duration. Based on CMS and relative percentage damage to membrane data, these two were reported as less sensitive to moisture stress [55]. Three contrasting wheat genotypes, namely PBW175, WH542, and HD2402, were studied for antioxidant enzyme (APX, GR, and nonspecific peroxidase) activities under water stress [56]. PBW175 showed higher membrane stability due to less lipid peroxidation and significantly up-regulated the activities of APX, GR, and POX, along with higher CHL and carotenoids content, whereas WH542 showed the highest lipid peroxidation and lowest antioxidant activity, membrane stability, chlorophyll, and carotenoids and, hence, termed as susceptible to drought. The genotype HD2402 was reported with intermediate values. In another study, drought stress was imposed for ten days at 50, 60, and 70 days after sowing, to examine the physiological and biochemical responses of wheat varieties (C306, Hira, HW24, A9-30-1) [57]. Plant height, total dry matter, and proline accumulation were recorded under water stress conditions. The lowest percent decline in NR and CHL under drought conditions was recorded in C306 with highest in Hira. Hira showed a considerable decline in RWC, carotenoid content, and membrane stability and the lowest ABA accumulation [57]. The genotypes that have been identified as drought tolerant, based on biochemical features, also proved their potential when evaluated for physiological traits or any other complementing trait, and vice versa. The genotypes C306, NI5439, Lok1, documented as drought tolerant based on physiological traits, also proved their potential when tested for biochemical traits. Better yield and low DSI (0.9) at anthesis, along with better biochemical functioning (APX, GR, CAT, SOD, and POX) indicated that PBW343 is a good performer undera drought stress environment. However, contrasting results were highlighted by some other authors, which showed a drastic reduction in CHL and carotenoids, along with grain yield. Similarly, for HD2733, the results are conflicting and need further validation. HD3016 was reported as a higher yielder, with higher STI, with less per cent decline in RWC, MSI, CHL, leaf area under moisture stress. Under drought, PBW175 maintained higher DRI values due to accumulation of solutes, higher membrane stability, and less lipid peroxidation. A significant increase in antioxidant enzymes, in multiple research studies, along with higher content of photosynthetic pigments and good root growth, indicate its potential as a drought-tolerant genotype.

3.1.3. Classification of Genotypes Based on Molecular Traits/Markers

In modern genetics, functional genomics approaches, such as, transcriptomics, proteomics and metabolomics, are utilized to identify drought-responsive genes. The expression of different genes varies in different plants, to help them in optimizing their growth and development in drought stress conditions. Plant hormone abscisic acid (ABA) regulates the expression of many target genes under drought stress through ABA-responsive element (ABRE)-binding proteins/ABRE-binding factor (AREB/ABF) transcription factors. AREB/ABF-regulated genes constitute a regulon, known as AREB/ABF regulon. These key genes also code proteins, different transcription factors (DREB, AP2/ERF, NAC, bZIP, MYC, and MYB), signaling protein kinases, and protein phosphatases. [58].

Differential expression of cytochrome P450, dehydrins, heat shock proteins, proteinase inhibitors, glutathione transferase, and regulatory proteins, including transcription factors, is a common response to drought stress conditions. In drought-tolerant wheat genotypes, multiple transcription factors, such as bHLH, ERF, NAC, bZIP, HD-ZIP, and WRKY, were differentially expressed, as compared to drought-susceptible genotypes [59]. These stress-responsive genes, including transcription factors (TFs), play important roles in multiple abiotic stress (heat, drought, and salt) responses, by regulating downstream stress-responsive genes. Molecular markers are being used to identify the location of drought-induced genes and for gene mapping and tagging of different traits, useful in marker-assisted breeding (MAB). Molecular markers were used exceedingly in crop improvement, but their success for complex traits, such as drought tolerance, is limited by the identification of strong marker-trait association. Genetic analysis of complex charac-

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teristics requires a suitable mapping population, which can be utilized as a tool for the identification of drought-associated QTLs. Tomar et al. [37] identified polymorphism in a set of 91 markers, between HD2877 and HW2004, as contrast parents for drought tolerance. To verify whether other parents involved in the development of the recombinant inbred lines (RILs) are also polymorphic, a survey for polymorphism was conducted. Out of 91 markers, 75.82% of Simple-sequence repeats (SSR) markers were polymorphic in C306 and MACS2496, 63.74% were polymorphic between HD2851 and HD2888, 60.44% were polymorphic between C306 and HD2851, and 57.14% polymorphism was observed between NI5439 and HD2012 contrast parents. Based on this molecular analysis, these eight genotypes and their mapping population were grouped into drought-tolerant and sesceptible clusters for understanding the drought-tolerance mechanism. By use of microsatellites, Röder et al. [60] highlighted analogous results between Triticum aestivum and Triticum durum. By using polymorphic DArT markers, Zhang et al. [61] reported that the presence of drought tolerance markers was more frequent on the B genome, but very rare on the D genome. However, Akbari et al. [62] reported comparatively low polymorphism by DArT markers. This corroborates that, among wheat ABD genomes, the highest level of polymorphism is exhibited by the B genome, whereas the D genome exhibits the lowest level of polymorphism for drought tolerance.

Tomar et al. [63] utilized thirty SSR markers to analyze genetic variation in a population of 158 wheat genotypes (72 Australian and 86 Indian genotypes). Based on the UPGMA cluster, STRUCTURE, and main coordinate analyses, the genotypes were divided into three subgroups: extremely tolerant, sensitive, and moderately sensitive, with tolerant as an intermediate group. Cluster-I had eight genotypes, viz. HD2851, HD2877, MACS2496, HD2012, HD2189, HD2932, Bijaga Yellow (durum) and NP846. Cluster-II included four genotypes, namely K65, PBW373, PBW343, and HD2329. Cluster-III consisted of nine well-known drought-tolerant genotypes, Mukta, C591, C306, HW2004, HD2888, NI5439, NP824, NP4, and HS240, whereas Cluster-IV consisted of ten genotypes, viz. Raj1555, Jairaj (both durum), WR544, Kharchia Local, GW366, Agra Local, Raj3765, UP2338, Sonalika and HD2687. The SSR analysis revealed a wide range of genotype variability, with the A genome having the highest value compared to the B and D genomes. In the current study, the SSR marker-based analysis, employing UPGMA tree, population structure, and primary coordinates, to analyze wheat genotypes in response to drought stress, was shown to be meaningful because the majority of the groups were co-linear in all grouping approaches. To detect alleles characteristics of cultivars from the distant genetic backgrounds, the suitability of SSRs was proven by the clustering of genotypes. C306 is directly associated with droughttolerant genotype HD2888, HW2004 (C306/T.sphaerococcum//HW2004) and NI5439, to a great extent, which reflects selection for genomic regions existing in the drought-tolerant varieties. In an SSR-based structure, population-I consisted of 17 genotypes, ranging from moderate sensitive to moderate tolerant genotypes, such as Mukta, NP4, C591, NP824, and HS240. Population II had highly drought-tolerant C306, HD2888, HW2004, and NI5439 genotypes and two durum wheat genotypes, Raj1555 and Jairaj, while the other eight genotypes of population III had intermediate response for drought. Such studies will provide a platform for identifying genotypes, utilizing SSR markers based on root and shoot attributes under drought stress. The expression studies by Tomar et al. [63] highlighted that SSR markers offer the benefit of co-dominance and uniform genome coverage in drought-stress-tolerant wheat genotypes, leading to the development of a highly segregating mapping population.

A preliminary study on an intervarietal mapping population (C306/HUW206) of recombinant inbred lines (RILs) was done by Kumar et al. [64] and further evaluation for drought tolerance was done by recording the traits, such as CHL, leaf temperature (L_{Temp}), PS II (Fv/Fm), and grain yield/plant (Gyp) under stress. Between the parents, 560 markers, that cover the entire wheat genome, were screened for polymorphism. The discovered QTLs provided a first insight into the genetics of drought tolerance in C306. Iquebal et al. [65] reported that WL711 (drought susceptible) and NI5439 (drought tolerant)

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were used to produce almost 78.2 GB of data for the responses of roots in wheat under drought conditions and 45,139 differentially expressed genes (DEGs), 288 miRNAs, 640 pathways, 13,820 TF, and 435,829 putative markers were found. They reported the molecular mechanism of wheat root drought responsiveness, through an irrigation withdrawal method using contrasting varieties at Zadok's scale. Kadam et al. [66] said that qDSI4B.1 appears to be the most significant genomic region for wheat variety C306. This QTL is present on the chromosome 4B region, which is responsible for drought tolerance [67–72]. Dashti et al. [72] identified QTL for the stress susceptibility index on chromosome 4B, linked to Rht1b gene. However, Pinto et al. [69] did not find linkage with any known Rht genes in Seri/Babax mapping population, suggesting that linkage between drought tolerance and plant height in the WL711/C306 population may be coincidental. By avoiding the segregation of genes, the probability of gene identification for minor effects is increased in comparison with other cereals. Few studies report on genetic analysis of root traits in wheat under reproductive stage in drought [73]. Chromosome 4B is responsible for grain yield under drought and it also helps in root and shoot biomass, with trait-enhancing allele coming from the drought-tolerant C306. In a region syntenic to wheat chromosome 4B, genomic regions have been known for grain yield under drought and root volume on rice chromosome 3 [74–76]. Chromosome 4B is more important due to the co-localization of multiple QTLs for the shoot and root biomass, with trait-enhancing allele coming from the drought-tolerant parent C306. Deeper roots, particularly the seminal roots, are thought to be crucial for wheat growth under drought [77,78]. Ren et al. [79] reported QTLs for total root length, lateral root length, and root tip number for seminal roots, at the seedling stage on wheat chromosome 4B. This depicts that wheat chromosome arm 4B hasthe main genes for improving root traits and has a key role to play in the drought tolerance of wheat variety C306.

Shukla et al. [80] found QTL qGYWD.3B.1 present on chromosome 3B, with positive allele being contributed by C306, which accounts for a large percentage of phenotypic variation. This QTL was co-located with QTLs for yield, canopy temperature, and flowering and was independent of plant height. Another major novel and consistent QTL qGYWD.3B.2 was associated with WL711, mainly participating in grain yield. Other important QTLs for grain yield, drought susceptibility index (DSI), thousand-grain weight, and biomass were mapped on chromosome arms 7BL, 3BL, 6AS, and 4AL. They are in consonance with the QTLs reported earlier for yield, yield components, and drought tolerance-related traits and/or genes either in rice or barley [81,82].

Gupta et al. [83] conducted a study in which they analyzed the expression behavior of five members of the DREB family, along with four other abiotic stress-responsive genes, in two wheat genotypes, C306 and HUW468, at the seedling stage. They found DREB2B to be up-regulated more significantly under drought stress, compared to other family members. DREB are important transcription factors that induce a set of abiotic stress-related genes and impart stress tolerance to plants. Accumulation of NAC transcription factor was observed higher in C306 compared to HUW468, while other stress-responsive gene (SCARECROW and Cu protein) accumulation was lower in C306. Increased accumulation in NAC protein in C306 may indicate its active involvement in drought stress conditions. Kumar et al. [84] used WL711 and NI5439 and carried out the expression analysis for different stress-responsive genes under lab conditions. An oxidative stress-responsive gene, FeSOD, was found to be induced only in NI5439. A variation in transcript expression was observed under drought stress conditions among all the tested genes. SHN1, DREB6, NHX2s and AVP1 gene expression was always found higher under drought stress conditions in wheat. Very meager information exists on transcription factors and other stress-responsive genes studies in Indian wheat varieties under drought stress conditions. However, the available information on such studies is compiled in Table 1. Advanced functional genomics research is now being used to gain a better knowledge on the wheat genome and to aid in its modification. Approaches, such as RNA interference, next-generation sequencing, CRISPR/Cas9, Sustainability **2022**, 14, 3957

and genome-wide association analysis (GWAS), will be useful in the induction of the desired phenotype.

Table 1. Trait-based classification of wheat genotypes for drought responsiveness.

Biochemical Biochemical Biochemical Biochemical Biochemical	SN	Variety	Drought Responsiveness	Trait(s)	Year of Release	Pedigree	Reference			
1 C306 Drought tolerant Biochemical, Molecular 1905 3/C217/N14//C281 52,53,57,63,64,64	Category 1: Drought Tolerant Genotypes (36)									
2 Ni5439 Drought tolerant Physiological, Molecular Molecular Molecular Selection from Kharchia Isoal EG953 Isoa Isoa	1	C306	Drought tolerant		1965		[34,37–40,42,44, 52,53,57,63,64,66]			
1974 1974 1974 1974 1975 1974 1975	2	NI5439	Drought tolerant	Physiological,	1973	REMP 80/3*NP710	[37,38,47,52,53,63, 65,84]			
5 WH147 Drought tolerant Physiological 1979 E4870/C286/C273/ 4/S339/PV18 [63] 6 HD2687 Drought tolerant - 1999 CPAN2009/HD2329 [63] 7 VL421 Drought tolerant Physiological 1979 SON64/Y50E/GTO [34,40] 8 WL711 Drought tolerant Physiological 1979 S308/CHR/KAL [52,65,80,84] 9 K7410 (SHEKHAR) Drought tolerant - 1980 K812'S'/KALYANSONA [34] 10 LOK1 Drought tolerant - 1983 PW5/Y53 [34] 11 AJANTA Drought tolerant - 1983 PW5/Y53 [34] 12 WL1562 Drought tolerant - 1985 PV18/K68 [34] 14 K78 Drought tolerant - 1985 PV18/K68 [34] 15 WH1021 Drought tolerant Physiological 2008 NYOT95/SONAK [43,47] 16 V110** Drought tol	3	K65	Drought tolerant	Physiological	1974		[34,40]			
Final Content Final Conten	4	HYB65	Drought tolerant	-	1976	GB-AUS/A115	[40]			
7 VI.421 Drought tolerant Physiological 1979 SON64/Y50E/GTO [34,40] 8 WL711 Drought tolerant Biochemical, Molecular 1979 S308/CHR/KAL [52,65,80,84] 9 K7410 (SHEKHAR) Drought tolerant - 1980 K812'S'/KALYANSONA [34] 10 LOK1 Drought tolerant - 1983 PW5/Y53 [34] 11 AJANTA Drought tolerant - 1983 PW5/Y53 [34] 12 WL1562 Drought tolerant - 1985 PV18/K68 [34] 14 K78 Drought tolerant - 1985 JANAK/K816//K65 [34] 15 WH1021 Drought tolerant Physiological 2008 NYOT95/SONAK [43,47] 16 V110 *** Drought tolerant Physiological - - [46] 17 PBW175 Drought tolerant Biochemical 1991 BB/KAL//WL711/ PBW65 [52] 18 PBW299 Drou	5	WH147	Drought tolerant	Physiological	1979		[63]			
8 WL711 Drought tolerant Biochemical, Molecular 1979 \$308/CHR/KAL [52,65,80,84] 9 K7410 (SHEKHAR) Drought tolerant - 1980 K812'S'/KALYANSONA [34] 10 LOK1 Drought tolerant Physiological Biochemical 1981 \$308/S331 [42,52,54] 11 AJANTA Drought tolerant - 1983 PW5/Y53 [34] 12 WL1562 Drought tolerant - 1985 PV18/K68 [34] 14 K72 Drought tolerant - 1985 JANAK/K816//K65 [34] 15 WH1021 Drought tolerant - 1985 JANAK/K816//K65 [34] 15 WH1021 Drought tolerant Physiological 2008 NYOT95/SONAK [43,47] 16 V110*** Drought tolerant Physiological - - [46] 17 PBW175 Drought tolerant Biochemical 1991 BB/KAL//WL711/PBW65 [52] 18 PBW299	6	HD2687	Drought tolerant	-	1999	CPAN2009/HD2329	[63]			
9 K7410 (SHEKHAR) Drought tolerant - 1980 K812'S'/KALYANSONA [34] 10 LOK1 Drought tolerant Physiological Biochemical 1981 S308/S331 [42,52,54] 11 AJANTA Drought tolerant - 1983 PW5/Y53 [34] 12 WL1562 Drought tolerant - 1985 PV18/K68 [34] 13 K72 Drought tolerant - 1985 PV18/K68 [34] 14 K78 Drought tolerant - 1985 JANAK/K816//K65 [34] 15 WH1021 Drought tolerant Physiological - - [46] 17 PBW175 Drought tolerant Physiological - - [46] 17 PBW299 Drought tolerant Biochemical 1991 BB/KAL//WL711/ PBW65 [52] 19 HPW42 Drought tolerant Physiological 1992 'S'APVNS'/CBB/CNO'S'/3/ JAR/OR 2'S' [40] 20 HD2932 Drought	7	VL421	Drought tolerant	Physiological	1979	SON64/Y50E/GTO	[34,40]			
1980 K812'S'/KALYANSONA 34 1980 K812'S'/KALYANSONA 34 10 LOK1 Drought tolerant Physiological Biochemical 1981 S308/S331 [42,52,54] 11 AJANTA Drought tolerant - 1983 PW5/Y53 34 12 WL1562 Drought tolerant Physiological 1984 KAL/JN//UP301 [40] 13 K72 Drought tolerant - 1985 PV18/K68 [34] 14 K78 Drought tolerant - 1985 JANAK/K816//K65 [34] 15 WH1021 Drought tolerant Physiological 2008 NYOT95/SONAK [43,47] 16 V110 ** Drought tolerant Physiological [46] 17 PBW175 Drought tolerant Physiological 1988 HD2160/WG1025 [42,52,53,56] 18 PBW299 Drought tolerant Biochemical Physiological 1991 BB/KAL//WL711/ PBW65 [52] 1992 'S'/4PVN'S'//CBB/CNO'S'/3/ [40] JAR/OR 2'S' 20 HD2932 Drought tolerant Physiological 1996 KAUZ/STAR// HD2643 [36] 21 PBW396 Drought tolerant Biochemical 1996 NON'S'/3/SER182 [52] 22 HI1531 Drought tolerant - 2006 HI1182/CPAN1990 [34] 23 MP3173 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,4	8	WL711	Drought tolerant	Biochemical, Molecular	1979	S308/CHR/KAL	[52,65,80,84]			
10	9		Drought tolerant	-	1980	K812'S'/KALYANSONA	[34]			
12 WL1562 Drought tolerant Physiological 1984 KAL/JN//UP301 [40] 13 K72 Drought tolerant - 1985 PV18/K68 [34] 14 K78 Drought tolerant - 1985 JANAK/K816//K65 [34] 15 WH1021 Drought tolerant Morphological, Physiological, Physiological 2008 NYOT95/SONAK [43,47] 16 V110 ** Drought tolerant Physiological - - [46] 17 PBW175 Drought tolerant Biochemical Physiological 1988 HD2160/WG1025 [42,52,53,56] 18 PBW299 Drought tolerant Biochemical 1991 BB/KAL//WL711/ PBW65 [52] 19 HPW42 Drought tolerant Physiological 1992 'S'/4PVN'S'/CBB/CNO'S'/3/ [40] [40] 20 HD2932 Drought tolerant Physiological 2008 KAUZ/STAR// HD2643 [36] 21 PBW396 Drought tolerant Biochemical 1996 CN067/MFD// NON'S'/3/SERI82	10	LOK1	Drought tolerant		1981	S308/S331	[42,52,54]			
13 K72 Drought tolerant - 1985 PV18/K68 [34] 14 K78 Drought tolerant - 1985 JANAK/K816//K65 [34] 15 WH1021 Drought tolerant Morphological, Physiological 2008 NYOT95/SONAK [43,47] 16 V110 ** Drought tolerant Physiological - - [46] 17 PBW175 Drought tolerant Biochemical Physiological 1988 HD2160/WG1025 [42,52,53,56] 18 PBW299 Drought tolerant Biochemical 1991 BB/KAL//WL711/ PBW65 [52] 19 HPW42 Drought tolerant Physiological 1992 'S'/4PVN'S' //CBB/CNO'S'/3/ [40] 20 HD2932 Drought tolerant Physiological 2008 KAUZ/STAR// HD2643 [36] 21 PBW396 Drought tolerant Biochemical 1996 CN067/MFD// NON'S'/3/SERI82 [52] 22 HI1531 Drought tolerant - 2006 HI1182/CPAN1990 [34]	11	AJANTA	Drought tolerant	-	1983	PW5/Y53	[34]			
14 K78 Drought tolerant - 1985 JANAK/K816//K65 [34] 15 WH1021 Drought tolerant Morphological, Physiological 2008 NYOT95/SONAK [43,47] 16 V110 ** Drought tolerant Physiological - - [46] 17 PBW175 Drought tolerant Biochemical Physiological 1988 HD2160/WG1025 [42,52,53,56] 18 PBW299 Drought tolerant Biochemical 1991 BB/KAL//WL711/PBW65 [52] 19 HPW42 Drought tolerant Physiological 1992 'S'/4PVN'S'//CBB/CNO'S'/3/ [40] 20 HD2932 Drought tolerant Physiological 2008 KAUZ/STAR//HD2643 [36] 21 PBW396 Drought tolerant Biochemical 1996 CN067/MFD//NON'S'/3/SERI82 [52] 22 HI1531 Drought tolerant - 2006 HI1182/CPAN1990 [34] 23 MP3173 Drought tolerant - 2009 HI1011/WH965-1 [34]	12	WL1562	Drought tolerant	Physiological	1984	KAL/JN//UP301	[40]			
15	13	K72	Drought tolerant	-	1985	PV18/K68	[34]			
16	14	K78	Drought tolerant	-	1985	JANAK/K816//K65	[34]			
17 PBW175 Drought tolerant Biochemical Physiological 1988 HD2160/WG1025 [42,52,53,56] 18 PBW299 Drought tolerant Biochemical 1991 BB/KAL//WL711/ PBW65 [52] 19 HPW42 Drought tolerant Physiological 1992 'S'/4PVN'S'//CBB/CNO'S'/3/ [40] 20 HD2932 Drought tolerant Physiological 2008 KAUZ/STAR// HD2643 [36] 21 PBW396 Drought tolerant Biochemical 1996 CN067/MFD// NON'S'/3/SERI82 [52] 22 HI1531 Drought tolerant - 2006 HI1182/CPAN1990 [34] 23 MP3173 Drought tolerant - 2009 HI1011/WH965-1 [34] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42]	15	WH1021	Drought tolerant		2008	NYOT95/SONAK	[43,47]			
Physiological Physiologica	16	V110 **	Drought tolerant	Physiological	-	-	[46]			
PBW299 Drought tolerant Biochemical 1991 PBW65 [52]	17	PBW175	Drought tolerant		1988	HD2160/WG1025	[42,52,53,56]			
19 HPW42 Drought tolerant Physiological 1992 'S'/4PVN'S'//CBB/CNO'S'/3/ JAR/OR 2'S' [40] 20 HD2932 Drought tolerant Physiological 2008 KAUZ/STAR// HD2643 [36] 21 PBW396 Drought tolerant Biochemical 1996 CN067/MFD// NON'S'/3/SERI82 [52] 22 HI1531 Drought tolerant - 2006 HI1182/CPAN1990 [34] 23 MP3173 Drought tolerant - 2009 HI1011/WH965-1 [34] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42]	18	PBW299	Drought tolerant	Biochemical	1991		[52]			
20 HD2932 Drought tolerant Physiological 2008 HD2643 [36] 21 PBW396 Drought tolerant Biochemical 1996 CN067/MFD//NON'S'/3/SERI82 [52] 22 HI1531 Drought tolerant - 2006 HI1182/CPAN1990 [34] 23 MP3173 Drought tolerant - 2009 HI1011/WH965-1 [34] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42]	19	HPW42	Drought tolerant	Physiological	1992	'S'/4PVN'S'//CBB/CNO'S'/3	/ [40]			
21 PBW396 Drought tolerant Biochemical 1996 NON'S'/3/SERI82 [52] 22 HI1531 Drought tolerant - 2006 HI1182/CPAN1990 [34] 23 MP3173 Drought tolerant - 2009 HI1011/WH965-1 [34] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42]	20	HD2932	Drought tolerant	Physiological	2008		[36]			
23 MP3173 Drought tolerant - 2009 HI1011/WH965-1 [34] 24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. (TAUS)/FCT/3/2*WEAVER [34,42]	21	PBW396	Drought tolerant	Biochemical	1996		[52]			
24 WH1142 Drought tolerant Physiological 2015 CHEN/Ae.Sq. [34,42]	22	HI1531	Drought tolerant	-	2006	HI1182/CPAN1990	[34]			
24 WH1142 Drought tolerant Physiological 2015 (TAUS)/FCT/3/2*WEAVER	23	MP3173	Drought tolerant	-	2009	HI1011/WH965-1	[34]			
25 HD3016 ** Drought tolerant Physiological - PBW65/2-PASTOR [38]	24	WH1142	Drought tolerant	Physiological	2015		[34,42]			
	25	HD3016 **	Drought tolerant	Physiological		PBW65/2-PASTOR	[38]			

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 Table 1. Cont.

SN	Variety	Drought Responsiveness	Trait(s)	Year of Release	Pedigree	Reference			
26	HW2004	Drought tolerant	Physiological, Molecular	1997	C306*7//TR380-14 #7/3 AG14	[42,54,56,63]			
27	HD2888	Drought tolerant	Molecular	2006	C306/T. sphaerococcum//HW2004	[37]			
28	RAJ1555	Drought tolerant	Physiological and morphological	1983	COCORIT71/ RAJ911	[43,64]			
29	DBW17	Drought tolerant	Morphological Biochemical	2007	CMH79A.95/3* CNO-79//RAJ-3777	[36,43,53]			
30	PBW226	Drought tolerant	Morphological	1989	C591/RN//JN/3/ CHR/HD1941	[43]			
31	NIAW34	Drought tolerant	Physiological	1997	CNO79/PRL"S"	[42]			
32	HW1098	Drought tolerant	Physiological	2015	NP201 (Mutant developed through 20 Kr irradiation)	[42]			
33	WH1126 **	Drought tolerant	Physiological	-	WBLL1*2/VIVTSII	[42]			
34	WH1181 **	Drought tolerant	Biochemical	-	CNO79//PF70354/MUS/3/ PASTORI4IBAV92IS/FRET2/ KUKUNAJ/RET2/6/MILAN/ KAUZL/PRINIA/3/BAV92	[42]			
35	WH1182 **	Drought tolerant	Physiological	-	KLDR/PEWITI// MILAN/DUCULA	[42]			
36	RAJ3765	Drought tolerant	Physiological	1996	HD2402/VL639	[42,63]			
Category 2: Drought Sensitive Genotypes (18)									
37	PBW373	Drought sensitive	Physiological	1997	ND/VG9144//KAL/BB/ 3/YCO"S'/4/VEE#5 'S'	[38]			
38	HD2967	Drought sensitive	Physiological	2011	ALD/COC//URES/ HD2160M/HD2278	[38]			
39	HD2133 ** Drought sensitive Physic		Physiological	-	-	[46]			
40	HD2428	2428 Drought sensitive - 1989 HD1949/HD2160		[45]					
41	HD1941 (Hira)	Drought sensitive	Physiological Biochemical	1972	E5477/S64	[57]			
42	GW273	Drought sensitive	Physiological	1997	CPAN2084/VW205	[54]			
43	GW366	Drought sensitive	Physiological	2007	DL802-3/GW232	[54]			
44	GW173	moderately susceptible	Physiological	1994	TW275/7/6/1/ LOK1	[54]			
45	GW322	moderately susceptible	Physiological	2002	GW173/GW196	[54]			
46	GW496	moderately susceptible	Physiological	1990	HD2285/4/CNO /NO//CC/INIA 66/3/KAL/BB	[54]			
47	HUW468	Sensitive	Molecular	1999	CPAN1962/TONI// LIRA'S'/PRL'S'	[34]			
48	HD2189	Sensitive	-	1979	HD1963/HD1931	[63]			
49	HD2329	Drought sensitive	Biochemical, Physiological	1985	HD1962/E4870//XX 65/HD1553/UP262	[38,52,63]			

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Table 1. Cont.

SN	Variety	Drought Responsiveness	Trait(s)	Year of Release	Pedigree	Reference		
50	HUW234	Drought sensitive	Biochemical Physiological	1985	HUW12*2/CPAN1666//HUW1	2 [34,52]		
51	HD2877	Drought sensitive	Molecular	=	CDWR9549/HD2347//HD2402	[37,63]		
52	HD2012 **	Drought sensitive	Molecular	-	S307XNP875/ HD1592	[37,63]		
53	HD2851	Drought sensitive	Molecular	2005	CPAN3004/WR426//HW2007	[37]		
54	MACS2496	Drought sensitive	Molecular	1991	VEERY #5 or SERI"S"	[37]		
Category 3: Mixed Reaction Genotypes (2)								
55	PBW343	Drought toler- ant/Drought sensitive	Biochemical Physiological	1995	ND/VG9144//KAL/BB/3/ YACO'S'/4/VEE#5'S'	[38,39,42,52,53, 63]		
56	HD2733	Mixed reaction	Physiological	2001	Attila/3/Tui/Carc// Chen/CHTO/4/Attila	[38,47]		
Category 4: Needs further investigation (3)								
57	PBW644	-	Physiological	2012	PBW175/HD2643	[42]		
58	UP2425	-	Physiological	1999	HD2320/UP2263	[42]		
59	NW1014	-	Physiological	1998	CEB148/KA/7/HK/38MA/4/ 4777//REI/Y/3/KT/5/YR/6/ TUC	[42]		

^{**} Indicates that the enlisted genotype is not a released variety.

3.2. Global Genotypes

Drought is a serious threat to both irrigated and rainfed agriculture systems around the world. Reduced rainfall and enhanced evapo-transpiration are expected to intensify drought situations, in many locations in the twenty-first century. However, a diverse pattern was noted at the global level, with agriculture being the most severely affected sector among the several sectors [85]. In order to develop drought-tolerant wheat genotypes, researchers have conducted experiments all over the world. An experiment was conducted with 34 diverse wheat genotypes (including local and commercial cultivars, landraces, and genotypes), under three different irrigation regimes (100%, 75%, and 50% Field capacity) [86]. Based on the high Yield Index (YI), RWC, SOD, and low DSI, genotypes 30ESWYT200, 30ESWYT173 and Akbari were identified to be tolerant genotypes. In another study, 25 wheat genotypes, including cultivars and advanced lines, were screened for drought tolerance in a split-plot design, with three replications under control and drought treatment. Wheat genotypes BARI Gom-24 and SATYN-9 were found to be highly drought tolerant on the basis of DSI [87]. During field research on 50 local wheat genotypes/lines, some drought-related indices and yield features were recorded [88]. Based on high Mean Productivity (MP), Geometric Mean Productivity (GMP), Tolerant Index (TOL), and Stress Susceptibility Index (SSI) values, GA-02, Sehar-06, Faisalabad-83, 9444, Kohistan-97, and Pirsabak-04 were found to be drought tolerant, whereas genotypes Chenab-00, Parwaz-94, Kohsar-95, and Kohenoor-83 were found to be drought sensitive. In a similar kind of study, an Iranian wheat cultivar, Azar 2, was found to have the highest grain yield under stress and non-stress conditions [89]. Mohammed et al. [90] found MP, GMP, and STI to be more effective in the identification of high-yield genotypes in drought-stressed, as well as normal irrigated, field conditions. Principal Component Analysis (PCA) findings suggested G1 and G10 as tolerant and G25 and G26 as sensitive genotypes, in drought stress conditions. Haque et al. [91] tested ten wheat genotypes, under 100% and 30% of field capacity, and two wheat genotypes, Sourav and Sonalika, were highlighted as tolerant, while Durum

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and Pavon-76 were categorized as intermediate for drought stress tolerance, based on the results of morphological studies and drought-linked marker data. In a greenhouse study, Kanbar et al. [92] evaluated nine winter wheat genotypes for some field and morphological traits (plant height, heading time, biomass, seeds/plant, yield/plant, harvest index, root length, and root dry mass) and found Plainsman V and GK Berény as tolerant under a water-deficient condition. Fifty-two bread wheat genotypes were selected based on the prior studies and evaluated at five locations, using phenotype traits and 20 SSR markers, to find divergent and complementary parents for drought stress tolerance breeding. Based on the phenotypic data, SSR analysis, and cluster analysis, three genotypes (10 (ETW17-295), 37 (ETW17-385), and 38 (ETW17-386)) were identified as the most divergent and were recommended for drought-tolerance breeding by Belete et al. [93]. In a glasshouse experiment, Ali et al. [94] compared different physiological and biochemical traits associated with drought adaptation in twelve wheat genotypes. The least reduction in dry weight, RWC and leaf area, as well as the lowest increase in H_2O_2 , was observed in Pirsabak-2004. Pirsabak-2004 was also found to be the most drought-tolerant genotype based on the drought tolerance index.

In another drought study, two wheat genotypes (Luhan7 and Yangmai16) were studied under intermittent water deficit conditions and recovery responses were recorded, based on the agronomic, physiological, and biochemical traits, by Abid et al. [95]. Yield decline was insignificant in drought-tolerant cultivars due to higher photosynthetic rates during water stress and swift recovery after re-watering. These findings suggest that the ability of a plant to maintain functions under drought and recover fast after re-watering during vegetative stages is critical in determining the final productivity. Drought stress was enforced by restricting irrigation during the grain-filling period, in a pot experiment conducted with eight wheat cultivars, to study the contribution of reserves in culm and sheath to yield under drought. Based on the changes in dry weights of leaves, culm with sheath, spikes, grains, and contribution of culm water-soluble carbohydrates (WSCs) to grain yield, BARI Gom 24 was demarcated as drought tolerant, while Kanchan as drought sensitive. BARI Gom 24 showed higher drought tolerance and revealed potential to grow under water deficit conditions, in comparison to other cultivars [96].

In a laboratory experiment, one-hundred wheat genotypes were tested under different osmotic stress conditions (PEG treatment) to find drought-tolerant genotypes at the early seedling stage. Based on the rate of germination (%), final germination (%), root and shoot dry weight and vigor index, BD-480, BD-498, BD-501, BD-513, BD-514, BD-519, BD-592, BD-618, and BD-633 were declared as drought tolerant. To study the impact of water deficit on Wafaq-2001 and Chakwal-50, another experiment was carried out under different osmotic stress levels (by PEG). Based on the recorded traits, such as germination, mean germination time, seedling length, chlorophyll contents, leaf membrane stability, relative water content, gas exchange measurements, and yield attributes, Chakwal-50 was found to be more drought tolerant. However, Wafaq-2001 showed a significant reduction in all physiological, biochemical, and other recorded parameters. Metabolites produced by wheat seedlings, in response to drought stress, were investigated to determine the tolerance mechanism from the cross of HX10 x YN211 with ultra-performance liquid chromatographymass spectrometry [97]. It was observed that HX10 exhibited higher growth indices than YN211 due to the accumulation of phenolic compounds, amino acids, alkaloids, organic acids, flavonoids, and thymine. Drought tolerant, as well as susceptible wheat genotypes identified at the global level, have been listed in Table 2.

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Table 2. Trait-Based Classification of Global Wheat Genotypes for Drought Responsiveness.

SN	Variety/Genotype	Drought Responsiveness	Trait(s)	Source	Reference
1	ETW17-295	Drought tolerant	Morpho-physiological, Molecular	CIMMYT-MEXICO	[93]
2	ETW17-385	Drought tolerant	Morpho-physiological, Molecular	CIMMYT-MEXICO	[93]
3	ETW17-386	Drought tolerant	Morpho-physiological, Molecular	CIMMYT-MEXICO	[93]
4	Hanxuan10	Drought tolerant	Physiological, Metabolomics	China	[97]
5	BARI Gom 24	Drought tolerant	Morpho-physiological, Molecular	Bangladesh	[87,96]
6	Akbari	Drought tolerant	Physiological Biochemical	Iran	[86]
7	30ESWYT173	Drought tolerant	Physiological	CIMMYT-MEXICO	[86]
8	30ESWYT200	Drought tolerant	Biochemical	CIMMYT-MEXICO	[86]
9	Maxi-Pak	Drought tolerant	Physiological	Pakistan	[98]
10	SATYN-9	Drought tolerant	Physiological	Bangladesh	[87]
11	Luhan7	Drought tolerant	Physiological, biochemical	China	[95]
12	Pirsabak-2004	Drought tolerant	Physiological, biochemical	Pakistan	[94]
13	GA-02	Drought tolerant	Grain yield, drought tolerance indices	Pakistan	[88]
14	Faisalabad-83	Drought tolerant	Grain yield, drought tolerance indices	Pakistan	[88]
15	Sehar-06	Drought tolerant	Grain yield, drought tolerance indices	Pakistan	[88]
16	Pirsabak-04	Drought tolerant	Grain yield, drought tolerance indices	Pakistan	[88]
17	Kohistan-97	Drought tolerant	Grain yield, drought tolerance indices	Pakistan	[88]
18	Azar 2	Drought tolerant	Grain Yield, drought tolerance indices	Iran	[89]
19	G1	Drought tolerant	Grain yield, drought tolerance indices	Iraq	[90]
20	G10	Drought tolerant	Grain yield, drought tolerance indices	CIMMITY-MEXICO	[90]
21	BD-480	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
22	BD-498	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
23	BD-501	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
24	BD-513	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
25	BD-514	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
26	BD-519	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
27	BD-592	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
28	BD-618	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
29	BD- 633	Drought tolerant	Physiological, Biochemical	Bangladesh	[99]
30	Sourav	Drought tolerant	Molecular, morphological	Bangladesh	[91]
31	Sonalika	Drought tolerant	Molecular, morphological	Bangladesh	[91]
32	Durum	Drought tolerant	Molecular, morphological	Bangladesh	[91]
33	Pavon-76	Drought tolerant	Molecular, morphological	Bangladesh	[91]
34	Plainsman V	Drought tolerant	Agro-morphological	Kansas, USA	[92]
35	GK Berény	Drought tolerant	Agro-morphological	Hungary	[92]
36	Yunong211	Drought Sensitive	Physiological, Metabolomics	China	[97]
37	KC161	Drought Sensitive	Physiological	Iran	[86]
38	30ESWYT120	Drought Sensitive	Biochemical	CIMMYT-MEXICO	[86]
39	Shiraz	Drought Sensitive	Physiological	Iran	[86]
40	Chenab-00	Drought Sensitive	Grain yield, drought tolerance indices	Pakistan	[88]

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SN	Variety/Genotype Drought Responsiveness		Trait(s)	Source	Reference
41	Kohsar-95,	Drought Sensitive	Grain yield, drought tolerance indices	Pakistan	[88]
42	Parwaz-94	Drought Sensitive	Grain yield, drought tolerance indices	Pakistan	[88]
43	Kohenoor-83	Drought Sensitive	Grain yield, drought tolerance indices	Pakistan	[88]
44	G25	Drought Sensitive	Grain yield, drought tolerance indices	CIMMITY-MEXICO	[90]
45	G26	Drought Sensitive	Grain yield, drought tolerance indices	CIMMITY-MEXICO	[90]
46	Yangmai16	Drought Sensitive	Physiological biochemical	China	[95]

4. Conclusions

To mitigate the adverse effects arising due to the current situation of incessant declining resources and receding underground water, the most imperative task is to develop varieties with high-yield potential, under low water conditions. Most of the key traits and genotypes studied for drought tolerance have been illustrated in the review and the practical use of the given information can lead to the significant improvement in wheat adaptability and resistibility in the future. This review depicts that many genotypes were tested for drought stress tolerance, both under lab and field conditions, and selected for particular traits with the hidden potential, and should be used in wheat improvement programs, indisputably. Some stable genotypes for drought response are highlighted in Figure 1, which can confidently be used in research programs. At the global level, also, many potential genotypes for drought tolerance were reported, which can be utilized in establishing tolerance into the wheat-breeding programs under the changing climate scenario. Most drought-related studies are reported to be based on drought tolerance indices, metabolomics, and SSR marker-based screening at the international level. Identifying and labeling a genotype as tolerant or susceptible is highly dependent on the cultivation environment. Designing a universal drought-tolerant genotype is a hypothetical concept, as the interaction of GXE is ever-changing and highly unpredictable. Still, however, the current review provides a reliable platform for the selection of stable and widely adapted wheat genotypes for drought-related wheat improvement programs.

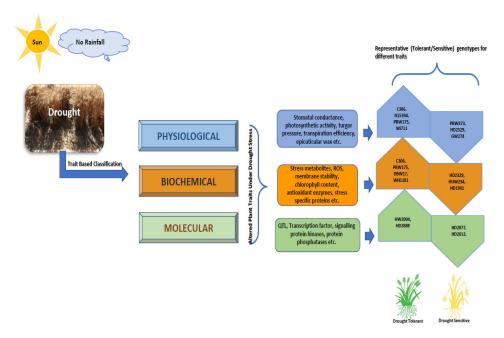


Figure 1. Schematic representation of selected stable Indian wheat genotypes for drought response.

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