Wheat Water Ecophysiology: A Review on Recent Developments

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Abstract: With exceptional tolerance to a wide range of climatic circumstances, from temperate to desert, and from warm to cold regions; wheat (Triticum aestivum L.) is an important food crop on a worldwide scale. This flexibility is linked to the crop's highly flexible DNA (Deoxyribonucleic acid), which is complicated in nature. The impacts of climate change and other stresses on wheat ecophysiology and productivity remain topics of concern despite our very thorough knowledge of wheat physiology, growth, and development. This study emphasizes the implementation of new information in breeding and crop management techniques while concentrating especially on the ecophysiology of water usage in wheat plants. The focus is on comprehending physiological processes at the level of the whole plant and organ, giving breeders and agronomist insightful information. Where necessary to explain physiological responses seen at higher organizational levels, cellular-level explanations are presented. Various topics, including wheat physiology, ecological interactions, and yield determination, are covered in this review that emphasizes recent developments in our knowledge of yield production. The knowledge gathered from this study may be used to help build crop production systems that maximize yield potential. Additionally, this study offers physiological and ecological methods for creating wheat production systems that are high-yielding, resource-efficient, and quality-focused. Although there is a wealth of information on wheat physiology that directly aids agronomists and breeders, more research is needed to fully grasp yield under stress. However, using already available physiological information provides encouraging potential for further development. The review prioritizes yield and yield-forming processes because they have the biggest potential impact on global wheat production, even though other factors like lodging resistance, growth regulator application, weed competition, soil mechanical impedance, and nutrient imbalances are not covered.

Keywords: Crop growth, Drought, Physio biochemical traits, Wheat, Yield.

INTRODUCTION

As one of the main staple food crops, wheat plays a key role in feeding the world's population. It is grown on around 220 million hectares of land and is the secondmost significant cereal crop in the world. Wheat is essential for supplying the present food demand, with a remarkable 716 million tons of cereal grain produced each year and an average yield of 3.2 tons per hectare [1]. But when we move into the future, it becomes clear that we must boost wheat output much more in order to reach the goal of 858 million tons by 2050, given the expanding world population [2]. In order to meet this objective and feed the world's growing population, an annual rise of around 1.5% over the next three decades should be considered. Additionally, it is important to keep in mind that 37% of wheat cultivation is done under rainfed circumstances, leaving it vulnerable to the ongoing drought limitation that severely reduces wheat output [3-5]. Drought stress effect on plant growth and reduces leaf area, decrease

These effects impact on plant yield, growth and physiology. So in present study, to best of our understanding, we have provided the detailed information about effects of water deficit conditions on wheat plant, its ecophysiology, yield and different wheat penal. This study will provide comprehensive knowledge in selecting drought tolerant wheat genotype by identifying the biochemical physiological traits involved in drought tolerance mechanisms. WHEAT PHYSIOLOGY

> Abiotic stress is the term used to describe environmental factors or their mixtures that have a detrimental effect on a plant's ability to grow, develop, and reproduce [6]. In the past, relieving environmental stress via practices like irrigation, soil management, and fertilizer usage has been the main strategy for doing so. Although these approaches have economic and ecological drawbacks, there is considerable

> reserves mobilization, kernel abortion and further

decline amyloplasts numbers in grain. In response to

drying conditions various processes are stimulated in

wheat plants such as reduction in photosynthetic rate,

closure of stomata and incline in leaf temperature.

and

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interest in studying plant genetic tolerance to environmental pressures. Abiotic environmental conditions in the United States are responsible for 71% of the potential yield decrease in annual crops [7]. Wheat yields are notably impacted by a number of conditions, such as soil salinity, poor soil fertility (especially nitrogen deficiency), heat, drought, and cold temperatures. Significant effects on wheat development, growth, and yield result from these conditions.

Water stress is a common occurrence in nature and results from a crop's inability to absorb enough water to keep up with air evaporation. Water stress is primarily caused by two processes: (i) crop water uptake, which is influenced by root traits and soil physical characteristics, and (ii) crop evapotranspiration, which is influenced by atmospheric factors like net radiation and vapor pressure deficit (VPD), as well as crop traits like ground cover and stomatal conductance. Wheat may undergo water stress in every area, regardless of the differences in the surrounding circumstances [3]. Crop evapotranspiration (ET), in particular crop transpiration, has a positive linear association with grain production in C3 and C4 plants. Consequently, a reduction in yield is a natural consequence of water stress [4].

EMERGENCE TO DOUBLE RIDGE

In both bread and durum wheat, water stress during the first growth stage (GS1) has been shown to extend the phyllochron, or the delay between the appearance of succeeding leaves [8, 9]. Different abiotic stresses influence leaf growth, its turgor and water potential and leaf elongation. Leaf growth measurement is considered as important indicator to show drought stress conditions. Drought stress reduce leaf growth rate in wheat which involve in reduction in leaf sheath and lamina elongation. This subsequently leads to decline in total cumulative plant leaf growth as well the reduction in water potential threshold. It is crucial to remember that leaf expansion is especially susceptible to water stress, and under extreme circumstances, leaf development may be severely slowed down when leaf water potentials reach values between -0.7 and -1.2 MPa [10]. Furthermore, tillering is significantly impacted by water stress, with dry circumstances possibly resulting in a roughly 50% decrease in tiller development. As a result, the most adversely impacted physiological process at this stage is the development of the leaf area index. A reduction in the quantity of spikelet primordia at this crucial time may also be

caused by a water shortage that occurs shortly before the start of blooming [11].

DOUBLE RIDGE TO ANTHESIS

After anthesis (GS2), wheat plants continue to develop for around ten days, including their roots, leaves, stems, and ears. This is a phase of rapid plant growth. A decline in cell development and leaf area during this phase may lower photosynthesis per unit area by reducing the amount of water available to the plant. Net photosynthesis reduces as a result of stomata that are partially closed when the water shortage becomes worse. When leaf water potentials drop below -1.5 MPa, wheat stomata start to shut [12, 13]. Reduced leaf internal CO₂ (Ci) levels impede electron transport, which might harm the system and produce photo-inhibition [14]. Photo-inhibition is a condition brought on by excessive light-harvesting system excitation without enough electron transport. Therefore, keeping the plant's water levels sufficient and its stomata open is essential for maintaining high CO₂ conductance, which enables the continuation of photosynthetic dark reactions and correct electron transport, as well as for cooling. Measurements of chlorophyll fluorescence, which reveal excessive light harvesting beyond the capability of dark responses, are often used to identify the impacts of stress on crops [15].

Grain number is significantly impacted by water stress during the spike growth stage, with a severe decrease being seen. Ten days before to spike emergence is when water stress results in the greatest yield loss. Water stress at this time also reduces the number of viable tiller, spikelets per spike [16, 17] and may kill the distal and basal florets in the spikes. At this developmental stage, carbon and nitrogen availability are crucial for spike growth, and both are decreased in the presence of water stress.

ANTHESIS TO MATURITY

Wheat plants may grow more quickly if there is a water shortage just before anthesis (the blooming stage) [18]. As a result, there is less soluble carbohydrate buildup in the stem between anthesis and the linear phase of grain development [18]. Reduced photosynthesis caused by water stress highlights the need of remobilizing pre-anthesis assimilates to the growing grain. Total non-structural carbohydrates, especially fructans and sucrose, which are obtained from wheat leaves and stems, are essential for promoting grain development [19].

Water stress does not affect the quantity of fertile tillers or the number of kernels per ear (KNO) during the grain-filling stage, but it does cause a decrease in grain weight. This decrease is a result of increased senescence, which shortens the grain-filling time [20]. Senescence is caused by high temperatures and terminal dryness. Barley and tall bread wheats, compared to semi-dwarf wheats, consistently show superior drought resilience, whereas durum wheats are the most sensitive [21, 22].

WATER DEFICIT AND GRAIN YIELD

The yield of a dryland crop can be calculated by multiplying transpiration (T), transpiration efficiency (TE), and harvest index (HI), represented as:

where GY refers to grain yield [23].

It has been frequently utilized to pinpoint features that improve grain production in winter cereals under drought stress, according to Equation 7 which expresses this connection [24]. It has been shown that genotypes that can maintain their stomata open under water stress produce more under these circumstances [25].

Measurements of gas exchange provide light on TE variation. However, their use in crop development programs has been constrained by the difficulty of integrating instantaneous gas exchange observations across time and place [26]. It is possible to estimate TE at the plant level using carbon isotopic discrimination. Wheat TE and grain yield are negatively and linearly linked to the degree of selectivity against the heavier carbon isotope (13C) in the photosynthetic process, respectively [27, 28, 29]. Thus, 13C discrimination may be used in genetic improvement programs for areas with less rainfall as an indirect metric of TE [30]. Wheat has genetic diversity in 13C discrimination, making it possible to identify high-yielding lines with better TE. It is crucial to remember that vapor pressure deficit (VPD) has a significant impact on TE, thus any comparisons should be made on a VPD basis.

When there is regular rainfall in agricultural regions, there may be significant soil water evaporation from the soil surface, particularly if the crop cover is insufficient and leaves some of the soil exposed to sunlight. The majority of the overall evapotranspiration (ET) is often accounted for by the evaporation of soil water. Therefore, by increasing water-use efficiency via proper crop management strategies, grain yield of dryland crops may be significantly increased [31, 32]. The quantity of water lost during grain filling and the current TE are used to calculate the harvest index in dry settings. The attainable yield is generally in the range of 10 to 15 percent of the biomass present at anthesis if there is no water available for transpiration after anthesis.

DROUGHT RESISTANCE

Grain yield under drought circumstances is a popular basis for evaluating wheat's drought tolerance. But in addition to its intrinsic yield potential, the genotype's phenology also affects the grain production of wheat during droughts [33]. Utilizing yield stability indices for various conditions and drought susceptibility indices have both been used to quantify drought resistance [34]. These indices are essential for assessing how well wheat genotypes perform and react to drought stress. The apparent characters like morphology and physiology that depicts the drought resistance can possibly be categorized based on how they relate to the crop's water uptake or loss. Root development, osmotic adjustment, associated solutes, membrane stability are morphological and physiological characteristics associated with an increase in water absorption [35]. Leaf color [36], leaf movements, trichomes on the leaf surface, stomatal behavior and epicuticular wax [37], transpirational efficiency, and air to canopy temperature differentials [38, 39] are the traits of morphology and physiology linked to minimize the efficiency of transpiration [38, 39].

Mainly production of wheat is affected by many different biotic and abiotic stresses. Water stress is the abiotic stress, which affects the vegetative growth and in turns affects the wheat crop yield (Figure 1) [40]. Drought stress accounts as the heavily pronounced aspect for the best yield of crops which affects the stability of crop production throughout the world [40]. Furthermore, the intervals of erratic rainfall in rainfed areas is also the key factor which results in limiting productivity of crops in semiarid regions. In conclusion, due to the scarcity of rainfall that fails to expedite the requirements of water for the crops life cycle in specific regions usually results in the total failure of crop growth. Ground water usage for crops is a common practice, but this ground water is becoming unavailable for crops because of its in-judicious use, which results in lamentable effects on the ground water table [41]. Consequently, techniques and strategies including water conservation measures should be adopted to



Figure 1: Diagrammatic sketch of drought stress on growth, physiological processes, and overall yield. Here ROS is abbreviation of Reactive oxygen species.

encounter this critical condition, and to solve the problem of conservation of rainfall water to keep in rhizospheric zone that can possibly help in the production of crops ultimately [42, 43].

It has been evaluated, while comparing near isogenic lines the durum and bread wheat segregating lines depicted a high capability of osmotic adjustment that exhibited a yield uplift (11 to 17 % as in case of bread wheat and 7 % in durum wheat) without this characteristic [44]. Higher temperatures adversely limit the yield of wheat accelerating the development of plants more specifically the floral organs, photosynthetic functionality and formation of fruits. Despite the fact that there is a basic correlation amid stress of water and heat in plants, the focus shall be put on one of them specifically, heat stress and it will be assumed that wheat crops do not experience the water constraints. However, it is typically necessary to combine tolerance to these two stressors for the purpose of breeding.

The main mechanism for energy desolation is transpiration, a method of heat avoidance. An effective heat avoider may be a crop that sustains transpirational chilling, which indicates that in the fields the plant organs temperature should be several degrees different than the ambient temperature. With a higher transpiration rate, this discrepancy widens. The leaf to air temperature differences for wheat that does not have a water scarcity in the soil rises linearly with the differences in vapor pressure [45]. The temperature of the leaf may increase above the ambient temperature if there is a water scarcity and the stomata start to shut down. In cool-grown wheat leaves, photosynthesis is severely impacted as soon as the temperature rises over 25°C; however, leaves that have been used to high temperatures begin to exhibit a comparable reduction as soon as the temperature goes above 35°C. Leaf photosynthesis may be reduced by 50% at 45°C. Wheat grain production and total above-ground biomass are both decreased by heat stress. The earlier-mentioned growth phases (Figure 1) will be applied in order to analyze the impacts of heat stress. Each of these stages is impacted differently by temperature [46, 47]. Wheat grain yield is most susceptible to temperature at the GS2 stage, which is when KNO is calculated.

SEED GERMINATION TO PLANT EMERGENCE

At higher temperatures of soil, the fatality of seedlings from seeding stage to crop onset and

consequently its formulation, this is usually a major concern. Plant sprouting and their population establishment accounts for the initiation of crop growth. However, in hot conditions, it is found that when surface of soil is exposed and barren, it suffers strong radiation intensity, the highest possible soil temperature in the primary layer of soil may surpass the air temperature range of about 10° to 15°C. Highest temperature of soil may possibly reach up to 40 to 45 °C in such circumstances, seriously affecting the seedling formulations. The original plant population might drop to the lowest of 100 plants/m threshold, which is thought to be detrimental to crop yield. For wheat to germinate, the grain must have 35 to 45 percent of its weight in water [48]. Germination can take place anywhere from 4° to 37°C, with 12° to 25°C being ideal while seed size has an impact on yield, growth, and development. In comparison with the smaller seeds, big seeds have a variety of benefits, including quicker seedling development, more fertile tillers on each plant, and better yield of grains [49]. Production of crops under stressful conditions of environment, notably under drought stress the benefit of larger seeds is considerably evident [50].

The seed embryo contains three to four leaf primordia and about half of them have already begun when crop emergence starts to happens [51-53]. The coleoptile that guards the formulation of the first crop leaf, grows after seminal roots during course of germination. The length of coleoptile, which varies with genotype and only modestly elongates when seeds are placed deeper, regulates the sowing depth [54]. Tall wheat plants have longer coleoptiles than semi-dwarf wheat. The main shoot leaves' axils are where the wheat tillers emerge. The corresponding tillers counts depends upon the particular genotype, specifically in flowering forms, winter varieties have a comparatively huge count. The majority of semi dwarf wheat cultivars have several tillers. Tiller appearance and bud differentiation into tillers often come to an end right before stem elongation begins [52]. Other research, however, suggests that tillering is influenced by a variety of genetic and environmental variables rather than coming to an end at any one stage of wheat growth [55].

WHEAT DEVELOPMENT

Differentiation of organ occurs at different stages during development of wheat. The stages which are most evident physiologically including germination, formulation, tillerring, floral initiation or double ridge, terminal spikelet, boot, spike emergence, first node or beginning of stem elongation, anthesis and maturity are critical to illustrate. Germination to emergence (E), growth stage 1 (GS1) from emergence to double ridge, growth stage 2 (GS2) from double ridge to anthesis, and growth stage 3 (GS3), which also includes the grain filling phase, from anthesis to maturity. Typically, the flag leaf and spikes become yellow at the point of physiological maturity [56]. Each development phase's duration is largely influenced by the genotype, ambient temperature, day length, and sowing date. The development stages of wheat may be shortened by many environmental conditions, most notably heat but also water and salinity.

BIOCHEMICALS, MORPHO-PHYSIOLOGICAL AND WHEAT YIELD CHARACTERISTICS IN RESPONSE TO DRYING ENVIRONMENT

The most restraining factors in crop growth is the availability of water which acutely affect the morphological traits and physiology of crops, transform the biochemical characteristics of shoots, grains and final yield of crops [57]. The efficient management for the use of water resources for the crops is currently required urgently. Water deficiency for crops badly biochemical characteristics, affects physiological processes and vegetative growth of shoots, grains and overall biomass [58] (Figure 2). Furthermore, depletion of water overall also affects the transpiration rate, photosynthesis. osmotic potential. stomatal conductance, relative water contents of crops [59]. While dynamics of proteins and carbohydrates, amylopectin and amylose constituents, photochemical efficiency, rubisco efficiency, abscisic acid generation, reactive oxygen species. proline accumulation. antioxidants defense system, generation of polyamines. Increasing oxidative enzymes are all affected greatly by the drought stress [60].

WHEAT MORPHOLOGICAL CHARACTERISTICS IN RESPONSE TO WATER DEFICIT

A very strong association between WUE and drought have been commonly observed in agricultural systems as in crop husbandry [60]. Many different protocols and practices to enhance WUE are considered valuable to manage the expense of overall production for many crops, mainly cereals which in turns helps in conservation of water and N inputs individually. The morphological traits of wheat crop specifically the leaf characteristics *i.e.* leaf area, size,



Figure 2: Morpho-physiological and biochemical patterns of plants influenced by water stress.

shape, leaf hairs, expansion and waxiness, leaf senescence, its pubescence and cuticle resilience of wheat crop is largely altered due to limited water conditions [61, 62].

Correspondingly, root traits *i.e.* density, dry weight and length of roots are severely altered due to limiting soil moisture condition in rhizosphere [63]. Plants adopted to improved strategies which includes modification of their life cycles as a result of abiotic stress (i.e. water deficit) early maturation, small plant size and reduced area of leaf for tolerance of drought stress [64]. It is noticed that length of leaf is increased while no apparent change was found in leaf width under limited water condition [65]. Therefore, leaf expansion occurs due to evacuated water from the rhizosphere by roots while having possible plentitude in the tissues of plants [66]. Subsequently, under limited water conditions lower number of leaves, size and its vitality to be observed and possibly even their unavailability [67]. The development of leaf growth in wheat crops greatly affected by the decrease in overall soil moisture which in turns decrease the overall plant biomass. Improved morphological traits could possibly be attained having low overall production cost under co-limitation of water in soil. Hence, Water use efficiency (WUE) in wheat crops can be improved using photosynthesis, mesophyll conductance and stomatal conductance which ultimately results in increasing uptake of N and overall nitrogen use efficiency (NUE) [68].

WHEAT BIOCHEMICAL ATTRIBUTES UNDER WATER STRESS

The accumulation of metabolites can help plants to withstand under limited water conditions [69]. These metabolites can play crucial roles in regulating plant growth under stressful environments [70-71]. Under drought stress, proline is accumulated in a large amount under dehydration [72]. The antioxidation enzymes can scavenge ROS production via, several osmo-protection processes. In which includes membrane stability, osmotic adjustment and gene signaling [72]. Drought stress tolerance in wheat is strongly dependent on sufficient amount of proline [73]. The genotypes planted in rainfed regions comprised more proline content over irrigated cultivars [74]. In plants, different physiological pathways take place to cope with the drought stress. Under water stress, plant growth is arrested and stomatal closure are regulated, guard cell ion translocation alters via, translocation of ABA from roots to shoots [75]. In wheat crops less ABA content in shoots are highly susceptible to drought stress compared to more ABA ones [76]. Similarly, high proline content in wheats cultivars shows better water use efficiency. Water deficit conditions limits indole acetic acid (IAA) contents in wheat [77]. The POD, H_2O_2 , glutathionse (GSH), proline, and malondialdehyde (MDA) contents increases with drought stress [78].

YIELD AND YIELD CONTRIBUTORS

Yield contributors are linked crop productivity. In water limited regions, these traits are complex and polygenic [79]. Drought stress highly influence yield and yield traits of wheat over well water environment [80]. In water stress conditions, wheat with thousand kernel weight was lowered by 16% which led to overall yield loss [81]. Wheat grains are the most important yield contributor suppressed by water stress [82]. All yield traits were strongly influenced by water stress, while the influence was more prominent for grain weight and grain number [83].

Water stress can severely affect grain size and number which reveals high plasticity over other counterparts [79]. A low plasticity of grain size in water deficits environments leading to a better transport for pre anthesis assimilation to sink [84]. Water stress negatively affect crop plant reproduction stages. Cereal crops shows several adaptive mechanisms to cope water deficit conditions by activating antioxidants defense system [85]. The efficient use of limited water and N are key options for wheat yield [86].

Photosynthesis is the prerequisite for crop production [87]. Water use efficiency can assess yield formation and is considered a key factor in yield determination [88]. Water application in crop management strongly affect WUE. This can provide information to researchers to choose best crop management options towards improved water use efficiency [89]. Limited irrigation and fertilization during growth can increase WUE and wheat yield [90].

APPROACHES TO IMPROVE WUE

Agronomic Perspectives

Agronomic practices *i.e.*, tillage practices, drought resistant and adaptive cultivars, soil fertility and pest

management can improve WUE [91]. The crop yield increases under no till system by affecting soil moisture availability [59]. Optimum sowing window, row spacing and seed rate can boost wheat crop WUE and production [92]. Decreasing row spacing and increasing plant size can improve soil moisture content and consequently increase WUE [93]. Optimum row spacing benefits the crop to efficiently uptake nutrients and water [94]. Sustainable agriculture is one of the critical topic needs to be addressed today. Application of straw mulching and decline in tillage are the important measures that are being adopted and utilized in various arid and semi-arid areas [95]. Mulching and tillage both effect crop productivity by impacting the soil environment of plant. Along with mulching, intercropping technique is also being utilized in the field to enhance soil organic matter, maintain soil moisture content and reduce water loss. These mulching techniques are playing important role in increasing crop production and yield by improving the soil water storage and prominently enhancing the water use efficiency [96].

Drought resistant varieties can result in high WUE over susceptible cultivars [97]. The laser leveling is an effective option in terms of germination, irrigation time saving, pest control and cost effective [30]. The application of silicon, selenium, potassium, and hydrogel increases WUE in wheat under water stress. This also can enhance bioavailability of nutrients, photosynthetic efficiency and better light harvesting [30].

PHYSIOLOGICAL AND ANATOMICAL PERSPEC-TIVE

Stomatal Physiology and Biochemistry Dynamics

High stomatal conductance requires high water fixation per unit leaf area to enhance soil and water use





during transpiration [98]. To boost WUE, during peak growth under high transpiration may high by blocking water loss from leaves by prevention via sensitivity of stomata. Through transpiration which facilitates CO₂ uptake [99]. Thus stomata play a key role for boosting WUE and controls water loss [100]. Stomata opening and closing is regulated by the environmental conditions [101]. Stomatal moment is controlled by transport and osmotically active solute content as well guard cells [102]. Generally, plant leaves, stomata are separated by an epidermal cell creating space for opening and closing [103]. In certain plants, the clustering of stomata is considered an efficient option to lower water loss under drought stress [104].

Crop Environment, Root Architecture and Harvest Index Enhancement

Growing crops under environments with less transpiration can result in higher WUE. Identification and allocation of such areas with less transpiration are identified by spatial and temporal scale [105]. Improvements in harvest index improves WUE which offers a new research window to enhance WUE under drought [106]. Water stress can suppress harvest index during reproductive stage of wheat, hence certain strategies need to be used for water conservation particularly in reproductive stages [107]. Similarly, root architectures are the key to uptake soil moisture [108]. Root density, root angle, root hairs, root type and root length can uptake water from various soil depths [109]. In wheat stele and xylem number are important factors under water stress due to xylem developmental plasticity [110]. In wheat, the metaxylem diameter and density can enhance WUE.

High soil moisture content can improve physiological processes and thus increase wheat production [109]. Severe drought spells due to climate change can negatively affect agriculture system, and aquatic water bodies' ecosystem [111]. Climate drought cross talk exposes the crops to reduce crop growth and yield [112]. Erratic rainfall, temperature events are caused by climate change which affects farmer's decisions for cultivar selection and crop management [113].

CONCLUSIONS

Wheat is staple food crop for 35% global population. Studying wheat physiology is important for wheat production to tackle abiotic stresses. Drought stress is the key factor that limits wheat yield in dryland agroecosystem. It is crucial to understand how drought affects eco-physiological pathways and biochemical traits of wheat, and its adaptive mechanisms under stress. The present study reveals impacts of water deficit environment on wheat (Triticum aestivum L.) ecophysiology and yield, and adaptive mechanisms Drought under stress. stress affects wheat morphological, physiological, biochemical, qualitative changes and yield traits and consequently water use efficiency. For increasing wheat yield, yield traits are very important component and incline in grain yield under drought conditions can be obtained by manipulating different yield traits. Wheat plant cope with drying conditions by storing leaf area and plant biomass. Moreover, plants accumulate different compatible solutes like sugar, protein and proline in response to osmotic stress. So present study highlighted the plant adaptation strategies by reducing oxidative damage at cell level, and manipulating the yield trait at crop production level. In conclusion, this review provided the detail mechanisms of wheat ecophysiology under drying conditions and the recent developments in this era however more research can be done to select plant markers and wheat genotypes that are more drought tolerant.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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REFERENCES

- Cakmak I, Kutman UÁ. Agronomic biofortification of cereals with zinc: a review. European Journal of Soil Science, 2018; 69, 172-80. https://doi.org/10.1111/ejss.12437
- [2] Stevenson JR, Villoria N, Byerlee D, Kelley T, Maredia M. Green Revolution research saved an estimated 18 to 27 million hectares from being brought into agricultural production. Proceedings of the National Academy of Sciences of the United States of America, 2013; 110(21), 8363-8368.

https://doi.org/10.1073/pnas.1208065110

- [3] Sedri MH, Amini A, Golchin A. Evaluation of nitrogen effects on yield and drought tolerance of rainfed wheat using drought stress indices. Journal of Crop Science and Biotechnology, 2019; 22, 235-42. <u>https://doi.org/10.1007/s12892-018-0037-0</u>
- [4] Younis H, Abbas G, Naz S, Fatima Z, Ali MA, Ahmed M, Khan MA, Ahmad S. Advanced production technologies of wheat. Agronomic Crops, 2019; 223-236. Springer,

Singapore. https://doi.org/10.1007/978-981-32-9151-5 12

- [5] Shiferaw B, Smale M, Braun HJ, Duveiller E, Reynolds M, Muricho G. Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. Food Security, 2013; 5, 291-317. https://doi.org/10.1007/s12571-013-0263-y
- [6] Anwar A, Kim JK. Transgenic breeding approaches for improving abiotic stress tolerance: Recent progress and future perspectives. International Journal of Molecular Sciences, 2020; 21(8), 2695. https://doi.org/10.3390/iims21082695
- Boyer JS. Plant productivity and environment. Science, 1982; 218, 443-448. https://doi.org/10.1126/science.218.4571.443
- [8] Krenzer EG, Nipp TL, McNew, RW. Winter wheat main stem leaf appearance and tiller formation vs. moisture treatment. Agronomy Journal, 1991; 83, 663-667. https://doi.org/10.2134/agronj1991.00021962008300040003x
- [9] Simane B, Peacock JM, Struik PC. Differences in development and growth rate among drought-resistant and susceptible cultivars of durum wheat (*Triticum turgidum* L. var. durum). Plant Soil, 1993; 157: 155-166. https://doi.org/10.1007/BF00011044
- [10] Eastham J, Oosterhuis DM, Walker S. Leaf water and turgor potential threshold values for leaf growth of wheat. Agronomy Journal, 1984; 76, 841-847. https://doi.org/10.2134/agronj1984.00021962007600050029x
- [11] Oosterhuis DM, Cartwright PM. Spike differentiation and floret survival in semidwarf spring wheat as affected by water stress and photo-period. Crop Science, 1983; 23, 711-716. <u>https://doi.org/10.2135/cropsci1983.0011183X002300040026</u>
- [12] Kobata T, Palta JA, Turner NC. Rate of development of post anthesis water deficits and grain filling of spring wheat. Crop Science, 1992; 32, 1238-1242. <u>https://doi.org/10.2135/cropsci1992.0011183X003200050035</u> x
- [13] Palta JA, Kobata T, Turner NC, Fillery IR. Remobilization of carbon and nitrogen in wheat as influenced by post-anthesis water deficits. Crop Science, 1994; 34, 118-124. <u>https://doi.org/10.2135/cropsci1994.0011183X003400010021</u>
- [14] Cooper M, Messina CD. Breeding crops for drought-affected environments and improved climate resilience. The Plant Cell, 2023; 35(1), 162-186. <u>https://doi.org/10.1093/plcell/koac321</u>
- [15] Seaton GR, Walker DA. Chlo-rophyll fluorescence as a measure of photosynthetic carbon assimilation. Proceedings of the Royal Society, Lond. B, 1990; 242, 29-35. <u>https://doi.org/10.1098/rspb.1990.0099</u>
- [16] Hochman ZVI. Effect of water stress with phasic development on yield of wheat grown in a semi-arid environment. Field Crops Research, 1982; 5, 55-67. <u>https://doi.org/10.1016/0378-4290(82)90006-5</u>
- [17] Moustafa MA, Boersma L, Kronstad WE. Response of four spring wheat cultivars to drought stress. Crop Science, 1996; 36, 982-986. https://doi.org/10.2135/cropsci1996.0011183X003600040027 x
- [18] Nicholas ME, Turner NC. Use of chemical desiccants and senescing agents to select wheat lines maintaining stable grain size during post-anthesis drought. Field Crops Research, 1993; 31, 155-171. https://doi.org/10.1016/0378-4290(93)90058-U
- [19] Bidinger FR, Musgrave RB, Fischer RA. Contribution of stored pre-anthesis assimilates to grain yield in wheat and barley. Nature, 1977; 270, 431-433. <u>https://doi.org/10.1038/270431a0</u>

- [20] Benbella M, Paulsen GM. Efficacy of treatment for delaying senescence of wheat leaves. II. Senescence and grain yield under field conditions. Agronmy Journal, 1998; 90: 332-338. https://doi.org/10.2134/agronj1998.00021962009000030004x
- [21] Sojka RE, Stolzy LH, Fischer RA. Seasonal response of selected wheat cultivars. Agronmy. Journal, 1981; 73, 838-844.

https://doi.org/10.2134/agronj1981.00021962007300050022x

- [22] Abid M, Tian Z, Zahoor R, Ata-Ul-Karim ST, Daryl C, Snider JL, Dai T. Pre-drought priming: A key drought tolerance engine in support of grain development in wheat. Advances in Agronomy, 2018; 152, 51-85. https://doi.org/10.1016/bs.agron.2018.06.001
- [23] Passioura JB. Grain yield harvest index and water use of wheat. The Journal of the Australian Institute of Agricultural Science, 1977; 43, 117-120.
- [24] Duvnjak J, Lončarić A, Brkljačić L, Šamec D, Šarčevi'c H, Branka Salopek-Sondi B, Špani'c V. Morpho-physiological and hormonal response of winter wheat varieties to drought stress at stem elongation and anthesis stages. Plants, 2023; 12(418), 21. https://doi.org/10.3390/plants12030418
- [25] Venora G, Calcagno F. Study of stomatal parameters for selection of drought resistance varieties in *Triticum durum* Desf. Euphytica, 1991; 57, 275-283. https://doi.org/10.1007/BF00039674
- [26] Menendez CH, Hall AE. Heritability of carbon isotope discrimination and correlations with harvest index in cowpea. Crop Science, 1996; 36, 233-238. <u>https://doi.org/10.2135/cropsci1996.0011183X003600020003</u> <u>x</u>
- [27] Farquhar GD, Richards RA. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Australian Journal of Plant Physiology, 1984; 11, 539-552. https://doi.org/10.1071/PP9840539
- [28] Masle J, Farquhar GD. Effect of soil strength on the relation of water use efficiency, carbon isotope discrimination and dry matter partitioning during early growth in sunflower. Australian Journal of Plant Physiology, 1988; 17, 207-214.
- [29] Wang M, Wang S, Liang Z, Shi W, Gao C, Xia G. From genetic stock to genome editing: gene exploitation in wheat. Trends in Biotechnology, 2018; 36(2), 160-172. <u>https://doi.org/10.1016/j.tibtech.2017.10.002</u>
- [30] Abd El-Mageed TA, El-Samnoudi IM, Ibrahim AE, Abd El Tawwab AR. Compost and mulching modulates morphological, physiological responses and water use efficiency in sorghum (bicolor L. Moench) under low moisture regime. Agricultural Water Management, 2018; 208, 431-9. https://doi.org/10.1016/j.agwat.2018.06.042
- [31] Harris H, Cooper, P.JM, Pala M. Soil and crop management for improved water use efficiency. Aleppo, Syria, ICARDA. 1991; 352.
- [32] Rezzouk FZ, Romero AG, Kefauver SC, Taladriz MTN, Serret MD, Araus JL. Durum wheat ideotypes in Mediterranean environments differing in water and temperature conditions. Agricultural Water Management, 2022; 259, 107257. https://doi.org/10.1016/j.agwat.2021.107257
- [33] Cann DJ, Schillinger WF, Hunt JR, Porker KD, Harris FAJ. Agroecological advantages of early-sown winter wheat in semi-arid environments: A comparative case study from southern Australia and Pacific Northwest United States. Frontiers in Plant Science, 2020; 11, 568. https://doi.org/10.3389/fpls.2020.00568
- [34] Fischer RA, Maurer R. Drought resistance in spring wheat cultivars. I. Grain yield responses. Australian Journal of Agricultural Research, 1978; 29, 897-912. https://doi.org/10.1071/AR9780897

- [35] Acevedo E, Hsiao TC. Henderson DW. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiology, 1971; 48, 631-636. <u>https://doi.org/10.1104/pp.48.5.631</u>
- [36] Van Oosterom EJ, Acevedo E. Adaptation of barley (Hodeum vulgare L.) to harsh Mediterranean environments. I. Morphological traits. Euphytica, 1992; 62, 1-14. <u>https://doi.org/10.1007/BF00036082</u>
- [37] Van Loon AF. Hydrological drought explained. Wiley Interdisciplinary Reviews: Water, 2015; 2(4), 359-92. <u>https://doi.org/10.1002/wat2.1085</u>
- [38] Blum A, Jordan WR. Breeding crop varieties for stress environments. Critical Reviews in Plant Sciences, 1985; 2(3), 199-238. <u>https://doi.org/10.1080/07352688509382196</u>
- [39] Rees D, Sayre K, Acevedo E, Nava E, Lu Z, Zeiger E, Limon A. Canopy temperatures of wheat: relationship with yield and potential as a technique for early generation selection. 1993; Wheat Special Report No. 10. Mexico, DF, CIMMYT.
- [40] Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, Sadia S, Nasim W, Adkins S, Saud S, Ihsan MZ. Crop production under drought and heat stress: plant responses and management options. Frontiers in Plant Science, 2017; 8, 1147. https://doi.org/10.3389/fpls.2017.01147
- [41] Sahrawat KL, Wani SP, Pathak P, Rego TJ. Managing natural resources of watersheds in the semi-arid tropics for improved soil and water quality: A review. Agricultural Water Management, 2010; 97(3), 375-81. <u>https://doi.org/10.1016/j.agwat.2009.10.012</u>
- [42] Ullah H, Santiago-Arenas R, Ferdous Z, Attia A, Datta A. Improving water use efficiency, nitrogen use efficiency, and radiation use efficiency in field crops under drought stress: A review. Advances in Agronomy, 2019; 156, 109-157. <u>https://doi.org/10.1016/bs.agron.2019.02.002</u>
- [43] Kumar A, Nayak AK, Das BS, Panigrahi N, Dasgupta P, Mohanty S, Kumar U, Panneerselvam P, Pathak H. Effects of water deficit stress on agronomic and physiological responses of rice and greenhouse gas emission from rice soil under elevated atmospheric CO₂. Science of the Total Environment, 2019; 650, 2032-50. https://doi.org/10.1016/j.scitotenv.2018.09.332
- [44] Morgan J, Condon AG. Water use, grain yield and osmoregulation in wheat. Australian Journal of Plant Physiology, 1986; 13, 523-532. https://doi.org/10.1071/PP9860523
- [45] Idso SB., Reginate RJ, Hatfield JI, Pinter PJ, Jr. Measuring yield reducing plant water potential depression in wheat by infrared thermometry. Irrigation Science, 1984; 2, 205-212. <u>https://doi.org/10.1007/BF00258374</u>
- [46] Shpiler L, Blum A. Differential reaction of wheat cultivars to hot environments. Euphytica, 1986; 35, 483-492. https://doi.org/10.1007/BF00021856
- [47] Havrlentová M, Kraic J, Gregusová V, Kovácsová B. Drought stress in cereals - A review. Agriculture (Poľnohospodárstvo), 2021; 67, 47-60. <u>https://doi.org/10.2478/agri-2021-0005</u>
- [48] Evans LT, Wardlaw IF, Fischer RA. Wheat. In L.T. Evans, ed. Crop physiology, 1975; 101-149. Cambridge, UK, Cambridge University Press.
- [49] Spilde LA. Influence of seed size and test weight on several agronomic traits of barley and hard red spring wheat. Journal of Production Agriculture, 1989; 2, 169-172. https://doi.org/10.2134/jpa1989.0169
- [50] Mian MAR, Nafziger ED. Seed size and water potential effects on germination and seedling growth of winter wheat. Crop Science, 1994; 34, 169-171. <u>https://doi.org/10.2135/cropsci1994.0011183X003400010030</u> <u>X</u>

- [51] Baker CK, Gallagher JN. The development of winter wheat in the field. Relation between apical development and plant morphology within and between seasons. The Journal of Agricultural Science, 1983a; 10, 327-335. https://doi.org/10.1017/S0021859600037631
- [52] Baker CK, Gallagher JN. The development of winter wheat in the field. The control of primordium initiation rate by temperature and photoperiod. The Journal of Agricultural Science 1983b; 101, 337-344. <u>https://doi.org/10.1017/S0021859600037643</u>
- [53] Hay RKM, Kirby EJM. Convergence and synchrony a review of the coordination of development in wheat. Australian Journal of Agricultural Research, 1991; 42, 661-700. https://doi.org/10.1071/AR9910661
- [54] Kirby EJM. Effect of sowing depth on seedling emergence, growth and development in barley and wheat. Field Crops Research, 1993; 35, 101-111. https://doi.org/10.1016/0378-4290(93)90143-B
- [55] Longnecker N, Kirby EJM, Robson A. Leaf emergence, tiller growth, and apical development of nitrogen-deficient spring wheat. Crop Science, 1993; 33, 154-160. <u>https://doi.org/10.2135/cropsci1993.0011183X003300010028</u> <u>x</u>
- [56] Hanft JM, Wych RD. Visual indicators of physiological maturity of hard red spring wheat. Crop Science, 1982; 22, 584-587. <u>https://doi.org/10.2135/cropsci1982.0011183X002200030036</u> <u>x</u>
- [57] Rane J, Singh AK, Kumar M, Boraiah KM, Meena KK, Pradhan A, Prasad PVV. The adaptation and tolerance of major cereals and legumes to important abiotic stresses. International Journal of Molecular Sciences, 2021; 22(23), 12970. https://doi.org/10.3390/ijms222312970
- [58] Chakraborty D, Nagarajan S, Aggarwal P, Gupta VK, Tomar RK, Garg RN, Sahoo RN, Sarkar A, Chopra UK, Sarma KS, Kalra N. Effect of mulching on soil and plant water status, and the growth and yield of wheat (*Triticum aestivum* L.) in a semi-arid environment. Agricultural Water Management, 2008; 95(12), 1323-34. https://doi.org/10.1016/j.agwat.2008.06.001
- [59] Ali H, Iqbal N, Shahzad AN, Sarwar N, Ahmad S, Mehmood A. Seed priming improves irrigation water use efficiency, yield, and yield components of late-sown wheat under limited water conditions. Turkish Journal of Agriculture and Forestry, 2013; 37(5), 534-44. https://doi.org/10.3906/tar-1207-70
- [60] Gómez DS, Rodríguez PP. Sustainable agriculture through perennial grains: Wheat, rice, maize, and other species. A review. Agriculture, Ecosystems & Environment, 2022; 325, 107747.

https://doi.org/10.1016/j.agee.2021.107747

- [61] Shahid S, Ali Q, Ali S, Al-Misned FA, Maqbool S. Water deficit stress tolerance potential of newly developed wheat genotypes for better yield based on agronomic traits and stress tolerance indices: physio-biochemical responses, lipid peroxidation and antioxidative defense mechanism. Plants, 2022; 11(3), 466. https://doi.org/10.3390/plants11030466
- [62] Zang U, Goisser M, Häberle KH, Matyssek R, Matzner E, Borken W. Effects of drought stress on photosynthesis, rhizosphere respiration, and fine-root characteristics of beech saplings: A rhizotron field study. Journal of Plant Nutrition and Soil Science, 2014; 177(2), 168-77. https://doi.org/10.1002/jpln.201300196
- [63] Zhang X, Wang Y, Sun H, Chen S, Shao L. Optimizing the yield of winter wheat by regulating water consumption during vegetative and reproductive stages under limited water supply. Irrigation Science, 2013; 31(5), 1103-12. <u>https://doi.org/10.1007/s00271-012-0391-8</u>

- [64] Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM. The role of root exudates in rhizosphere interactions with plants and other organisms. Annual Review of Plant Biology, 2006; 57, 233-66. <u>https://doi.org/10.1146/annurev.arplant.57.032905.105159</u>
- [65] Ackerly D. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecological Monographs, 2004; 74(1), 25-44. https://doi.org/10.1890/03-4022
- [66] Dijkstra FA, Cheng W. Moisture modulates rhizosphere effects on C decomposition in two different soil types. Soil Biology and Biochemistry, 2007; 39(9), 2264-74. <u>https://doi.org/10.1016/j.soilbio.2007.03.026</u>
- [67] Freschet GT, Swart EM, Cornelissen JH. Integrated plant phenotypic responses to contrasting above-and belowground resources: Key roles of specific leaf area and root mass fraction. New Phytologist, 2015; 206(4), 1247-60. <u>https://doi.org/10.1111/nph.13352</u>
- [68] Moyano FE, Manzoni S, Chenu C. Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. Soil Biology and Biochemistry, 2013; 59, 72-85. <u>https://doi.org/10.1016/j.soilbio.2013.01.002</u>
- [69] Kurepin LV, Ivanov AG, Zaman M, Pharis RP, Allakhverdiev SI, Hurry V, Hüner NP. Stress-related hormones and glycinebetaine interplay in protection of photosynthesis under abiotic stress conditions. Photosynthesis Research, 2015; 126(2-3), 221-35. https://doi.org/10.1007/s11120-015-0125-x
- [70] Reddy AR, Chaitanya KV, Vivekanandan M. Droughtinduced responses of photosynthesis and antioxidant metabolism in higher plants. Journal of Plant Physiology, 2004; 161(11), 1189-202. <u>https://doi.org/10.1016/j.jplph.2004.01.013</u>
- [71] Chen H, Jiang JG. Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. Environmental Reviews, 2010; 309-19. https://doi.org/10.1139/A10-014
- [72] Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, Ahmad A. Role of proline under changing environments: a review. Plant signaling & Behavior, 2012; 7(11), 1456-66. https://doi.org/10.4161/psb.21949
- [73] Wassmann R, Jagadish SV, Heuer S, Ismail A, Redona E, Serraj R, Singh RK, Howell G, Pathak H, Sumfleth K. Climate change affecting rice production: the physiological and agronomic basis for possible adaptation strategies. Advances in Agronomy, 2009; 101, 59-122. <u>https://doi.org/10.1016/S0065-2113(08)00802-X</u>
- [74] Ullah A, Manghwar H, Shaban M, Khan AH, Akbar A, Ali U, Ali E, Fahad S. Phytohormones enhanced drought tolerance in plants: a coping strategy. Environmental Science and Pollution Research, 2018; 33, 33103-18. <u>https://doi.org/10.1007/s11356-018-3364-5</u>
- [75] Marcińska I, Czyczyło-Mysza I, Skrzypek E, Filek M, Grzesiak S, Grzesiak MT, Janowiak F, Hura T, Dziurka M, Dziurka K, Nowakowska A. Impact of osmotic stress on physiological and biochemical characteristics in droughtsusceptible and drought-resistant wheat genotypes. Acta Physiologiae Plantarum, 2013; 35(2), 451-61. <u>https://doi.org/10.1007/s11738-012-1088-6</u>
- [76] Hong-Bo S, Xiao-Yan C, Li-Ye C, Xi-Ning Z, Gang W, Yong-Bing Y, Chang-Xing Z, Zan-Min H. Investigation on the relationship of proline with wheat anti-drought under soil water deficits. Colloids and Surfaces B: Biointerfaces, 2006; 53(1), 113-9. https://doi.org/10.1016/j.colsurfb.2006.08.008
- [77] Chakraborty U, Pradhan B. Oxidative stress in five wheat varieties (*Triticum aestivum* L.) exposed to water stress and study of their antioxidant enzyme defense system, water stress responsive metabolites and H₂O₂ accumulation.

Brazilian Journal of Plant Physiology, 2012; 24(2), 117-30. https://doi.org/10.1590/S1677-04202012000200005

- [78] Cattivelli L, Rizza F, Badeck FW, Mazzucotelli E, Mastrangelo AM, Francia E, Marè C, Tondelli A, Stanca AM. Drought tolerance improvement in crop plants: an integrated view from breeding to genomics. Field Crops Research, 2008; 105(1-2), 1-4. https://doi.org/10.1016/j.fcr.2007.07.004
- [79] Wang JY, Xiong YC, Li FM, Siddique KH, Turner NC. Effects of drought stress on morphophysiological traits, biochemical characteristics, yield, and yield components in different ploidy wheat: A meta-analysis. Advances in Agronomy, 143, 139-173.

https://doi.org/10.1016/bs.agron.2017.01.002

- [80] Mwadzingeni L, Shimelis H, Tesfay S, Tsilo TJ. Screening of bread wheat genotypes for drought tolerance using phenotypic and proline analyses. Frontiers in plant science, 2016; 7, 1276. https://doi.org/10.3389/fpls.2016.01276
- [81] Hafez EM, Gharib HS. Effect of exogenous application of ascorbic acid on physiological and biochemical characteristics of wheat under water stress. International Journal of Plant Production, 2016; 10(4), 579-96.
- [82] Samarah NH, Alqudah AM, Amayreh JA, McAndrews GM. The effect of late-terminal drought stress on yield components of four barley cultivars. Journal of Agronomy and Crop Science, 2009; 195(6), 427-41. <u>https://doi.org/10.1111/j.1439-037X.2009.00387.x</u>
- [83] Suneja Y, Gupta AK, Bains NS. Stress adaptive plasticity: Aegilops tauschii and Triticum dicoccoides as potential donors of drought associated morpho-physiological traits in wheat. Frontiers in Plant Science, 2019; 10, 211. https://doi.org/10.3389/fpls.2019.00211
- [84] Farooq M, Gogoi N, Barthakur S, Baroowa B, Bharadwaj N, Alghamdi SS, Siddique KH. Drought stress in grain legumes during reproduction and grain filling. Journal of Agronomy and Crop Science, 2017; 203(2), 81-102. https://doi.org/10.1111/jac.12169
- [85] Mancosu N, Snyder RL, Kyriakakis G, Spano D. Water scarcity and future challenges for food production. Water, 2015; 3, 975-92. <u>https://doi.org/10.3390/w7030975</u>
- [86] Driever SM, Lawson T, Andralojc PJ, Raines CA, Parry MA. Natural variation in photosynthetic capacity, growth, and yield in 64 field-grown wheat genotypes. Journal of Experimental Botany, 65(17); 4959-73. https://doi.org/10.1093/jxb/eru253
- [87] Blum A. Drought resistance, water-use efficiency, and yield potential-are they compatible, dissonant, or mutually exclusive?. Australian Journal of Agricultural Research, 2005; 56(11), 1159-68. https://doi.org/10.1071/AR05069
- [88] Waraich EA, Ahmad R, Ashraf MY, Saifullah, Ahmad M. Improving agricultural water use efficiency by nutrient management in crop plants. Acta Agriculturae Scandinavica, Section B-Soil & Plant Science, 2011; 61(4); 291-304. https://doi.org/10.1080/09064710.2010.491954
- [89] Tavakkoli AR, Oweis TY. The role of supplemental irrigation and nitrogen in producing bread wheat in the highlands of Iran. Agricultural Water Management, 2004; 65(3), 225-36. <u>https://doi.org/10.1016/j.agwat.2003.09.001</u>
- [90] Trethowan RM, Reynolds M, Sayre K, Ortiz-Monasterio I. Adapting wheat cultivars to resource conserving farming practices and human nutritional needs. Annals of Applied Biology, 2005; 146(4), 405-13. <u>https://doi.org/10.1111/j.1744-7348.2005.040137.x</u>
- [91] Johnson JF, Allmaras RR, Reicosky DC. Estimating source carbon from crop residues, roots and rhizodeposits using the national grain-yield database. Agronomy journal, 2006; 98(3), 622-36. https://doi.org/10.2134/agronj2005.0179

- [92] Hatfield JL, Sauer TJ, Prueger JH. Managing soils to achieve greater water use efficiency: a review. Agronomy journal, 2001; 93(2), 271-80. <u>https://doi.org/10.2134/agronj2001.932271x</u>
- [93] Chauhan BS. Weed ecology and weed management strategies for dry-seeded rice in Asia. Weed Technology, 2012; 26(1), 1-3. <u>https://doi.org/10.1614/WT-D-11-00105.1</u>
- [94] Debaeke P, Aboudrare A. Adaptation of crop management to water-limited environments. European Journal of Agronomy, 2004; 21(4), 433-46. https://doi.org/10.1016/j.eja.2004.07.006
- [95] Du C, Li L, Effah Z. Effects of straw mulching and reduced tillage on crop production and environment: a review. Water, 2022; 14, 2471. <u>https://doi.org/10.3390/w14162471</u>
- [96] Scavo A, Fontanazza S, Restuccia A, Pesce GR, Abbate C, Mauromicale G. The role of cover crops in improving soil fertility and plant nutritional status in temperate climates. A review. Agronomy for Sustainable Development, 2022; 42, 93.

https://doi.org/10.1007/s13593-022-00825-0

- [97] Li Y, Li H, Li Y, Zhang S. Improving water-use efficiency by decreasing stomatal conductance and transpiration rate to maintain higher ear photosynthetic rate in drought-resistant wheat. The Crop Journal, 2017; 5(3), 231-9. https://doi.org/10.1016/j.cj.2017.01.001
- [98] Papanatsiou M, Petersen J, Henderson L, Wang Y, Christie JM, Blatt MR. Optogenetic manipulation of stomatal kinetics improves carbon assimilation, water use, and growth. Science, 2019; 363(6434), 1456-9. <u>https://doi.org/10.1126/science.aaw0046</u>
- [99] Bertolino LT, Caine RS, Gray JE. Impact of stomatal density and morphology on water-use efficiency in a changing world. Frontiers in Plant Science, 2019; 10, 225. https://doi.org/10.3389/fpls.2019.00225
- [100] Casson SA, Hetherington AM. Environmental regulation of stomatal development. Current Opinion in Plant Biology, 2010; 13(1), 90-5. https://doi.org/10.1016/j.pbi.2009.08.005
- [101] Nadeau JA. Stomatal development: new signals and fate determinants. Current Opinion in Plant Biology, 2009; 12(1), 29-35. <u>https://doi.org/10.1016/j.pbi.2008.10.006</u>
- [102] Sibbernsen E, Mott KA. Stomatal responses to flooding of the intercellular air spaces suggest a vapor-phase signal between the mesophyll and the guard cells. Plant Physiology, 2010; 153 (3), 1435-42. <u>https://doi.org/10.1104/pp.110.157685</u>
- [103] Franks PJ, Farquhar GD. The mechanical diversity of stomata and its significance in gas-exchange control. Plant

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Physiology, 2007; 143(1), 78-87. https://doi.org/10.1104/pp.106.089367

- [104] Tardieu F. Plant response to environmental conditions: assessing potential production, water demand, and negative effects of water deficit. Frontiers in Physiology, 2013; 4, 17. https://doi.org/10.3389/fphys.2013.00017
- [105] Richards RA. Physiological traits used in the breeding of new cultivars for water-scarce environments. Agricultural Water Management, 2006; 80(1-3), 197-211. <u>https://doi.org/10.1016/j.agwat.2005.07.013</u>
- [106] Wasaya A, Zhang X, Fang Q, Yan Z. Root phenotyping for drought tolerance: a review. Agronomy, 2018; 8(11), 241. https://doi.org/10.3390/agronomy8110241
- [107] Maeght JL, Rewald B, Pierret A. How to study deep rootsand why it matters. Frontiers in Pant Science, 2013; 4, 299. https://doi.org/10.3389/fpls.2013.00299
- [108] Farooq M, Hussain M, Siddique KH. Drought stress in wheat during flowering and grain-filling periods. Critical Reviews in Plant Sciences, 2014; 33(4), 331-49. https://doi.org/10.1080/07352689.2014.875291
- [109] Schoppach R, Wauthelet D, Jeanguenin L, Sadok W. Conservative water use under high evaporative demand associated with smaller root metaxylem and limited transmembrane water transport in wheat. Functional Plant Biology, 2014; 41(3), 257-69. <u>https://doi.org/10.1071/FP13211</u>
- [110] Ye Y, Liang X, Chen Y, Liu J, Gu J, Guo R, Li L. Alternate wetting and drying irrigation and controlled-release nitrogen fertilizer in late-season rice. Effects on dry matter accumulation, yield, water and nitrogen use. Field Crops Research, 2013; 144, 212-24. https://doi.org/10.1016/j.fcr.2012.12.003
- [111] Saud SF, Yajun CI, Hammad HMN, Jr AA. Alharby H. Effects of nitrogen supply on water stress and recovery mechanisms in Kentucky Bluegrass plants. Frontiers of Plant Science, 2017; 8, 983. <u>https://doi.org/10.3389/fpls.2017.00983</u>
- [112] Saud S, Li X, Chen Y, Zhang L, Fahad S, Hussain S, Sadiq A, Chen Y. Silicon application increases drought tolerance of Kentucky bluegrass by improving plant water relations and morphophysiological functions. The Scientific World Journal, 2014; 2014, 1-10. <u>https://doi.org/10.1155/2014/368694</u>
- [113] Danish S, Zafar-ul-Hye M, Fahad S, Saud S, Brtnicky M, Hammerschmiedt T, Datta R. Drought stress alleviation by ACC deaminase producing achromobacter xylosoxidans and enterobacter cloacae, with and without timber waste biochar in maize. Sustainability, 2020; 12(15), 6286. <u>https://doi.org/10.3390/su12156286</u>