Review Article

Managing drought stress in wheat (*Triticum aestivum* L.) production: strategies and impacts

Maltase Mutanda [1,2], **Hussein Shimelis** [2], **Vincent Chaplot** [2,3] and **Sandiswa Figlan** [1]

[1]Department of Agriculture and Animal Health, University of South Africa, Florida, South Africa
[2]School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa
[3]Institut de Recherche pour le Dévelopement (IRD), Laboratory of Oceanography and Climate, Experiments and Numerical Approaches (LOCEAN), UMR, IRD/C NRS/UPMC/MNHN, IPSL, Paris, France
*Corresponding author, Email: figlas@unisa.ac.za

Drought stress is a major constraint to sustainable wheat production worldwide, including sub-Saharan Africa, where environmental and poor agronomic practices exacerbate the yield gap. Drought disrupts physiological, biochemical, and molecular processes, negatively impacting crop growth, grain yield and quality. This review outlines a range of effective management strategies to cope with drought stress in wheat, including the adoption of drought-tolerant wheat cultivars, advanced agronomic practices, and precision irrigation techniques. The review emphasises the role of carbon isotope discrimination (CID) in breeding programs, enhancing water-use efficiency, and crop resilience under drought conditions. Collaborative efforts among researchers, farmers, and policymakers are essential to enhance adaptive capacity and promote food security amidst growing climate variability. Future research should focus on developing and deploying drought-tolerant cultivars and integrating CID technology in wheat-breeding programmes to build climate-resilient agriculture systems.

Keywords: carbon isotope discrimination, crop resilience, irrigation strategies, molecular breeding, water-use efficiency

Introduction

Bread wheat (*Triticum aestivum* L., 2n = 6× = 42, AABBDD) is the third most important cereal crop globally after maize (*Zea mays*) and rice (*Oryza sativa*) (FAO 2023). Wheat grain has vital human dietary contents such as starch, protein, vitamin B, calcium and iron (Sewore et al. 2023). Nonetheless, sustaining and increasing wheat output to meet growing demand faces significant challenges, including climate change, increasing population, agricultural land loss and competing demands for water (FAO 2023). In sub-Saharan Africa (SSA) the total wheat production is low, forcing several nations to rely on wheat imports to meet local demands (Silva et al. 2023). The mean grain yield of wheat under dryland production in SSA is 2.00 t ha^{-1}, significantly lower than the potential yield of 10 t ha^{-1} based on irrigated conditions (Shamuyarira 2018). In South Africa, the yield gap ranges from 1.58 t ha^{-1} to 3.13 t ha^{-1}, representing the achievement of only 38% of the yield potential (Soba et al. 2020). The low grain yields in SSA have been attributed to the slow progress in the development of drought-tolerant cultivars and recurrent drought associated with climate change (Tadesse et al. 2018).

Omotoso et al. (2023) highlighted that drought is a prominent threat to human livelihoods. Drought is becoming prevalent in SSA due to low and erratic rainfall and rising air temperatures (Rezaly and Shabri 2024). For instance, Zimbabwe declared drought as a national disaster in 2024 (FAO 2024). Unpredictable rainfall patterns are the primary drivers of long-term drought stress in drylands across the SSA region (Ayugi et al. 2022). Prolonged droughts affect crop growth and development, leading to reduced grain yield (Schweiger et al. 2023). Recent studies have indicated that drought affects agro-morphological, physiological and biochemical traits, limiting potential yield (Yılmaz et al. 2023). Therefore, developing and deploying wheat varieties with high water use efficiency (WUE) will assist in mitigating the adverse effects of drought stress.

Water use efficiency is defined as the amount of biomass or grain yield per unit of water applied (Hussain et al. 2022). Water use efficiency can be measured using various methods, including biomass parameters and carbon isotope discrimination (Mutanda et al. 2024). High WUE indicates that a wheat genotype can produce a high grain yield with less water applied (Martínez-Goñi et al. 2023). However, the impact of drought stress on WUE differs according to drought intensity, genotype, environment and genotype × environment interaction effects (Mbava et al. 2020; Hussein et al. 2022). Various approaches, such as

precision irrigation (Feng et al. 2023), agronomic management practices (Mallareddy et al. 2023) and organic and inorganic mulching (Li et al. 2018) are used to minimise the impact of drought stress on wheat. High throughput phenotyping (HTP) tools, such as the LeasyScan and liquid chromatography-mass spectrometry (LC-MS) (Hall et al. 2022) have been widely used to identify traits and metabolites associated with improved drought tolerance and WUE.

Water use efficiency and drought tolerance in wheat are complex traits controlled by polygenes, and various environmental conditions influence their expressions. Several researchers have also shown that, at cellular and metabolite levels, many compounds are increased to provide osmoprotective functions, prevent the dissociation of enzymes, and reduce reactive oxygen species in the plant cell (Mwadzingeni et al. 2016; Agami et al. 2019). Hence the link between WUE, drought tolerance, and the associated genetic and metabolic foundations remains vital to developing wheat genotypes. In addition, the association between the metabolome and transcriptome is an effective method for identifying metabolites involved in drought response. For instance, the correlation between the metabolome and transcriptome revealed that amino acid biosynthesis, downstream pathways, and secondary metabolite biosynthesis were co-regulated during drought stress (Lv et al. 2022). Zhang et al. (2021a) found that purine metabolism and phenylpropanoid biosynthesis were key metabolic pathways responding to drought stress in plants.

Approaches such as measuring WUE, drought indices, and simultaneous trait selection and analysis have been employed to identify superior wheat varieties. Assessing WUE using biomass measurement methods and CID is essential to evaluate the efficiency of crop genotypes in drought-prone regions (Mutanda et al., 2024). Semahegn et al. (2020) reported increased selection efficiency of drought-tolerant wheat genotypes using drought indices. In addition, correlation and path analysis provide insights into the complex relationships between agronomic traits, drought indices, WUE, and metabolites. These associations will help plant breeders pinpoint key traits contributing to high WUE. In light of the above, the objectives of this review were to document (i) the impact of drought stress on wheat agro-morphological, physiological, and biochemical changes and WUE, (ii) the cultural practices and modern technologies that can be used to improve WUE, and (iii) the screening methods to select wheat genotypes with WUE and tolerance to drought.

Drought stress

Causes of drought stress
Climate change has emerged as a pressing concern in Africa, causing increased temperatures and unpredictable rainfall patterns and significantly contributing to drought stress in economically important crops (Amoak et al. 2023). The mean annual air temperature has increased by 0.9°C, while the mean annual rainfall decreased by 16.09 mm in Africa in the 21st century (Scholes and Engelbrecht 2021).

Even with adequate soil moisture, various edaphic factors can induce water stress in crop plants. These factors include salinity, low soil temperatures, and flooding, all of which impede the plant's ability to absorb water through its roots (Muhammad et al. 2023).

Impact of drought stress on wheat performance
Drought stress causes significant alterations at different agro-morphological, biochemical, and physiological levels. The major changes associated with drought stress are presented in Figure 1.

Impact of drought stress on agro-morphological changes
Drought stress significantly impacts agro-morphological traits in wheat during heading, anthesis, and grain filling (Table 1). It reduces grain size, weight, and quality (Sattar et al. 2020) mainly when drought occurs during the grain-filling stage. Some wheat genotypes mature earlier under drought as a survival strategy (Mathew et al. 2019). The early-maturing genotypes display reduced assimilation and poor source-to-sink mobilisation (Semahegn et al. 2020). Drought causes protoplasm dehydration and loss of turgidity, leading to reduced plant height (Salam et al. 2022). Mwadzingeni et al. (2016) reported that drought stress reduced plant height by 5.78% compared to non-stressed conditions. The decrease in plant height under drought stress conditions further reduces spike length. Reportedly, Mathew et al. (2019) indicated a 12.50% decrease in spike length in wheat due to drought conditions. Low spike length is associated with height controlling genes regardless of the induced stress (Thabet et al. 2020). Fewer tillers per plant due to tiller mortality under drought conditions results in fewer spikes (Mmbando 2025). Likewise, Shamuyarira et al. (2022) reported that fewer tillers are associated with reduced productive spikes. In addition, reduced water availability, impaired photosynthesis, restricted growth, and premature senescence reduce grain yield under drought stress (Wan et al. 2022). This is consistent with findings from Shamuyarira et al. (2022), who noted a significant decline in yield ($p < 0.05$). While shoot biomass typically decreases under drought conditions, root biomass often increases as plants adapt to enhance water absorption capacity (Yan et al. 2023). This adaptive response highlights the complex interplay between aboveground and belowground traits in response to water stress. Therefore, understanding these traits is crucial for developing effective strategies to mitigate the impacts of drought on wheat production. Future research should focus on identifying and breeding for traits that enhance drought tolerance while maintaining productivity.

Impact of drought stress on biochemical changes
Drought stress impacts biochemical processes, causing alterations in metabolic activities in crop plants (Bhandari et al. 2023). In the rhizosphere, drought stress elevates respiratory carbon loss, consequently decreasing adenosine triphosphate production (Zahoor et al. 2020). Energy generation through oxidative phosphorylation in mitochondria is disrupted under drought conditions, causing reactive oxygen species formation. Under these conditions, only 0.1 to 2.0% of electrons effectively progress through
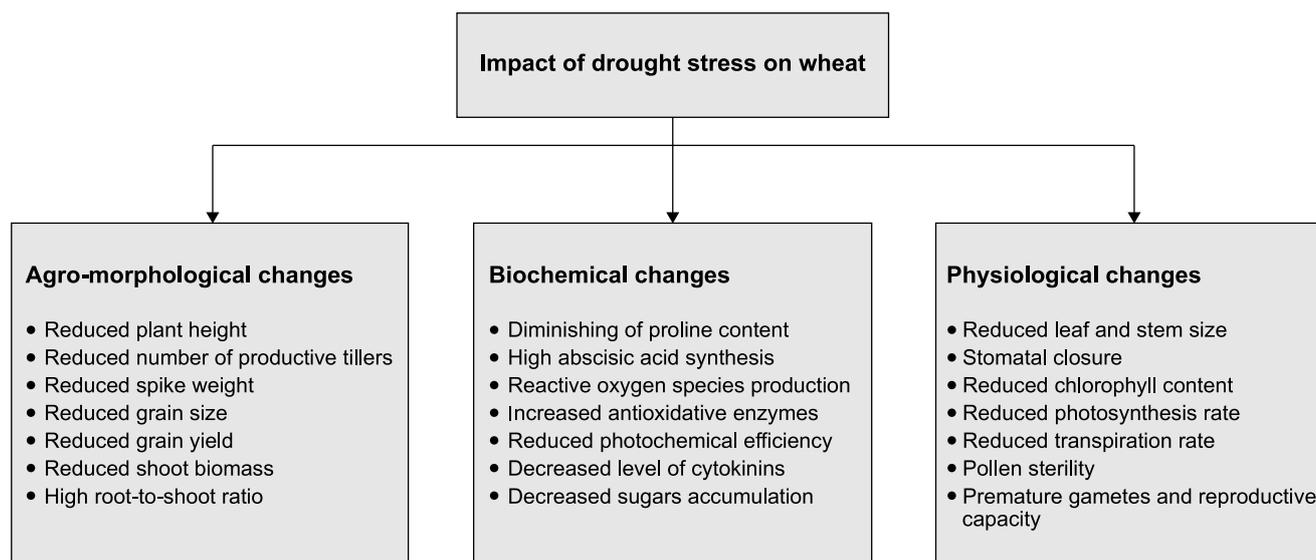
Figure 1: Summary of agro-morphological, biochemical and physiological changes in wheat under drought stress conditions (Source: Adapted with modification from Davies et al. 2005; Mwadzingeni et al. 2016; Mathew et al. 2019; Zahra et al. 2021; Salam et al. 2022; Vassileva et al. 2023; Nyaupane et al. 2024)

the electron transport chain, resulting in incomplete oxygen reduction and superoxide radical formation (Szechyńska-Hebda et al. 2022). In addition, drought stress increases abscisic acid synthesis for stomal closure, reducing photosynthesis (Davies et al. 2005). The reduction in photosynthesis rate limits carbon uptake and sugar accumulation. Proline levels rise under water stress but diminish rapidly due to variations in cytosolic synthesis and mitochondrial breakdown rates (Mwadzingeni et al. 2016). Therefore, the interplay between these biochemical processes illustrates a complex network where drought influences the pathways and metabolic framework of wheat plants. Understanding these interactions provides insights into potential breeding strategies for developing drought-tolerant wheat genotypes.

Impact of drought stress on physiology
Drought stress significantly alters wheat physiology and results in critical changes in various physiological traits. Under drought conditions, chlorophyll content, osmotic potential, leaf water potential, and turgor pressure are decreased (Figure 1). These changes hinder the plant's ability to maintain cellular function. For instance, Liang et al. (2002) reported that low water potential reduces stomatal conductance, leading to low CO_2 uptake and decreased photosynthetic rate. The reproductive organ development is compromised under drought stress, causing several physiological defects, including impaired ovule development and fertilisation. This leads to premature gamete abortion and reproductive sterility (Nyaupane et al. 2024). The physiological moisture requirements of reproductive structures lead to reduced pollen viability and poor fertilisation (Arathi and Smith 2023). The inability of plants to absorb water from the soil under drought conditions leads to decreased turgor

pressure. This reduces growth by limiting cell extensibility and embryo development (Vassileva et al. 2023). The decline in leaf water potential directly impacts gaseous exchange through stomatal conductance and transpiration rates (Li et al. 2020). In response to drought stress, wheat plants close their stomata to conserve water, which reduces carbon uptake (Kimura et al. 2020). During flowering, wheat typically exhibits peak chlorophyll content. However, this can be significantly reduced under drought stress, leading to reduced photosynthesis. Nikolaeva et al. (2010) noted that drought stress reduced chlorophyll content by 15% due to the activation of chlorophyllase and enzyme inactivation. Drought-sensitive stages of pollen development, such as meiosis and microsporogenesis, are vulnerable, resulting in pollen sterility which leads to reduced yield (Zahra et al. 2021). Furthermore, reactive oxygen species generated during photosynthesis and respiration can cause oxidative damage in chloroplasts and mitochondria (Sachdev et al. 2021). This oxidative stress further exacerbates the physiological challenges faced by wheat under drought conditions, illustrating how interconnected biochemical processes affect the physiological processes. Therefore, understanding the integrated physiological responses is crucial for drought-tolerance breeding programs in the face of climate change.

Impact of drought stress on water use efficiency
Water use efficiency reflects the ability of plants to utilise water effectively for shoot biomass, root biomass and grain yield production (Plett et al. 2020). However, drought stress significantly impacts WUE, leading to lower grain yield (Zou et al. 2021). During drought stress various agro-morphological responses occur, including reduced stem and leaf size to maintain water balance (Wu et al. 2022).

Table 1: Influence of drought stress on wheat yield reduction and yield components during critical growth stages

Agronomic traits	Percentage reduction (%)	Drought intensity and induction period	Site	Number of genotypes evaluated	References
Number of tillers	20.8	35% field capacity from flowering to maturity	field and greenhouse	78	Shamuyarira et al. (2018)
Spike length	28.7				
Thousand kernel weight	26.8				
Grain yield	54.7				
Fresh biomass	43.1				
Plant height	17.0	30% field capacity from flowering to maturity	field and greenhouse	97	Shamuyarira et al. (2022)
Number of tillers	27.7				
Shoot biomass	31.8				
Root biomass	30.1				
Grain yield	41.3				
Shoot biomass	32.3	30% field capacity from 5 weeks after crop emergence.	field and greenhouse	100	Mathew et al. (2019)
Root biomass	32.1				
Root-to-shoot ratio	14.0				
Grain yield	45.0				
Total plant biomass	35.2				
Plant height	5.8	35% field capacity from 50% heading to physiological maturity	field and greenhouse	96	Mwadzingeni et al. (2015)
Number of productive tillers	24.5				
Grain yield	40.6				
Plant height	7.5	35% field capacity from anthesis to physiological maturity	Field and greenhouse	60	Makebe et al. (2024)
Shoot biomass	31.4				
Root biomass	20.1				
Grain yield	38.3				
Grain yield	40.0	Severe stress for 10 days during the heading stage	field	100	Tshikunde et al. (2018)
Grain yield	30.6	Severe stress from 50% heading to grain filling stage	field	256	Amare et al. (2019)
Grain filling period	41.7	Severe stress from 50% heading to maturity	field	144	Lemma et al. (2021)
Number of kernels per spike	16.3				
100 grain weight	18.3				
Grain yield	48.3				
Grain yield	44.3	Severe stress from anthesis to grain filling	field	5	Kimurto et al. (2003)
Grain yield	62.2	Severe stress from the seedling stage to maturity			
Grain yield	52.7	Severe stress from tillering to maturity			
Number of productive tillers	1.2	Severe stress from 50% flowering to physiological maturity	rainout shelter	28	Thungo et al. (2020)
Grain yield	20.2				
Number of productive tillers	8.5	Severe stress from 50% flowering to physiological maturity	greenhouse		
Grain yield	71.1				
Grain yield	50.9	Severe stress at pre-anthesis	field and greenhouse	15	Mdluli et al. (2020)
Grain yield	39.9	Severe stress during post-anthesis			

This limits carbon uptake, leading to reduced carbon assimilation and WUE (Harrison et al. 2020). Furthermore, the impact of drought stress on WUE varies in different environmental conditions (Hussein et al. 2022). For instance, Hu et al. (2006) reported that drought stress significantly decreased WUE in wheat genotypes evaluated in China, whilst Alotaibi et al. (2023) found an increased WUE in wheat under limited water environments in Saudi Arabia. These differences reflect the diversity of adaptive strategies and physiological mechanisms that plants employ to cope with water scarcity under different conditions. Some wheat genotypes exhibit inherent traits associated with higher WUE such as a deep root system and reduced stomatal density. In addition, the genetic variation within wheat genotypes contributes to differences in drought response and WUE, offering opportunities for selective breeding and genetic improvement of crops. Air temperature and humidity also influence plant water relations and WUE under drought-stressed conditions (Yu et al. 2021). Furthermore, the severity and duration of drought stress significantly impact yield production (Schweiger et al. 2023).

Methodologies for improving water use efficiency

Drought stress is a major constraint in wheat production and is threatening global food security. Various strategies should be adopted to enhance wheat production and WUE. This section outlines key mitigation strategies to minimise the impact of drought stress on wheat production.

Cultural practices
Mulching
Mulching is the action of covering the soil surface with organic or inorganic material to preserve moisture and moderate soil temperature (He et al. 2023), thus improving WUE and grain yield production. Mhazo et al. (2016) highlighted that mulching reduces surface water flow during rainstorms by improving infiltration into the soil profile, leading to increased WUE. A study conducted by Ali et al. (2018) evaluated different mulching practices and found that the addition of wheat residue at 5 t ha^{-1} coupled with an irrigation of 350 mm increased WUE of plants by 35%. Another study by Wang et al. (2021) evaluated the impact of ridge-furrow mulching farming systems in Kenya and found that they increased wheat grain yield and WUE by more than 74% and 89%, respectively. In addition, Li et al. (2018) evaluated the effectiveness of plastic and straw mulches on the WUE of plants and found that plastic mulch increases WUE by 29% as compared to a 6% increase under straw mulch. These results concur with Liu et al. (2014), who found higher WUE under plastic much than under no mulch. Zhang et al. (2017) also reviewed mulch's effect on WUE of maize plants under a dryland farming system and indicated that mulch increased WUE by 61% and grain yield by 51%. Despite the demonstrated benefits of mulching, the widespread adoption of mulching practices by smallholder farmers remains limited due to lack of awareness. Notable efforts have been made to educate smallholder farmers through the Sustainable Land Management Project in Ethiopia and Zambia through the Sasakawa-Global 2000 program (Ito et al. 2007; Bwalya et al. 2023).

Precision irrigation
Application of water through irrigation improves wheat production. Enhancing irrigation management is critical in reducing drought stress and increasing WUE under limited water environments (Kumar et al. 2023). However, to apply water efficiently during irrigation, the use of precision irrigation methods such as drip irrigation and micro-sprinklers are encouraged. These methods deliver water directly to the root zone of crops, thereby reducing water loss due to runoff (Abioye et al. 2020). Furthermore, the utilisation of precision irrigation in commercial wheat farms increases profitability by achieving higher yields per hectare while using less water, fertiliser, and energy resources. Studies show that adopting precision irrigation technologies can significantly improve crop yield and WUE (Adeyemi et al. 2017; Brar et al. 2022), making them essential for sustainable water management in agricultural systems. Despite the importance of precision irrigation, adoption in SSA is limited because of poor access to technology, lack of irrigation water, and low awareness among smallholder farmers. Therefore, there is a pressing need to embrace innovative irrigation strategies to sustain agricultural productivity with the prevalence of unpredictable rainfall patterns and increasing water scarcity.

Soil Management Practices
Organic matter
The practices that increase soil organic matter content positively affect the soil water holding capacity (Dengxiao et al. 2024). Hudson (1994) asserted that an increase in organic matter content from 0.5 to 3%, resulted in more than double the available soil water capacity for a wide range of environments. This phenomenon has been reported to be relevant in the SSA region. For instance, in Ghana, Mensah and Frimpong (2018) demonstrated that soil organic matter amendments using compost and biochar enhanced soil water retention capacity and reduced water stress. Similarly, investigations by Sithole et al. (2016) in South Africa indicated that integrating green manures into agricultural systems increased soil organic matter content, leading to improved soil structure and water-holding capacity. These findings suggest that adopting soil management practices to increase organic matter content improves soil water-holding capacity, increasing plant WUE.

Tillage practices
Tillage practices significantly impact WUE in agricultural systems and SSA dryland regions. Conservation tillage methods, such as no-till and reduced tillage, have been shown to improve soil water retention. For instance, a study by Mashingaidze et al. (2019) conducted in Zimbabwe demonstrated that conservation tillage practices led to significant increases in soil water content compared to conventional tillage methods. This improvement is attributed to reduced soil disturbance, which minimises soil compaction and preserves soil structure, facilitating better water infiltration and reducing surface runoff. Similarly, Oyekale et al. (2017) found that adopting reduced tillage improves soil moisture retention and WUE. However, the great significance of reduced tillage in increasing WUE has been recognised when mulching is applied as well. For instance, a study by Peng et al. (2019) reported that a combination of mulch and reduced tillage increased wheat grain yield by 22% and WUE by 26%. Wang et al. (2015) reported that ridge-furrow mulching increased the yields of wheat by 18% and WUE by 20.11%. These findings highlight the potential of conservation tillage practices to mitigate water scarcity in wheat production. In the Western Cape Province of South Africa, approximately 90% of farmers used no-till that enhanced yield gains (Liebenberg et al. 2020). Despite the proven benefits, the adoption of no-till is still low in SSA because of cultural preferences for traditional tillage methods. Nonetheless, efforts to promote conservation tillage are underway in countries such as Kenya and Zimbabwe, where government-supported programs promote reduced tillage.

Strategies for selecting WUE crops
Breeding for improved WUE and drought tolerance
Breeding for improved WUE is a pressing challenge intensified by the increasing frequency of drought events in

the African region. Developing drought tolerance and water-use-efficient varieties of wheat has become the major focus in reducing the adverse effects of drought stress on wheat yields. However, progress in developing WUE and drought tolerant cultivars remains elusive due to the complexity of this trait as it is influenced by environmental conditions and genes (Gahlaut et al. 2019). Understanding the genetic complexities requires deep knowledge across different plant science fields, which indicates the need for collaboration in breeding for improved WUE cultivars. Moreover, wheat's large genome size (17 gigabase, Gb) poses additional challenges to breeding and genetic progress (Bapela et al. 2022). The relationship between genetic factors and environmental conditions highlights the need to integrate both traditional and modern breeding techniques to improve WUE. Phenotypic selection, a cornerstone of conventional breeding, relies on discerning desirable traits such as deep root systems and delayed senescence (Hall et al. 2022). However, advancing breeding programs requires the integration of cutting-edge technologies such as biomarker applications and HTP techniques. The biomarker application offers valuable insights into the physiological and genetic basis of drought tolerance, which helps to make informed decisions during selection and variety development (Kaur et al. 2021).

Use of high-throughput and automated phenotyping techniques

Traditional phenotyping techniques primarily rely on manual measurements for data collection, and this tends to be time-consuming and tedious (Xiao et al. 2022). However, the accuracy and repeatability of measurements and data management using traditional phenotyping tools may limit the response to the selection of drought-tolerant and water-use-efficient cultivars (Xiao et al. 2022). This is exacerbated by the difficulties in understanding the genetic and physiological bases of WUE and drought tolerance on both phenotypic and genomic levels. Therefore, the convergence and adoption of HTP technologies and artificial intelligence (AI) has emerged as a transformative force in plant breeding for enhancing drought tolerance and WUE (Renó et al. 2024). These technologies facilitate accurate data collection and analysis of phenotypic, metabolomic and genotypic data. In addition, ground and remote sensing techniques based on infrared reflectance digital sensors, thermometers and cameras are used to precisely measure various phenotypic and genotypic traits (Hall et al. 2018; Buthelezi et al. 2023). The use of unmanned aerial vehicles and satellite imaging offers new opportunities to monitor and manage water resources (Acharya et al. 2021). In South Africa, there is a high throughput phenotyping facility at the Agricultural Research Council-Grain Crop in Potchefstroom to evaluate the response of crop plants to climate change (Brits 2023). These technologies enable high-resolution spatial and temporal monitoring of crop performance, water availability, and environmental conditions. Despite these factors, most SSA countries face significant barriers to adopting and implementing HTP and AI-driven phenotyping technologies because of limited funding (Kala 2023). Therefore, addressing this technological gap requires collaborative efforts from various stakeholders to empower local scientists with the expertise and tools to do so.

Identification of candidate genes controlling WUE

Water use efficiency is a physiological trait that is controlled by genes, particularly when plants are exposed to drought stress. Therefore, identifying and monitoring the genes that control WUE is crucial in improving the trait. Plant scientists have reported genes associated with WUE under drought conditions, such as *HaHB4* and *TaPYL1-1B* (González et al. 2019; Mao et al. 2022). Furthermore, candidate genes linked to disease resistance and environmental adaptability from wild wheat relatives, such as *Aegilops* species, remain untapped in breeding programs (Adhikari et al. 2023). Therefore, breeding programs could benefit from incorporating or manipulating these genes to enhance WUE in wheat varieties. For example, research by Jain et al. (2019) demonstrated the role of genes affecting abscisic acid synthesis in regulating stomatal conductance and water conservation, leading to improved WUE. Additionally, genes like *TaER1* and *TaER2* have been found to positively influence biomass, instantaneous WUE, and yield in wheat, suggesting their potential for breeding programs aimed at enhancing WUE and drought tolerance (Li et al. 2021).

Measurement and estimation of WUE

Biomass measurement method. Biomass measurement is a widely used method to measure the grain yield and biomass produced with the amount of water applied (Hussain et al. 2022). This technique involves destructive sampling and drying of plant material to assess weight (Mutanda et al. 2024). The amount of water used is the quantity of water applied through rainfall or irrigation during the growing cycle (Hussain et al. 2022). This approach was demonstrated in a study conducted in a wheat field by Li et al. (2017), where biomass was harvested and weighed alongside the quantification of water applied under various irrigation treatments. The efficacy of different irrigation strategies in optimising WUE can be evaluated by calculating the ratio of biomass produced to water used. Similarly, Zhao et al. (2020) investigated WUE in tomato cultivars by measuring water input and biomass accumulation under varying water availability conditions. Therefore, the application of biomass measurement coupled with water input to calculate WUE assists in optimising water management practices. However, estimating crop WUE using the manual measurement method is resource-consuming and expensive in large field experiments with multiple genotypes.

Carbon isotope discrimination. In this method, carbon isotopes are used to assess WUE. It involves measuring the carbon isotopic ratio in plant samples through mass spectrometry analysis (Mutanda et al. 2024). The technique offers valuable insights into a crop genotype potential and its ability to use water during photosynthesis for yield and biomass production optimally. Carbon isotope discrimination (CID) refers to the variation in the ratios of carbon isotopes (^{12}C and ^{13}C) between atmospheric carbon dioxide and the carbon assimilated by plants. When plants

are water-use-efficient, they discriminate less against the heavier isotope (^{13}C), resulting in higher carbon isotope ratios in their tissues. Conversely, lower WUE is often associated with increased discrimination against ^{13}C, leading to lower isotopic ratios. For example, Arslan et al. (1999) reported a strong negative correlation ($r = -0.85$) between WUE and CID in wheat genotypes from Austria, indicating that these genotypes exhibited low WUE. Similarly, Rao et al. (1993) pinpointed a negative correlation between WUE and CID in groundnuts, suggesting that lower WUE corresponds with higher CID values. However, Zhao et al. (2009) reported a positive association between WUE and CID in certain wheat genotypes, suggesting variable water efficiency for grain yield production. This variability highlights the influence of environmental conditions and experimental conditions on WUE. However, the use of CID should be viewed as a complementary tool for screening wheat genotypes for WUE.

Furthermore, integrating CID with other breeding tools such as marker-assisted selection (MAS) can create a more robust framework for developing drought-tolerant wheat varieties. The application of CID is not limited to wheat and can be expanded across various crops to develop water-use efficient cultivars. Integrating CID and MAS and other molecular breeding techniques would improve our understanding of how these approaches complement each other in enhancing artificial selection for climate resilience. Therefore, understanding the conditions under which correlations between CID and WUE occur is essential for accurately interpreting results and effectively applying them in breeding programs. The use of CID with advanced breeding techniques is crucial

for developing sustainable agricultural practices in the face of climate change.

Drought indices

Breeding of wheat varieties to improve their drought tolerance is a significant step in achieving food security. Selection measures are required to identify the drought-tolerant wheat genotypes for the effective breeding. Grain yield is considered the basis of genotype selection for improving drought tolerance in plants (Anwaar et al. 2020). However, high grain yield potential under optimum conditions does not guarantee drought tolerance under severe drought stress (Mzileni 2023). Several studies have considered yield under both non-stress and drought stress conditions, as this is more efficient when selecting drought-tolerant wheat genotypes (Anwaar et al. 2020; Semahegn et al. 2020). Therefore, many drought tolerance indices have been proposed to screen drought-tolerant wheat genotypes based on grain yield produced under drought and non-stress conditions (Semahegn et al. 2020). These yield-based drought indices are presented in Table 2. Understanding the utilization of these drought indices is crucial for selecting drought-tolerant wheat genotypes.

Metabolomic analysis

Drought stress causes the expression of genes that influence the regulation of various metabolites such as proline and malate (Zhang et al. 2021b). These metabolites play crucial roles in improving drought tolerance because they work towards osmotic adjustments and scavenging of reactive oxygen species (Iqbal et al. 2018). The accumulation of specific metabolites improves WUE in wheat, especially

Table 2: List of formulae used to calculate drought-tolerant indices

Indices	Formulae	Description	References
Tolerance index (TOL)	$TOL = Y_p - Y_s$	Measures the genotype's drought tolerance based on yield differences.	Rosielle and Hamblin (1981)
Stress susceptibility index (SSI)	$SSI = \dfrac{1 - \dfrac{Ys}{Yp}}{1 - \dfrac{\bar{Ys}}{\bar{Yp}}}$	Evaluates the relative susceptibility of a genotype to drought.	Fischer and Maurer (1978)
Mean productivity (MP)	$MP = \dfrac{Yp + Ys}{2}$	Calculates the average yield of a genotype.	Ramirez-Vallejo and Kelly (1998)
Geometric mean productivity (GMP)	$GMP = (Yp \times Ys)^{\frac{1}{2}}$	Accounts for variability in yield performance across environments.	Ramirez-Vallejo and Kelly (1998)
Harmonic mean (HM)	$HM = \dfrac{2(Ys \times Yp)}{Yp + Ys}$	Measures cultivar performance based on mean yield response.	Jafari et al. (2009)
Stress tolerance index (STI)	$STI = \dfrac{Yp \times Ys}{\bar{Y}_p^2}$	Quantify yield performance and drought tolerance.	Fernandez (1992)
Yield index (YI)	$YI = \dfrac{Ys}{\bar{Y}_s}$	Compares individuals' performance relative to the average of all the test genotypes.	Gavuzzi et al. (1997)
Yield stability index (YSI)	$YSI = \dfrac{Ys}{Yp}$	Assesses stability by comparing yields under stress to potential yields and discerns genotype ranking.	Bouslama and Schapaugh (1984)
Drought susceptibility index (DSI)	$DSI = \dfrac{Ys - Yp}{Yp}$	Measures the sensitivity of a genotype to drought based on yield performance.	Fischer and Maurer (1978)

Y_p = mean yield of the genotype under non-stress, Y_s = mean yield of the genotype under stress, $\bar{Y}_p$ = mean yield of all genotypes under non-stress, and $\bar{Y}_s$ = mean yield of all genotypes under stress

under drought stress conditions (Budak et al. 2015). During drought stress, amino acid metabolism plays a significant role in drought stress response by providing building blocks for proteins and signalling molecules (Ghorbanzadeh et al. 2023). The synthesis of proline has been shown to improve drought tolerance and WUE in wheat. This corroborates with Khan et al. (2025), who highlighted the importance of proline accumulation in enhancing drought resilience. Plant metabolism profiling has been done using technological platforms such as LC-MS (Hall et al. 2022) and others. These technological platforms identify specific metabolic pathways that modulate plant responses to drought stress and enhance WUE. The studies indicate that manipulating metabolic pathways involved in osmolyte biosynthesis and antioxidant biosynthesis offers the potential to improve drought tolerance.

Simultaneous selection of traits
Simultaneous selection of several traits is fundamental in plant breeding programs to release desirable varieties with the required product profiles. Hence, ascertaining the magnitude and trend of multiple traits is vital to guide selection and reveal their contribution in enhancing drought tolerance and WUE. Wheat varieties require a combination of traits to thrive in diverse environmental conditions. This provides an opportunity to meet the demands of modern agriculture. In addition, simultaneous selection for multiple traits in wheat breeding increases the value of cultivars. Several authors have targeted common traits such as yield potential (Mathew et al. 2019; Shamuyarira et al. 2022) and grain quality attributes to meet end-users' demand (Agami et al. 2019).

Correlation analysis plays a crucial role in simultaneously selecting several traits by evaluating the relationships between yield components (Akram et al. 2008). The high correlations between traits indicate shared genetic or physiological mechanisms. This facilitates the identification of key traits associated with drought tolerance and WUE (Singh et al. 2017). Understanding trait correlations helps to prioritise their selection, identify trade-offs and design breeding strategies for balanced and stable wheat varieties. Several studies have employed principal component analysis to investigate multivariate patterns of selection in wheat and make breeding strategies for improving yield and drought tolerance (Mwadzingeni et al. 2016; Mathew et al. 2019; Shamuyarira et al. 2022). Therefore, simultaneous selection of traits guided by correlation analysis and multivariate analysis presents a robust framework for understanding genetic and environmental factors affecting agronomic performances.

In addition, path coefficient analysis has been conducted on wheat genotypes to evaluate traits that contribute directly and indirectly to higher grain yield and drought tolerance (Jamro and Rashid 2017). This technique visualises the relationships between traits as interconnected pathways or networks. The analysis provides insights into trait interactions and trade-offs and helps inform breeding strategies to develop resilient wheat varieties. For instance, Denčić et al. (2000) found that agronomic traits directly influencing grain yield under stress included the number of tillers, grains per spike, and number of spikes. The substantial number of grains per spike

compensates for diminished grain weight under drought conditions (Mwadzingeni et al. 2016), indicating the importance of this trait in drought tolerance. Additionally, longer spikes boost grain number, which is valuable under stress conditions (Thomas et al. 2017). Therefore, path analysis assists in evaluating complex traits and guiding the development of the next generation of drought-tolerant wheat cultivars.

Conclusion

Drought stress presents significant challenges to wheat production and productivity, especially in arid regions. Addressing these challenges requires drought-tolerant cultivars, the application of conservation agriculture, and the use of CID. Innovations in molecular breeding and precision agriculture are vital for resilient cultivars and optimised resource use. Management strategies must align with sustainable agriculture practices. Collaboration among researchers, farmers, and policymakers is key to promoting food security under climate variability.

Author contributions — (Authors' name abbreviations: MM = Maltase Mutanda, HS = Hussein Shimelis, SF = Sandiswa Figlan and VC = Vincent Chaplot) Conceptualization: MM, HS, SF and VC; Writing original draft: MM, HS, SF and VC Writing review and editing: MM, HS, SF and VC; Funding acquisition: HS, SF and VC; Supervision: HS, SF and VC; Investigation: HS, SF and VC; Validation: HS, SF and VC; Project administration: HS and SF; Resources: SF and HS

Conflict of interest — The authors declare that they have no known competing financial interests or personal relationship that could have appeared to influence the work reported in this paper.

ORCID iDS

Maltase Mutanda — http://orcid.org/0009-0008-3881-5834
Hussein Shimelis — http://orcid.org/0000-0003-2793-8392
Vincent Chaplot — http://orcid.org/0000-0001-5430-362X
Sandiswa Figlan — http://orcid.org/0000-0003-0395-8612

References

Abioye EA, Abidin MSZ, Mahmud MSA, Buyamin S, Ishak MHI, Abd Rahman MKI, Ramli MSA. 2020. A review on monitoring and advanced control strategies for precision irrigation. *Computers and Electronics in Agriculture* 173: 105441.

Acharya BS, Bhandari M, Bandini F, Pizarro A, Perks M, Joshi DR, Sharma S. 2021. Unmanned aerial vehicles in hydrology and water management: Applications, challenges, and perspectives. *Water Resources Research* 57: e2021WR029925.

Adeyemi O, Grove I, Peets S, Norton T. 2017. Advanced monitoring and management systems for improving sustainability in precision irrigation. *Sustainability* 9: 353.

Adhikari L, Raupp J, Wu S, Koo DH, Friebe B, Poland J. 2023 Genomic characterization and gene bank curation of *Aegilops*: the wild relatives of wheat. *Frontiers in Plant Science.* 14:1268370.

Agami RA, Alamri SAM, Abd El-Mageed TA, Abousekken MSM. 2019. Salicylic acid and proline enhance water use efficiency, antioxidant defense system and tissues' anatomy of wheat plants under field deficit irrigation stress. *Journal of Applied Botany and Food Quality* 92: 360–370.

Akram Z, Ajmal SU, Munir M. 2008. Estimation of correlation coefficient among some yield parameters of wheat under rainfed conditions. *Pakistan Journal of Botany* 40: 1777–1781.

Ali S, Manzoor AJ, Sohail A, Khan A, Khan MI, Khan MI. 2018. Soil amendments strategies to improve water-use efficiency and productivity of maize under different irrigation conditions. *Agricultural Water Management* 210: 88–95.

Alotaibi M, El-Hendawy S, Mohammed N, Alsamin B, Refay Y. 2023. Appropriate application methods for salicylic acid and plant nutrients combinations to promote morpho-physiological traits, production, and water use efficiency of wheat under normal and deficit irrigation in an arid climate. *Plants* 12 : 1368.

Amare A, Mekbib F, Tadesse W, Tesfaye K. 2019. Screening of drought tolerant bread wheat (*Triticum aestivum* L.) genotypes using yield-based drought tolerance indices. *Ethiopian Journal of Agricultural Sciences* 29: 1–16.

Amoak D, Kwao B, Ishola TO, Mohammed K. 2023. Climate change induced ecological grief among smallholder farmers in semi-arid Ghana. *SN Social Sciences* 3: 131.

Anwaar HA, Perveen R, Mansha MZ, Abid M, Sarwar ZM, Aatif HM, Khan KA. 2020. Assessment of grain yield indices in response to drought stress in wheat (*Triticum aestivum* L.). *Saudi Journal of Biological Sciences* 27: 1818–1823.

Arathi HS, Smith TJ. 2023. Drought and temperature stresses impact pollen production and autonomous selfing in a California wildflower, *Collinsia heterophylla. Ecology and Evolution* 13: e10324.

Arslan A, Zapata F, Kumarasinghe KS. 1999. Carbon isotope discrimination as indicator of water-use efficiency of spring wheat as affected by salinity and gypsum addition. *Communications in Soil Science and Plant Analysis* 30: 2681–2693.

Ayugi B, Eresanya EO, Onyango AO, Ogou FK, Okoro EC, Okoye CO, Anoruo CM, Dike VN, Ashiru OR, Daramola MT, Mumo R. 2022. Review of meteorological drought in Africa: historical trends, impacts, mitigation measures, and prospects. *Pure and Applied Geophysics* 179: 1365–1386.

Bapela T, Shimelis H, Tsilo TJ, Mathew I. 2022. Genetic improvement of wheat for drought tolerance: Progress, challenges and opportunities. *Plants* 11: 1331.

Bhandari U, Gajurel A, Khadka B, Thapa I, Chand I, Bhatta D, Shrestha J. 2023. Morpho-physiological and biochemical response of rice (*Oryza sativa* L.) to drought stress: A review. *Heliyon* 9: 13744.

Bouslama M, Schapaugh WT. 1984. Stress tolerance in soybeans. I. Evaluation of three screening techniques for heat and drought tolerance 1. *Crop Science* 24: 933–937.

Brar AS, Kaur K, Sindhu VK, Tsolakis N, Srai JS. 2022. Sustainable water use through multiple cropping systems and precision irrigation. *Journal of Cleaner Production* 333: 130117.

Brits E. 2023. Phenotyping labs to test plant responses to climate change. *Nature Africa*. Assessed on 5 November 2024 https://doi.org/10.1038/d44148-023-00335-5.

Budak H, Hussain B, Khan Z, Ozturk NZ, Ullah N. 2015. From genetics to functional genomics: improvement in drought signalling and tolerance in wheat. *Frontiers in Plant Science* 6: 1012.

Buthelezi S, Mutanga O, Sibanda M, Odindi J, Clulow AD, Chimonyo VG, Mabhaudhi T. 2023. Assessing the prospects of remote sensing maize leaf area index using UAV-derived multi-spectral data in smallholder farms across the growing season. *Remote Sensing* 15: 1597.

Bwalya B, Mutandwa E, Chiluba BC. 2023. Awareness and Use of Sustainable Land Management Practices in Smallholder Farming Systems. *Sustainability 15*: 14660.

Davies WJ, Kudoyarova G, Hartung W. 2005. Long-distance ABA signalling and its relation to other signalling pathways in the detection of soil drying and the mediation of the plant's response to drought. *Journal of Plant Growth Regulation* 24: 285–295.

Denčić S, Kastori R, Kobiljski B, Duggan B. 2000. Evaluation of grain yield and its components in wheat cultivars and landraces under near optimal and drought conditions. *Euphytica* 113: 43–52.

Dengxiao Z, Hongbin J, Wenjing Z, Qingsong Y, Zhihang M, Haizhong W, Wei R, Shiliang L, Daichang W. 2024. Combined biochar and water-retaining agent application increased soil water retention capacity and maize seedling drought resistance in Fluvisols. *Science of the Total Environment* 907: 167885.

Feng S, Ding W, Shi C, Zhu X, Hu T, Ru Z. 2023. Optimizing the spatial distribution of roots by supplemental irrigation to improve grain yield and water use efficiency of wheat in the north China plain. *Agricultural Water Management* 275: 107989.

Fernandez GC. 1992. Effective selection criteria for assessing plant stress tolerance. In *Proceeding of the International Symposium on Adaptation of Vegetables and other Food Crops in Temperature and Water Stress, August. 13–16, Shanhua, Taiwan*. Pp 257–270.

Fischer RA, Maurer R. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. *Australian Journal of Agricultural Research* 29: 897–912.

Food and Agriculture Organization. 2023. *The State of Food Security and Nutrition in the World 2023*. Rome: FAO.

Food and Agriculture Organization. 2024. *FAO Statistical Yearbook 2024*. Rome: FAO.

Gahlaut V, Jaiswal V, Singh S, Balyan HS, Gupta PK. 2019. Multi-locus genome wide association mapping for yield and its contributing traits in hexaploid wheat under different water regimes. *Scientific Reports* 9: 19486.

Gavuzzi P, Rizza F, Palumbo M, Campanile RG, Ricciardi GL, Borghi B. 1997. Evaluation of field and laboratory predictors of drought and heat tolerance in winter cereals. *Canadian Journal of Plant Science* 77: 523–531.

Ghorbanzadeh Z, Hamid R, Jacob F, Zeinalabedini M, Salekdeh GH, Ghaffari MR. 2023. Comparative metabolomics of root-tips reveals distinct metabolic pathways conferring drought tolerance in contrasting genotypes of rice. *BMC Genomics* 24*: 1–20.

González FG, Capella M, Ribichich KF, Curín F, Giacomelli JI, Ayala F, Watson G, Otegui ME, Chan RL. 2019. Field-grown transgenic wheat expressing the sunflower gene HaHB4 significantly outyields the wild type. *Journal of Experimental Botany* 70: 1669–1681.

Hall O, Dahlin S, Marstorp H, Archila Bustos MF, Öborn I, Jirström M. 2018. Classification of maize in complex smallholder farming systems using UAV imagery. *Drones* 2: 22.

Hall RD, D'Auria JC, Ferreira ACS, Gibon Y, Kruszka D, Mishra P, Van de Zedde R. 2022. High-throughput plant phenotyping: a role for metabolomics?. *Trends in Plant Science* 27: 549–563.

Harrison EL, Arce Cubas L, Gray JE, Hepworth C. 2020. The influence of stomatal morphology and distribution on photosynthetic gas exchange. *The Plant Journal* 101*: 768–779.

He Q, Li Liu D, Wang B, Cowie A, Simmons A, Waters C, Li L, Feng P, Li Y, de Voil P, Huete A. 2023. Modelling interactions between cowpea cover crops and residue retention in Australian dryland cropping systems under climate change. *Agriculture, Ecosystems and Environment* 353: 108536.

Hu YC, Shao HB, Chu LY, Gang W. 2006. Relationship between water use efficiency (WUE) and production of different wheat

genotypes at soil water deficit. *Colloids and Surfaces B: Biointerfaces* 53: 271–277.

Hudson BD. 1994. Soil organic matter and available water capacity. *Journal of Soil and Water Conservation* 49: 189–194.

Hussain T, Hussain N, Tahir M, Raina A, Ikram S, Maqbool S, Fraz Ali M, Duangpan S. 2022. Impacts of drought stress on water use efficiency and grain productivity of rice and utilization of genotypic variability to combat climate change. *Agronomy* 12: 2518.

Iqbal MJ. 2018. Role of osmolytes and antioxidant enzymes for drought tolerance in wheat. *Global Wheat Production* 51: 51–66.

Ito M, Matsumoto T, Quinones MA. 2007. Conservation tillage practice in sub-Saharan Africa: the experience of Sasakawa Global 2000. *Crop Protection* 26: 417–423.

Jafari A, Paknejad F, Jami AM. 2009. Evaluation of selection indices for drought tolerance of corn (*Zea mays* L.) hybrids. *International Journal of Plant Production* 3: 33–38.

Jain M, Kataria S, Hirve M, Prajapati R. 2019. Water deficit stress effects and responses in maize. *Plant Abiotic Stress Tolerance: Agronomic, Molecular and Biotechnological Approaches*: 1: 129–151.

Jamro SA, Rashid A. 2017. Significance of chemical priming on yield and yield components of wheat under drought stress. *American Journal of Plant Sciences* 8: 1339–1344.

Kala ESM. 2023. Challenges of Technology in African Countries: A Case Study of Zambia. *Open Journal of Safety Science and Technology* 13: 202–230.

Kaur B, Sandhu KS, Kamal R, Kaur K, Singh J, Röder MS, Muqaddasi QH. 2021. Omics for the improvement of abiotic, biotic, and agronomic traits in major cereal crops: Applications, challenges, and prospects. *Plants* 10: 1989.

Khan P, Abdelbacki AM, Albaqami M, Jan R, Kim KM. 2025. Proline promotes drought tolerance in maize. *Biology* 14: 41.

Kimura H, Hashimoto-Sugimoto M, Iba K, Terashima I, Yamori W. 2020. Improved stomatal opening enhances photosynthetic rate and biomass production in fluctuating light. *Journal of Experimental Botany* 71: 2339–2350.

Kimurto PK, Kinyua MG, Njoroge JM. 2003. Response of bread wheat genotypes to drought simulation under a mobile rain shelter in Kenya. *African Crop Science Journal* 11: 225–234.

Kumar S, Yadav A, Kumar A, Hasanain M, Shankar K, Karan S, Dayal P. 2023. Climate Smart Irrigation Practices for Improving Water Productivity in India. A Comprehensive Review. *International Journal of Environment and Climate Change* 13: 333–348.

Lemma AZ, Hailemariam FM, Abebe KA, Bishaw Z. 2021. Evaluation of durum wheat (*Triticum turgdium* var *durum*) genotypes for drought tolerance using morpho-agronomic traits. *Journal of Plant Breeding and Crop Science* 13: 216–225.

Li H, Yang Y, Wang H, Liu S, Jia F, Su Y, Li, S, He F, Feng C, Niu M, Wang J. 2021. The receptor-like kinase ERECTA confers improved water use efficiency and drought tolerance to poplar via modulating stomatal density. *International Journal of Molecular Sciences* 22: 7245.

Li Q, Li H, Zhang L, Zhang S, Chen Y. 2018. Mulching improves yield and water-use efficiency of potato cropping in China: a meta-analysis. *Field Crops Research* 221: 50–60.

Li Y, Li H, Li Y, Zhang S. 2017. Improving water-use efficiency by decreasing stomatal conductance and transpiration rate to maintain higher ear photosynthetic rate in drought-resistant wheat. *The Crop Journal* 5: 231–239.

Li Y, Song X, Li S, Salter WT, Barbour MM. 2020. The role of leaf water potential in the temperature response of mesophyll conductance. *New Phytologist* 225: 1193–1205.

Liang Z, Zhang F, Shao M, Zhang J. 2002. The relations of stomatal conductance, water consumption, growth rate to leaf water potential during soil drying and rewatering cycle of wheat (*Triticum aestivum*). *Botanical Bulletin of Academia Sinica* 43.

Liebenberg A, van der Nest JR, Hardie AG, Labuschagne J, Swanepoel PA. 2020. Extent of soil acidity in no-tillage systems in the Western Cape Province of South Africa. *Land* 9: 361.

Liu J, Bu L, Zhu L, Luo S, Chen X, Li S. 2014. Optimizing plant density and plastic film mulch to increase maize productivity and water-use efficiency in semiarid areas. *Agronomy Journal* 106: 1138–1146.

Lv L, Chen X, Li H, Huang J, Liu Y, Zhao A. 2022. Different adaptive patterns of wheat with different drought tolerance under drought stresses and rehydration revealed by integrated metabolomic and transcriptomic analysis. *Frontiers in Plant Science* 13: 1008624.

Makebe A, Shimelis H, Mashilo J. 2024. Selection of M5 mutant lines of wheat (*Triticum aestivum* L.) for agronomic traits and biomass allocation under drought stress and non-stressed conditions. *Frontiers in Plant Science* 15: 1314014.

Mallareddy M, Thirumalaikumar R, Balasubramanian P, Naseeruddin R, Nithya N, Mariadoss A, Vijayakumar S. 2023. Maximizing water use efficiency in rice farming: A comprehensive review of innovative irrigation management technologies. *Water* 15: 1802.

Mao H, Jian C, Cheng X, Chen B, Mei F, Li F, Kang, Z. 2022. The wheat ABA receptor gene TaPYL1-1B contributes to drought tolerance and grain yield by increasing water-use efficiency. *Plant Biotechnology Journal* 20: 846–861.

Martínez-Goñi XS, Miranda-Apodaca J, Pérez-López U. 2023. Could buckwheat and spelt be alternatives to wheat under future environmental conditions? Study of their physiological response to drought. *Agricultural Water Management* 278: 108176.

Mashingaidze AB, Madakadze IC, Twomlow S, Hove L. 2019. Tillage systems for smallholder farmers under semi-arid conditions: Implications on soil hydrological properties, soil water content and maize yield. *Soil and Tillage Research* 194: 104329.

Mathew I, Shimelis H, Mutema M, Clulow A, Zengeni R, Mbava N, Chaplot V. 2019. Selection of wheat genotypes for biomass allocation to improve drought tolerance and carbon sequestration into soils. *Journal of Agronomy and Crop Science* 205: 385–400.

Mbava N, Mutema M, Zengeni R, Shimelis H, Chaplot V. 2020. Factors affecting crop water use efficiency: A worldwide meta-analysis. *Agricultural Water Management* 228: 105878.

Mdluli SY, Shimelis H, and Mashilo J. 2020. Screening for pre-and post-anthesis drought responses in selected bread wheat (*Triticum aestivum* L.) genotypes. *Acta Agriculturae Scandinavica, Section B—Soil and Plant Science* 70: 272–284.

Mensah AK, Frimpong KA. 2018. Biochar and/or compost applications improve soil properties, growth, and yield of maize grown in acidic rainforest and coastal savannah soils in Ghana. *International Journal of Agronomy* 1: 6837404

Mhazo N, Chivenge P, Chaplot V. 2016. Tillage impact on soil erosion by water: discrepancies due to climate and soil characteristics. *Agriculture, Ecosystems and Environment* 230: 231–241.

Mmbando GS. 2025. Tiller number: an essential criterion for developing high-yield and stress-resilient cereal crops. *Archives of Agronomy and Soil Science* 71: 1–21.

Muhammad M, Abdul W, Abdul W, Muhammad M, Muhammad N, Yong-Hong L, Li L, Wen-Jun L. 2023. Soil salinity and drought tolerance: An evaluation of plant growth, productivity, microbial diversity, and amelioration strategies. *Plant Stress* 11: 100319.

Mutanda M, Chaplot V, Shimelis H, Shamuyarira KW, Figlan S. 2024. Determinants of the accuracy of using carbon isotopes in estimating water use efficiency of selected cereal and legume crops: A global perspective. *Food and Energy Security* 13: e522.

Mwadzingeni L, Shimelis H, Tesfay S, Tsilo TJ. 2016. Screening of bread wheat genotypes for drought tolerance using phenotypic and proline analyses. *Frontiers in Plant Science* 7: 182193.

Mzileni LS. 2023. Investigation into response of wheat genotypes to drought and optimum conditions in the Eastern Cape Province, South Africa. PhD thesis, Fort Hare University, South Africa.

Nikolaeva MK, Maevskaya SN, Shugaev AG, Bukhov NG. 2010. Effect of drought on chlorophyll content and antioxidant enzyme activities in leaves of three wheat cultivars varying in productivity. *Russian Journal of Plant Physiology* 57: 87–95.

Nyaupane S, Poudel MR, Panthi B, Dhakal A, Paudel H, Bhandari R. 2024. Drought stress effect, tolerance, and management in wheat–a review. *Cogent Food and Agriculture* 10: 2296094.

Omotoso AB, Letsoalo S, Olagunju KO, Tshwene CS, Omotayo AO. 2023. Climate change and variability in sub-Saharan Africa: A systematic review of trends and impacts on agriculture. *Journal of Cleaner Production* 141: 137487.

Oyekale AS, Olalekan AF, Afolabi WA. 2017. Impact of Minimum Tillage Adoption on Farmers' Income in Nigeria: An Endogenous Switching Regression Approach. *Sustainability* 9: 868.

Peng Z, Wang L, Xie J, Li L, Coulter JA, Zhang R, Choudhary S. 2019. Conservation tillage increases water use efficiency of spring wheat by optimizing water transfer in a semi-arid environment. *Agronomy* 9: 583.

Plett DC, Ranathunge K, Melino VJ, Kuya N, Uga Y, Kronzucker HJ. 2020. The intersection of nitrogen nutrition and water use in plants: new paths toward improved crop productivity. *Journal of Experimental Botany* 71: 4452–4468.

Ramirez-Vallejo P, Kelly JD. 1998. Traits related to drought resistance in common bean. *Euphytica* 99: 127–136.

Rezaly R, Shabri A. 2024. Enhancing drought prediction precision with EEMD-ARIMA modelling based on standardized precipitation index. *Water Science and Technology* 89: 745–770

Rao RN, Williams JH, Wadia KDR, Hubick KT, Farquhar GD. 1993. Crop growth, water-use efficiency and carbon isotope discrimination in groundnut (*Arachis hypogaea* L.) genotypes under end-of season drought conditions. *Annals of Applied Biology* 122: 357–367.

Renó V, Cardellicchio A, Romanjenko BC, Guadagno CR. 2024. AI-assisted image analysis and physiological validation for progressive drought detection in a diverse panel of Gossypium hirsutum L. *Frontiers in Plant Science* 14: 1305292.

Rosielle AA, Hamblin J. 1981. Theoretical aspects of selection for yield in stress and non-stress environment 1. *Crop Science* 21: 943–946.

Sachdev S, Ansari SA, Ansari MI, Fujita M, Hasanuzzaman M. 2021. Abiotic stress and reactive oxygen species: Generation, signalling, and defense mechanisms. *Antioxidants* 10: 277.

Salam A, Ali A, Afridi MS, Ali S, Ullah Z. 2022. Agrobiodiversity: Effect of Drought Stress on the Eco-physiology and Morphology of Wheat. In: Öztürk M, Khan SM, Altay V, Efe R, Egamberdieva D, Khassanov FO (eds), *Biodiversity, Conservation and Sustainability in Asia*. Cham: Springer. https://doi.org/10.1007/978-3-030-73943-0_33.

Sattar A, Sher A, Ijaz M, Ullah MS, Ahmad N, Umar UU. 2020. Individual and combined effect of terminal drought and heat stress on allometric growth, grain yield and quality of bread wheat. *Pakistan Journal of Botany* 52: 405–412.

Scholes R, Engelbrecht F. 2021. Climate impacts in southern Africa during the 21st Century. *Report for Earthjustice and the Centre for Environmental Rights*. Global Change Institute, University of Witwatersrand, South Africa.

Schweiger R, Maidel AM, Renziehausen T, Schmidt-Schippers R, Müller C. 2023. Effects of drought, subsequent waterlogging and redrying on growth, physiology and metabolism of wheat. *Physiologia Plantarum* 175: e13874.

Semahegn Y, Shimelis H, Laing M, Mathew I. 2020. Evaluation of bread wheat (*Triticum aestivum* L.) genotypes for yield and related traits under drought stress conditions. *Acta Agriculturae Scandinavica, Section B—Soil and Plant Science* 70: 474–484.

Sewore BM, Abe A, Nigussie M. 2023. Evaluation of bread wheat (*Triticum aestivum* L.) genotypes for drought tolerance using morpho-physiological traits under drought-stressed and well-watered conditions. *PloS One* 18: e0283347.

Shamuyarira KW. 2018. Early generation selection of bread wheat (*Triticum aestivum L.*) genotypes for drought tolerance. PhD thesis, University of KwaZulu-Natal, South Africa

Shamuyarira KW, Shimelis H, Mathew I, Shayanowako A, Zengeni R, Chaplot V. 2022. Comparative genetic diversity analysis for biomass allocation and drought tolerance in wheat. *Agronomy* 12: 1457.

Silva JV, Jaleta M, Tesfaye K, Abeyo B, Devkota M, Frija A, Habarurema I, Tembo B, Bahri H, Mosad A. 2023. Pathways to wheat self-sufficiency in Africa. *Global Food Security* 37: 100684.

Singh O, Dwivedi SK, Shukla RS, Samaiya RK, Upadhayay A, Vasht D, Singh M, Prajapati BS. 2017. Correlation studies in diverse lines of wheat (*Triticum aestivum* L.) under Restricted Irrigation. *International Journal of Pure and Applied Bioscience* 5: 379–388.

Sithole NJ, Magwaza LS, Mafongoya PL. 2016. Conservation agriculture and its impact on soil quality and maize yield: A South African perspective. *Soil and Tillage Research* 162: 55–67.

Soba D, Shu T, Runion GB, Prior SA, Fritschi FB, Aranjuelo I, Sanz-Saez A. 2020. Effects of elevated [CO_2] on photosynthesis and seed yield parameters in two soybean genotypes with contrasting water use efficiency. *Environmental and Experimental Botany* 178: 104154.

Szechyńska-Hebda M, Ghalami RZ, Kamran M, Van Breusegem F, Karpiński S. 2022. To be or not to be? Are reactive oxygen species, antioxidants, and stress signalling universal determinants of life or death? *Cells* 11: 4105.

Tadesse W, Bishaw Z. Assefa S. 2018. Wheat production and breeding in Sub-Saharan Africa: Challenges and opportunities in the face of climate change. *International Journal of Climate Change Strategies and Management* 11: 696–715.

Thabet SG, Moursi YS, Karam MA, Börner A, Alqudah AM. 2020. Natural variation uncovers candidate genes for barley spikelet number and grain yield under drought stress. *Genes* 11: 533.

Thomas N, Marker S, Lal GM, Dayal A. 2017. Study of heterosis for grain yield and its components in wheat (*Triticum aestivum*) over normal and heat stress condition. *Journal of Pharmacognosy and Phytochemistry* 6: 824–830.

Thungo Z, Shimelis H, Odindo AO, Mashilo J. 2020. Assessment of terminal drought tolerance among elite wheat (*Triticum aestivum* L.) genotypes using selected agronomic and physiological traits. *Acta Agriculturae Scandinavica, Section B—Soil and Plant Science* 70: 177–194.

Tshikunde NM, Odindo A, Shimelis H, Mashilo J. 2018. Leaf gas exchange and water-use efficiency of dry-land wheat genotypes under water stressed and non-stressed conditions. *Acta Agriculturae Scandinavica, Section B—Soil and Plant Science* 68: 738–748.

Vassileva V, Georgieva M, Zehirov G, Dimitrova A. 2023. Exploring the genotype-dependent toolbox of wheat under drought stress. *Agriculture* 13: 1823.

Wan C, Dang P, Gao L, Wang J, Tao J, Qin X, Gao J. 2022. How does the environment affect wheat yield and protein content response to drought? A meta-analysis. *Frontiers in Plant Science* 13: 896985.

Wang JY, Mo F, Zhou H, Kavagi L, Nguluu SN, Xiong YC. 2021. Ridge–furrow with grass straw mulching farming system to boost rainfed wheat productivity and water use efficiency in semiarid Kenya. *Journal of the Science of Food and Agriculture* 101: 3030–3040.

Wang LF, Shangguan ZP. 2015. Water–use efficiency of dryland wheat in response to mulching and tillage practices on the Loess Plateau. *Scientific Reports* 5: 12225.

Wu J, Wang J, Hui W, Zhao F, Wang P, Su C, Gong W. 2022. Physiology of plant responses to water stress and related genes: A review. *Forests* 13: 324.

Xiao Q, Bai X, Zhang C, He Y. 2022. Advanced high-throughput plant phenotyping techniques for genome-wide association studies: A review. *Journal of advanced research 35:* 215-230.

Yan S, Weng B, Jing L, Bi W. 2023. Effects of drought stress on water content and biomass distribution in summer maize (*Zea mays* L.). *Frontiers in Plant Science* 14: 1118131.

Yılmaz P, Babat CF, Yılmaz C. 2023. Comparison of short-term physiological and biochemical effects of drought stress on two wheat cultivars. *Brazilian Archives of Biology and Technology* 66: e23220705.

Yu L, Zhao X, Gao X, Jia R, Yang M, Yang X, Siddique KH. 2021. Effect of natural factors and management practices on agricultural water use efficiency under drought: A meta-analysis of global drylands. *Journal of Hydrology* 594: 125977.

Zahoor I, Hasan H, Gul A, Khursheed A, Ali M, Amir R, Zarrar F. 2020. Molecular mechanism of drought tolerance in wheat. In *Climate Change and Food Security with Emphasis on Wheat*. Boston: Academic Press. pp 129–154.

Zahra N, Wahid A, Hafeez MB, Ullah A, Siddique KH, Farooq M. 2021. Grain development in wheat under combined heat and drought stress: Plant responses and management. *Environmental and Experimental Botany* 188: 104517.

Zhang C, Chen J, Huang W, Song X, Niu J. 2021a. Transcriptomics and metabolomics reveal purine and phenylpropanoid metabolism response to drought stress in Dendrobium sinense, an endemic orchid species in Hainan Island. *Frontiers in Genetics* 12: 692702.

Zhang L, Yan S, Zhang S, Yan P, Wang J, Zhang H. 2021b. Glutathione, carbohydrate and other metabolites of Larix olgensis A. Henry response to polyethylene glycol-simulated drought stress. *PloS One 16*: e0253780.

Zhang Q, Wang Z, Miao F, Wang G. 2017. Dryland maize yield and water-use efficiency responses to mulching and tillage practices. *Agronomy Journal* 109: 1196–1209.

Zhao H, Wang L, Liu L, Hou X, Zhang Y. 2020. Effects of different irrigation levels on water use efficiency and fruit quality of cherry tomatoes in greenhouses. *Agriculture* 10: 307**.**

Zhao H, Zhao Z, An L, Chen T, Wang X, Feng H. 2009. The effects of enhanced ultraviolet-B radiation and soil drought on water use efficiency of spring wheat. *Journal of Photochemistry and Photobiology B: Biology* 94: 54–58.

Zou Y, Saddique Q, Ali A, Xu J, Khan MI, Qing M, Siddique KH. 2021. Deficit irrigation improves maize yield and water use efficiency in a semi-arid environment. *Agricultural Water Management* 243:106483.