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DROUGHT TOLERANCE IN MAJOR CROPS: PHYSIOLOGICAL TRAITS AND BREEDING STRATEGIES

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ABSTRACT

Droughts are occurring more frequently and intensively due to climate change, posing a significant threat to crop cultivation and food security. This review examines the morphological traits, cellular adaptations, and breeding behaviours that enable major crops to endure drought. We highlight some of the most important characteristics: root growth, stomatal regulation, adaptation to water stress, resistance to oxidation, and the resistance of some plants to staying green. We discuss the mechanisms by which these characteristics are regulated by the hormone abscisic acid, by important genes such as DREB, NAC, and WRKY, protective proteins, and DNA modification. Other new breeding technologies, such as marker-assisted and genome-based selection, CRISPR editing, rapid screening of multiple plants, and the use of beneficial microbes, have accelerated the deployment of these traits and demonstrated real benefits in laboratory and field experiments. Nevertheless, drought tolerance is a multi-gene process, with limited field testing across various locations and social and policy barriers remaining. We propose an integrated workflow that combines multiple data types, AI to select the most suitable plants, and farmer-led experiments to introduce novel varieties sooner. We indicate that unpopular crops such as millets may be suitable for climate-smart breeding.

Keywords: Drought resilience, Physiological traits, Molecular mechanisms, Breeding, Climate-smart crops.

Introduction

Climate change is intensifying droughts and increasing their frequency, jeopardizing food security and agricultural output. According to reports from the Intergovernmental Panel on Climate Change (IPCC, 2022) and the Food and Agriculture Organisation (FAO, 2023), large areas of cropland worldwide are becoming vulnerable to water shortages. The effect of drought is to disrupt water relations, photosynthesis, and nutrient assimilation, and to cause significant yield losses, such as a 40% decrease in maize yield and a 2030% reduction in wheat yield under severe stress conditions (Aslam *et al.*, 2022; Mahobe *et al.*, 2025), but with genotypic and environmental variations in responses.

The mechanization of crop adaptation to drought relies on coordinated physiological changes. Stomatal control saves on water but reduces CO₂ uptake (Ramachandra *et al.*, 2024). Deep and extensive roots increase water absorption in soils and yield stability, as observed in sorghum genotypes with high root biomass (Frantova *et al.*, 2024). The use of compatible solutes and increased antioxidant activity is an osmotic adjustment that helps preserve cellular integrity during oxidative stress (Singh *et al.*, 2020).

Drought responses are coordinated at the molecular level by abscisic acid (ABA)-dependent signalling pathways and stress-sensitive transcription factors, including members of the DREB and NAC families. Empirical evidence supporting the positive

interplay between transgenic overexpression of the *DREB1A* transcription factor and yield stability has been demonstrated in rice (Hassan *et al.*, 2023). Other phenomena, such as epigenetics and DNA methylation patterns, also regulate stress adaptation in crop species, as demonstrated in *Zea mays* (Qiao *et al.*, 2025).

These understandings have been incorporated into breeding programs. The introgression of drought-associated QTLs in wheat has been enabled by marker-assisted selection (Gouda *et al.*, 2020), and genetic gain in complex traits in maize has been increased through genomic selection (Khahani *et al.*, 2021). CRISPR-Cas9 editing of genes associated with ABA has improved water-use efficiency in sorghum (Shaheen *et al.*, 2023), and transgenic methods have been used to insert stress-responsive genes into rice (Su *et al.*, 2006). Nevertheless, drought tolerance is also polygenic and environmentally specific, requiring multi-trait breeding and improved phenotyping platforms (Srivastava *et al.*, 2022). This review is a synthesis of physiological, molecular, and breeding approaches to drought tolerance in staple crops and sets priorities for producing climate-resistant varieties.

Physiological impacts of drought on crops

Drought stress disrupts plant function at various levels, from subcellular metabolism to overall plant growth. Water imbalance in soils disrupts water relations, carbon assimilation, and cellular redox balance, thereby limiting biomass growth and ultimate yield. The features that make drought adaptation and drought resilience possible are only possible with a clear understanding of these physiological disturbances.

Water relations

Water deficit in soils reduces turgor and water potential in plants, thereby limiting cell expansion and biomass accumulation. One of the main short-term responses is stomatal closure, which decreases transpiration but also limits CO₂ diffusion and photosynthesis (Ramachandra *et al.*, 2024). Maize in extreme drought has been found to experience rapid declines in leaf water potential, leading to stomatal closure within hours and limiting temporary productivity (Sultana *et al.*, 2025).

Photosynthesis

The effects of drought on photosynthesis are through stomatal (CO₂ restrictions) and non-stomatal (biochemical) pathways. Low CO₂ concentration, reduced Rubisco activity, and reduced ATP production inhibit carbon fixation, whereas excess light may lead to PSII photoinhibition (Wang *et al.*, 2018). As field

and chamber studies indicate, photosynthetic decreases of about 20-30 per cent are observed under moderate stress, and greater decreases are observed under extreme drought (Chen *et al.*, 2024). The C3 crops (rice, wheat) tend to be more sensitive than the C4 species, including sorghum (Wang *et al.*, 2012).

Oxidative stress

The lack of water disrupts electron transport in chloroplasts and mitochondria, leading to the overproduction of reactive oxygen species (ROS), including superoxide and H₂O₂. The damage to membranes, proteins and nucleic acids, facilitating the lipid peroxidation and cell viability loss, is promoted by ROS (Cruz *et al.*, 2008). The presence of antioxidant enzymes (superoxide dismutase, catalase, peroxidases) reduces ROS levels, although in extreme cases or during prolonged drought, these mechanisms can be overwhelmed; high levels of oxidative markers have been observed in stressed rice (Yaqoob *et al.*, 2022; Hasanuzzaman *et al.*, 2020).

Growth and development

Drought has been shown to limit vegetation growth and inhibit reproduction. Root reactions are subject- and condition-specific: some crops reduce root elongation during extreme deficit, and others, like sorghum, increase the rooting depth to access deeper water layers (Kang *et al.*, 2022). Growth of shoots, the increase in leaf area, and stem extension are reduced under water stress, and the growth phases are especially sensitive; drought at the anthesis stage of maize may not only shorten the period of grain-filling but also decrease the final yield (Kim *et al.*, 2023). These developmental effects highlight the need for breeding traits that can maintain vegetative and reproductive success in intermittent and terminal drought.

Main physiological traits for drought resilience

The emergence of drought resilience results in a restricted range of recurrent attributes to increase water acquisition, support water preservation, and maintain cellular integrity. The brief descriptions of traits that follow, along with example illustrations and breeding relevance, outline the main physiological characteristics, the mechanisms behind them, the crops they represent, and the selective implications, as summarised in Table 1.

Root architecture

The more extensive and deeper root systems enhance access to soil moisture and are frequently associated with greater yield consistency during water scarcity. Root depth loci introgressed to improve water

extraction (e.g., DRO1 in rice and others) have been shown to confer yield benefits under drought conditions (Adjah *et al.*, 2022; Ghazy *et al.*, 2024). Root ideotypes should be considered in relation to the particular soil profile and rainfall regime, as in some environments, deeper roots can be at the expense of early-season vigour.

Stomatal control and transpiration efficiency

Stomatal aperture and stomatal density are coordination mechanism that balances between the conservation of water and the uptake of CO₂. The experimental studies have shown that the stimulation of stomatal control mechanisms, e.g., *SIAREB1* in *Solanum lycopersicum*, reduces transpirational water loss; breeding programs to boost water-use efficiency (WUE) have also been shown to yield a measurably positive increase in wheat (Korwin *et al.*, 2023; Fan *et al.*, 2018). Even though these characteristics are beneficial under terminal or intermittent drought conditions, field validation would be required to assess the potential yield compromises accurately.

Osmotic adjustment and compatible solutes

Low water potential is compensated for by the accumulation of proline, glycine betaine, and other osmolytes, which help maintain cell turgor and enzyme activity. Osmotic adjustment tends to be associated with enhanced stress-induced growth maintenance; putative yield responses in maize and rice depend on genotype and stress severity (Ghosh *et al.*, 2021). The osmotic characteristics are polygenic and environmentally sensitive; in this case, selection should involve physiological screening, with molecular phenotypes where possible.

Leaf structural traits and stay-green

Water loss is minimized, and photosynthesis is extended in grain filling by leaf cuticle characteristics (wax load), lower specific leaf area and stay-green phenotypes. Waxier leaves and stay-green alleles (such as *Gpc-B1* effects in wheat and analogous effects in sorghum) have been linked to the enhancement of chlorophyll retention and grain-filling during drought (Mohammed *et al.*, 2018; Kamal *et al.*, 2019; Sultana *et al.*, 2021). The importance of these characteristics is determined by the timing of drought relative to the reproductive periods.

Antioxidant defences and cellular protection

The increased antioxidant activity, including superoxide dismutase (SOD), catalase, and peroxidases, and protective proteins, including the late embryonic abundant (LEA) proteins and dehydrins, removes oxidative damage and stabilizes cellular

structures when they are subjected to drought. Genotypes with drought tolerance are more likely to exhibit better reactive oxygen species (ROS) scavenging, which helps maintain membrane integrity and cell viability (Singh *et al.*, 2020). Breeding-wise, the introduction of the antioxidant defence system needs to be complemented by traits such as root system structure, stomatal control, and osmotic adjustment. Since drought tolerance depends on environmental conditions, a multi-trait selection approach with field validation is essential to achieve stable performance.

Molecular and Genetic Basis of Drought Tolerance

Drought tolerance is regulated by linked groups of molecules that respond to environmental cues and control how the plant reacts. The systems in the plant interact during drying, as illustrated in Figure 1. These links involve hormonal signalling, gene regulation, protein protection, and modifications in DNA packaging to control the plant's stress response.

ABA signalling pathway

Abscisic acid (ABA) is the primary hormone involved in stomata closure as well as activation of stress response genes in plants. The key participants include *NCED*, which generates ABA; *PYL* receptors; and *SnRK2* kinases, which induce downstream transcriptional responses. Manipulating these parts alters plant drought response, such as *NCED3* overexpression, which increases ABA and enables rice to conserve water (Ma *et al.*, 2024), and manipulating *PYL* or *SnRK2* activity can improve measured tolerance in maize and other crops (Kaderbek *et al.*, 2025; Kumar *et al.*, 2026). *SnRK2*s are ideal engineering targets due to their positive stress response, but their extensive biological effects on growth should be considered.

Transcription factors (TFs)

TF families such as *DREB*, *NAC*, and *WRKY* control gene clusters that help the plant respond to stress, including osmolyte production, ion transport, and chaperone activities. Enhancing TF activity has enabled the development of drought-tolerant varieties across various crops. *DREB2A* and other such genes, for instance, increase the activity of stress in wheat (Zhou *et al.*, 2020). The superior root characteristics and water balance in rice are associated with *SNAC1*-type *NAC*s (Liu *et al.*, 2014). TF strategies are powerful and may be disadvantageous. Their application in breeding or genetic engineering is more practical when tested in real field conditions and with stress- or tissue-specific promoters.

Protective proteins

During dehydration, membranes and proteins are stabilized by late embryogenesis abundant (LEA) proteins, dehydrins, and heat-shock proteins. Empirical evidence confirms that the expression of given LEA/dehydrin genes is associated with enhanced cellular hydration and greater yield stability under drought conditions (Goyal *et al.*, 2005; Sun *et al.*, 2021). These proteins are useful biomarkers and transgenic targets, particularly when coupled with features that maintain cellular water status.

Epigenetic regulation and stress memory

Histone modifications and chromatin remodelling, as well as DNA methylation, play key roles in regulating the expression of drought-responsive genes and may be involved in forming stress memory. Changes in methylation caused by drought have been linked to disparate performance in stress-sensitive genes in maize (Wang *et al.*, 2021); on the other hand, histone acetylation trajectories mediate the drought-sensitive expression of rice (Li *et al.*, 2021). Together with abscisic acid (ABA) signalling elements, transcription factors and protective proteins, epigenetic regulators are key molecular targets for crop enhancement. However, their effects are often genotype- and environment-specific, making the combination of physiological screening and multi-environment field validation invaluable for developing stable agronomic benefits.

Breeding and biotechnological approaches for drought tolerance

The drought-tolerant cultivar approach requires combining phenotypic selection with molecular and biotechnological modalities. The following is a brief, literature-based review of some of the most important

methodologies, outlining their strengths and weaknesses. Table 2 summarises the main breeding and biotechnological strategies, their underpinning, advantages, limitations, and suitability for complex traits.

Conventional breeding

Traditional breeding is a method of selecting for drought-adaptive phenotypes (canopy temperature, biomass partitioning, WUE) through multi-environment trials and progressively higher-throughput phenotyping (infrared thermography, canopy sensors). Thermal images have been used to identify cooler canopies associated with stress-induced yield benefit (Correia *et al.*, 2022). Traditional programs are not particularly ineffective but are time-consuming and benefit from integration with molecular tools.

Marker-assisted selection (MAS)

MAS targets QTLs that control important traits (such as root depth and stomatal behaviour). In specific backgrounds, introgression of *DRO1* and associated loci into rice has enhanced deep rooting and drought tolerance (Arai-Sanoh *et al.*, 2014; Adjah *et al.*, 2022). MAS reduces the time required to select for major-effect loci, but it is less effective for highly polygenic traits unless combined with genomic techniques (Gupta *et al.*, 2017).

Genomic selection (GS)

GS is a technique that predicts complex traits using genome-wide markers and also speeds up selection. The GS research on maize and other cereals reports quantitative genetic gains in the drought-adaptive indices under testing conditions (McMillen *et al.*, 2022; Khahani *et al.*, 2021). GS is effective for yield stability but requires extensive, well-organized training groups and strong phenotyping.

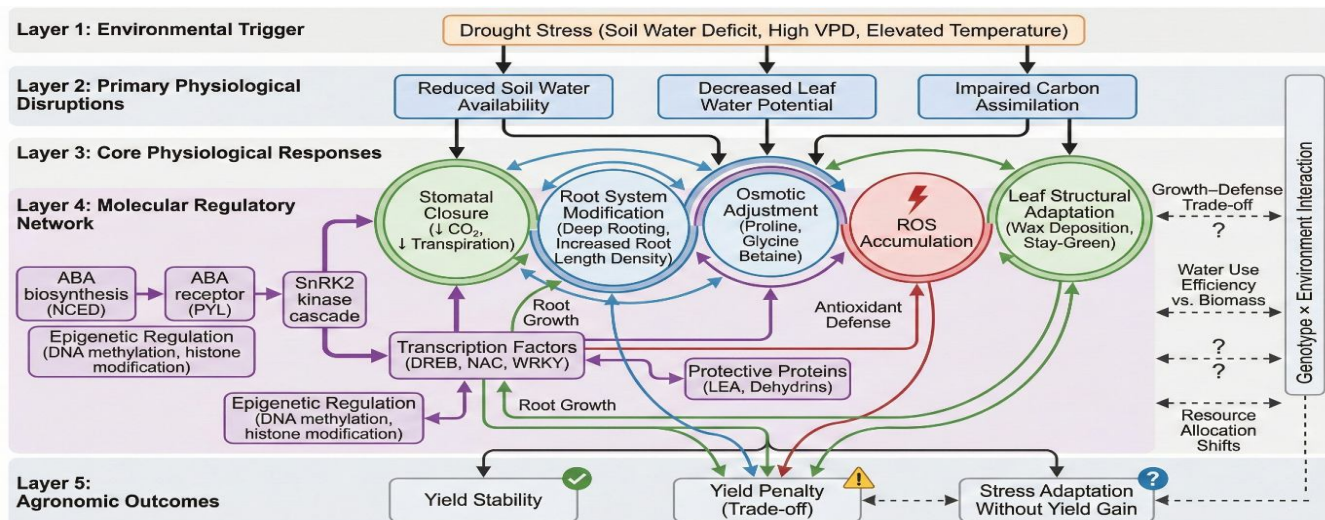


Fig. 1 : Integrated physiological and molecular responses of crops under drought stress.

(Conceptual model demonstrates the step-by-step response of crops to drought. The dry soil causes plants to lose water and use less carbon, hence plants change various processes such as their tiny openings (stomata), roots, water balance in the cell and antioxidants. These

changes are coordinated by the hormone ABA, stress genes, and changes that do not modify DNA. They jointly determine whether the crop is to retain its harvest or to make a loss as per the type of plant and the surrounding.)

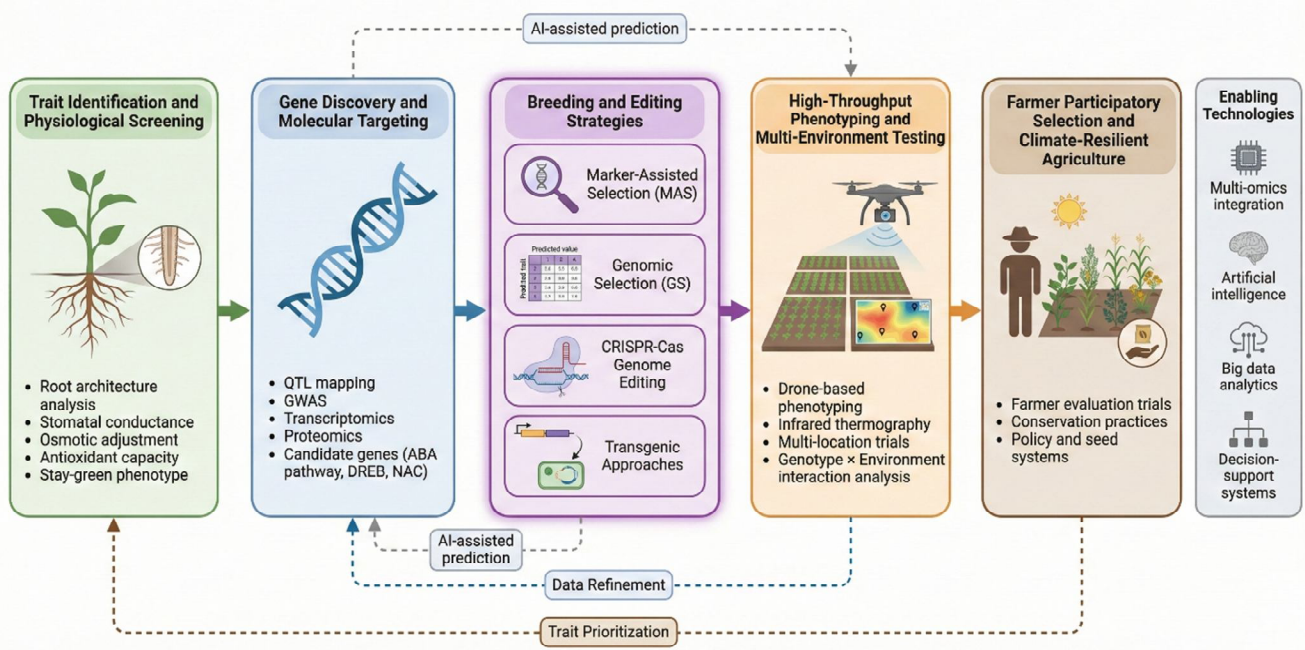


Fig. 2 : Integrated breeding pipeline for the development of drought-tolerant crop varieties.

(Flow diagram of a breeding system linking the acquisition of new traits to the farmers. The plan applies simple plant tests, gene analyses (such as QTL mapping and genomics), intelligent breeding (marker-assisted selection, genomic selection, gene editing), and rapid plant diagnostics with examinations in

numerous locations. It continues refining itself through the repetitive process based on the data provided by a great number of sources and AI. Farmers become engaged in testing and we apply the practices that can withstand the climate changes and the farmers embrace the new crops and they will gain benefits in the field.)

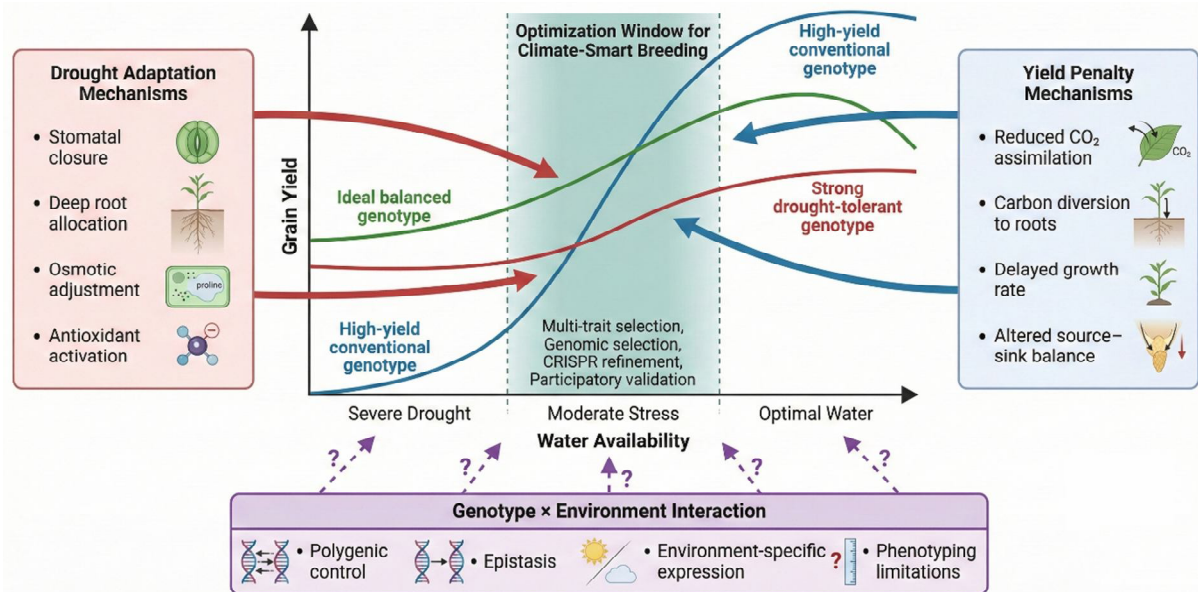


Fig. 3 : Conceptual trade-offs between drought tolerance and yield potential in crop breeding.

(In graphical model, the amount of water influence is displayed on the yield of grain in various varieties. Those that are high yielding perform well in the presence of sufficient water, but the yield reduces rapidly when water supply is limited. Drought adapted varieties remain stable, although they cannot achieve the same maximum yield. A balanced range of good results is the best breeding goal that can be attained with the help of choosing multiple good traits and enhancing genetics. The model illustrates the interaction of the plant genes with the environment and the number of genes in combination which dictate the stability of the yield under limited water supply.)

Genetic engineering and genome editing

Transgenic and CRISPR techniques have enabled researchers to modify genes associated with drought, such as the ABA pathway, stomatal development and transcription factors, with greater precision. For example, the ABA genes, including *OsERAI*, were edited, and changes in stomatal genes were introduced to enable rice and sorghum to use water more efficiently (Ma *et al.*, 2024; Kumar *et al.*, 2023). These methods have high payoffs but come with a checklist: they are regulated, prioritize safety, and are accepted by the public. Real-world testing and diligent examination for unintended side effects should be conducted.

Microbiome-assisted resilience

Interventions based on microbiomes, such as plant growth-promoting rhizobacteria (PGPR), can be used to promote drought resistance by stimulating root growth, enhancing nutrient uptake and altering stress-responsive signal transduction. Inoculation experiments with *Pseudomonas* and other beneficial strains have reported improved growth, yield, and root biomass under drought conditions in controlled and field-sampled conditions (Azeem *et al.*, 2022). Nevertheless, the microbiome-mediated effects are highly context-specific, as they differ across soils, climatic conditions, and cropping systems. To be used on a large scale, the application has to be standardized in formulations, deliveries have to be stable, and they must be multi-located and tested.

Integrated synthesis of breeding approaches

There is no particular breeding or biotechnological strategy that is adequate for stable drought tolerance. Favourable results will be more likely to be achieved through complementary loci phenotyping, marker-assisted selection, and genome editing of key individual regulators, the microbiome, or agronomic interventions that shield against environmental variability. Multi-trait testing, robust multi-environment testing, and farmer-based testing are needed to translate genetic gains into consistent on-

farm performance. The relationship between these components in terms of breeding is presented in Figure 2.

Challenges and Future Directions

Challenges

Although progress has been made in physiology and molecular breeding, it remains challenging to convert drought tolerance into stable increases in yield. Other characteristics that contribute to water conservation, such as stomatal closure, can also reduce carbon assimilation under non-stress conditions. Similarly, a greater distribution of assimilates to root systems may limit grain growth under certain conditions (Frantová *et al.*, 2024). These trade-offs explain the complexity of drought adaptation.

Also, drought tolerance is both polygenic and broadly an environment \times genotype interaction, making it challenging to select across different agroecological zones. Numerous molecular and microbiome-based interventions show promising outcomes in controlled settings but perform differently in soils, climates, and management systems. Strong multi-location validation is thus a significant bottleneck. Figure 3 demonstrates the theoretical relationship between drought tolerance and yield stability under water conditions.

Future directions and priorities

Further developments will involve combining multi-trait selection, large-scale multi-environment geographic testing, and sophisticated phenotyping systems. The new precision-selection models have improved trait discrimination in specific breeding scenarios (Sharma *et al.*, 2024; Resende *et al.*, 2024), and more predictive breeding models are being developed using genomics, transcriptomics, and metabolomics together with transcription factors as targets (e.g. *DREB2A*) (Wang *et al.*, 2021; Ma *et al.*, 2024). Pilot programs have shown that farmer-participatory trials, in conjunction with complementary agronomic methods such as mulching, have higher adoption rates and greater soil moisture protection (Sahoo *et al.*, 2025; FAO, 2023). Increased work on climate-resistant crops that are underutilised, especially millets, can also enhance adaptation mechanisms in water-scarce areas. All in all, sustainable advancement in drought-resilient breeding relies on context-specific, multi-trait approaches that link molecular innovation to stable field performance and equitable access to technology.

Conclusion

The ability of crops to endure drought is influenced by the interplay among physiological characteristics, molecular control, and breeding technology. Stress adaptation is based on characteristics such as enhanced root architecture,

controlled stomatal behaviour, and osmotic adjustment, as well as on ABA signalling, transcription factors, and protective proteins, which provide molecular control of these functions. Drought tolerance is polygenic and environmental, and improved marker-assisted selection, genomic selection, and genome-editing technologies have only increased the rate at which it is

integrated. Multi-trait breeding, strong field validation, and the combination of omics-based prediction and participatory evaluation are needed for sustainable progress. Enhancing these strategies, especially for crops that are not well exploited, such as millets, will play a crucial role in building climate-resilient agriculture.

Table 1 : Major physiological traits associated with drought tolerance in crops

Trait Category	Specific Trait	Mechanism of Action Under Drought	Representative Crops	Key Genes / QTLs	Reported Effect Under Drought	Limitations / Trade-offs	References
Root Architecture	Deep rooting	Access to deeper soil moisture; improved water extraction	Rice, Sorghum, Wheat	<i>DRO1</i> , <i>Rht-B1</i>	Improved yield stability under terminal drought; increased water uptake efficiency	Higher carbon allocation to roots may reduce early shoot vigor	Arai-Sanoh <i>et al.</i> , 2014; Adjah <i>et al.</i> , 2022; Ghazy <i>et al.</i> , 2024
Root Biomass & Distribution	Increased root length density	Enhances soil water foraging capacity	Sorghum, Maize	Multiple QTLs	Associated with higher drought resilience in field trials	Environment-dependent; soil-type specific response	Frantová <i>et al.</i> , 2024
Stomatal Regulation	Rapid stomatal closure; optimized density	Reduces transpirational water loss; conserves water	Wheat, Tomato	<i>SIAREB1</i> , <i>ERA1</i>	Reduced water loss and improved WUE under stress	Reduced CO ₂ assimilation may limit yield under non-stress	Korwin <i>et al.</i> , 2023; Fan <i>et al.</i> , 2018
Osmotic Adjustment	Proline & glycine betaine accumulation	Maintains turgor pressure; protects enzymes and membranes	Rice, Maize	<i>P5CS</i> and related genes	Improved stress tolerance; better maintenance of growth	Metabolic cost; variable correlation with yield	Ghosh <i>et al.</i> , 2021
Leaf Structural Traits	Wax deposition; reduced leaf area	Limits cuticular water loss	Wheat	Wax-related loci	Lower transpiration rates under drought	May affect photosynthetic efficiency	Mohammed <i>et al.</i> , 2018
Stay-Green Phenotype	Delayed senescence; chlorophyll retention	Sustains photosynthesis during grain filling	Wheat, Sorghum	<i>Gpc-B1</i> and related loci	Improved grain filling under post-anthesis drought	Can delay remobilization of nutrients	Kamal <i>et al.</i> , 2019; Sultana <i>et al.</i> , 2021
Antioxidant Defense	Elevated SOD, CAT, APX activity	Detoxifies ROS; protects membranes	Rice, Wheat	Multiple stress-responsive genes	Reduced oxidative damage; improved cellular stability	Effective mainly under moderate stress	Singh <i>et al.</i> , 2020
Protective Proteins	LEA proteins, dehydrins	Stabilize proteins and membranes during dehydration	Rice, Maize	<i>OsLEA3</i> , <i>DHN5</i>	Associated with improved cellular hydration and yield stability	Often requires genetic modification	Goyal <i>et al.</i> , 2005; Sun <i>et al.</i> , 2021

Table 2 : Breeding and biotechnological strategies for improving drought tolerance

Approach	Core principle	Example crops	Target traits / genes	Advantages	Limitations	Field validation status	Suitability for polygenic traits	References
Conventional breeding	Phenotypic selection across environments; recurrent selection	Wheat, Sorghum, Maize, Rice	Canopy temperature, WUE, root traits, phenology	Proven, low-tech, accepted by farmers	Slow, requires multi-year trials; limited for small-effect loci	Well validated in many programs; many varieties released	Moderate (best when large-effect traits exist)	Correia <i>et al.</i> , 2022; Baloch <i>et al.</i> , 2023
Marker-assisted selection (MAS)	Select for known QTLs/major genes using markers	Rice, Wheat	<i>DRO1</i> (root depth), stomatal conductance QTLs	Speeds introgression of major loci; reduces phenotyping load	Less effective for highly polygenic traits; QTL × environment interactions	Validated for specific QTL introgressions (e.g., <i>DRO1</i>)	Low–Moderate	Arai-Sanoh <i>et al.</i> , 2014; Gouda <i>et al.</i> , 2020; Gupta <i>et al.</i> , 2017
Genomic selection (GS)	Genome-wide marker-based prediction of breeding values	Maize, Wheat, Rice	Genome-wide improvement for yield stability, WUE indices	Captures small-effect loci; accelerates cycle time	Needs large training populations; high-quality phenotypes required	Demonstrated genetic gains in breeding programs	High	Khahani <i>et al.</i> , 2021; McMillen <i>et al.</i> , 2022
Transgenic approaches	Introduce/overexpress stress-responsive genes	Rice, Maize	<i>DREB1A</i> , LEA genes, dehydrins	Strong phenotypes possible; proof-of-concept for many genes	Regulatory, biosafety and public acceptance hurdles; pleiotropy risk	Several greenhouse/field reports; limited commercial deployment	Variable (depends on trait architecture)	Su <i>et al.</i> , 2006; Sun <i>et al.</i> , 2021
CRISPR / genome editing	Precise editing (knockout/allele introgression)	Rice, Sorghum, Wheat	ABA-pathway genes (<i>ERA1</i> , <i>NCED</i>), stomatal density genes	Precise, rapid generation of alleles; can use native alleles to avoid transgene footprint	Off-target/pleiotropy risks; regulatory status varies by country	Promising field-level reports but scale-up ongoing	Moderate–High (best for major-effect targets and allele refinement)	Ma <i>et al.</i> , 2024; Kumar <i>et al.</i> , 2023; Shaheen <i>et al.</i> , 2023
Microbiome-assisted strategies	Use PGPR/beneficial consortia to boost root growth and stress signalling	Maize, Wheat, Various vegetables	Root biomass, nutrient uptake, systemic tolerance	Low-cost agronomic option; complements genetic solutions	Variable efficacy across soils/climates; formulation and delivery challenges	Positive field trials reported; large-scale replication limited	N/A (complements genetic approaches)	Azeem <i>et al.</i> , 2022
High-throughput phenotyping (HTP) & integration	Remote/automated measurement of target traits to improve selection accuracy	All major crops	Canopy temp, spectral indices, growth dynamics	Improves accuracy of selection; enables GS and MAS integration	Equipment cost; data management and analysis needed	Increasing adoption in breeding programs; shown to improve selection	Supports polygenic trait selection (enables GS)	Correia <i>et al.</i> , 2022; McMillen <i>et al.</i> , 2022

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