World Journal of Agriculture and Forestry Sciences
ISSN: 2960-0227
DOI: https://doi.org/10.61784/wjafs3021

BREEDING CROPS FOR CLIMATE RESILIENCE: STRATEGIES AND CHALLENGES FOR HEAT, DROUGHT, AND FLOOD TOLERANCE

Hannah Boahemaa Addai*, Conficious Nkrumah, Benjamin Yennuna Konyannik, Akwasi Agyapong Oppong-Agyemang, Gladys Alabilla, Gloria Naa Lamiley Lamptey, Prosper Ntow, James Nii Armah Okine, Paul Laari, Abdul-Wahab Rabiu
Department of Agrobiotechnology, Institute of Agriculture, RUDN University, Moscow 117198, Russia.
Corresponding Author: Hannah Boahemaa Addai, Email: addaihannahboahemaa@gmail.com

Abstract: Climate change intensifies abiotic stresses heat, drought, and flooding jeopardizing global food security by disrupting crop physiology and causing substantial yield losses. While conventional breeding has developed resilient varieties like submergence-tolerant "Scuba" rice and drought-tolerant maize, its slow pace and limited genetic diversity are inadequate for rapidly changing climates. This review synthesizes advances in breeding for climate resilience, highlighting the integration of traditional methods with modern tools. Genomic selection accelerates genetic gain for complex traits, CRISPR enables precise editing of genes for root architecture and stomatal regulation, and speed breeding shortens generation cycles. High-throughput phenomics and artificial intelligence further enhance predictive breeding. However, critical gaps persist, including a lack of multi-stress field validation, underutilized crop wild relatives, and trade-offs between stress tolerance and yield. Future efforts must prioritize integrative strategies that combine genomics, phenomics, and participatory approaches to develop resilient crops capable of sustaining productivity under compound climatic stresses, ensuring food security in the 21st century.

Keywords: Climate-resilient crops; Heat stress; Drought tolerance; Plant breeding; Crispr-cas9; Food security

1 INTRODUCTION

Climate change represents a paramount threat to global food security in the 21st century, driven by rising temperatures and an increased frequency of extreme weather events, including heat waves, prolonged droughts, and flooding [1,2]. These abiotic stresses disrupt key physiological processes in crops such as photosynthesis and reproductive development leading to significant yield losses across major agricultural regions [3]. The vulnerability of agricultural systems is exacerbated because modern high-yielding cultivars were typically developed under relatively stable climatic conditions and lack the genetic diversity needed for resilience to concurrent and interacting stresses [4,5].

Conventional plant breeding, while responsible for foundational successes such as drought-tolerant maize and submergence-tolerant "Scuba" rice, faces significant constraints in addressing the pace and complexity of climate change. Its limitations include long breeding cycles of 8-12 years, low heritability of complex traits due to strong genotype by environment (G×E) interactions, and the genetic bottleneck of modern breeding pools [6,7]. Consequently, there is a compelling need to integrate novel tools including genomic selection, CRISPR-Cas9 gene editing, and speed breeding into crop improvement pipelines to accelerate genetic gain and enhance resilience under dynamic environmental stresses [8].

This review synthesizes current knowledge on breeding for resilience to heat, drought, and flooding, with emphasis on physiological and genetic mechanisms, advances in conventional and molecular breeding, and the role of emerging technologies. A primary objective is to consolidate progress, from the introgression of major genes like Sub1A to the application of artificial intelligence in predictive breeding [9,10]. A second key aim is to identify critical research gaps, such as the lack of multi-stress screening protocols, limited field validation of candidate genes, and the underutilization of genetic resources from crop wild relatives and landraces [7]. By integrating evidence across disciplines, this review aims to inform researchers, breeders, and policymakers in the global effort to build climate-resilient agricultural systems.

1.1 To Identify Critical Research Gaps and Future Opportunities

The second objective is to identify persistent knowledge gaps, technological limitations, and implementation barriers that hinder the development and deployment of climate-resilient varieties at scale. These include the lack of multi-stress screening protocols, despite the increasing frequency of compound stress events such as heat and drought or flood and salinity [11]. There are also limited breeding efforts in non-rice crops, particularly for flood tolerance in maize, soybean, and wheat, which remain highly vulnerable to extreme rainfall and waterlogging [12,13]. Poor heritability of complex traits due to strong genotype and environment (G×E) interactions reduces the efficiency of phenotypic selection [6]. Additionally, there is underutilization of genetic diversity from crop wild relatives and landraces, which harbor valuable alleles for stress adaptation but are often excluded from elite breeding programs [14]. Limited validation of gene-edited or transgenic traits under field conditions, especially in smallholder farming systems, further constrains progress [15].

Barriers to scaling, including high costs of advanced technologies, weak seed systems, and misalignment between breeder priorities and farmer needs, also pose major challenges [16,17].

In identifying these gaps, the review also highlights future opportunities for innovation, such as integrating multi-omics data including genomics, transcriptomics, and metabolomics to unravel cross-stress regulatory networks. Expanding speed breeding and AI-powered prediction models can accelerate genetic gain in resource-limited settings. Strengthening participatory breeding approaches that incorporate local knowledge and socio-economic factors into variety development will help ensure relevance and adoption. Finally, developing open-access digital platforms for sharing phenotypic and genotypic data across institutions and countries, such as the DivSeek initiative [18], represents a crucial step toward global collaboration and data integration.

2 HEAT TOLERANCE IN CROPS

2.1 Physiological Impacts of Heat Stress

Rising global temperatures due to climate change pose a significant threat to agricultural productivity, with heat stress emerging as a major abiotic constraint affecting crop growth, development, and yield. When plants are exposed to temperatures above their optimal range typically 5-10°C above species-specific thresholds a cascade of physiological disruptions occurs, including impaired photosynthesis, reproductive failure, and premature aging [19]. These effects are particularly severe during critical growth stages such as flowering and grain filling, leading to substantial yield losses in staple crops like wheat, maize, rice, and soybean.

2.1.1 Reduced photosynthesis

Photosynthesis is one of the most heat-sensitive physiological processes in plants. Elevated temperatures disrupt both the light-dependent reactions and the Calvin-Benson cycle, leading to a decline in carbon fixation and biomass accumulation. High temperatures, particularly those exceeding 35°C, destabilize the oxygen-evolving complex (OEC) of Photosystem II (PSII), impairing electron transport and increasing reactive oxygen species (ROS) production. This damage results in reduced quantum yield and photochemical efficiency (Fv/Fm), which are widely used indicators of photosynthetic health. The key carbon-fixing enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) also loses activity at high temperatures, while its activase (RCA) is even more thermolabile. In wheat, RCA denatures at temperatures above 30°C, limiting Rubisco activation and reducing CO_2 assimilation by up to 70%.

Heat stress further induces stomatal closure to reduce water loss, which restricts CO_2 diffusion into leaves. However, even when stomatal conductance is maintained, non-stomatal limitations such as reduced mesophyll conductance and metabolic dysfunction dominate photosynthetic decline [20]. In rice, exposure to 40°C during the vegetative stage reduced net photosynthetic rate by 45% and chlorophyll content by 30%, directly correlating with lower biomass and grain yield [21]. Similarly, in soybean, photosynthesis declined by 50% under chronic heat stress (38/30°Cday/night), primarily due to impaired electron transport and Rubisco activity [22].

2.1.2 Pollen sterility and reproductive failure

The reproductive phase is highly sensitive to heat stress, with pollen development and fertilization being particularly vulnerable. Even short episodes of high temperature during flowering can cause pollen sterility, poor anther dehiscence, and reduced pollen viability, leading to poor seed set and yield loss. Pollen grains are metabolically active and highly sensitive to thermal disruption. Heat stress reduces starch accumulation, alters tapetum development, and increases oxidative damage in anthers. In maize, exposure to 38°C during tasseling reduced pollen viability by 60% and kernel set by 50%. High temperatures also accelerate flower development, shortening the window for successful pollination. In rice, temperatures above 35°C during microspore development cause spikelet sterility, with each 1°C increase above 33°C reducing grain yield by 10%. Similarly, in wheat, heat stress during anthesis disrupts pollen tube growth and ovule viability, leading to unfertilized florets [23]. In legumes and vegetables, heat stress results in flower drop and poor fruit set. Tomato plants exposed to 35°C showed an 80% reduction in fruit set due to impaired pollen germination and style elongation. These reproductive failures are often irreversible, making heat tolerance during flowering one of the most critical targets in breeding programs for climate resilience.

2.1.3 Accelerated senescence

Heat stress accelerates leaf senescence, the programmed degradation of cellular components, leading to premature loss of photosynthetic capacity and reduced grain filling duration (see Table 1). Hormonal regulation plays a major role in this process, as heat stress increases ethylene and abscisic acid (ABA) levels while reducing cytokinins, thereby shifting the plant's metabolism toward catabolism. This hormonal imbalance triggers chlorophyll degradation, membrane disintegration, and nutrient remobilization. Elevated temperatures also cause oxidative stress by increasing the production of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2) and superoxide radicals, which can overwhelm antioxidant defense systems including superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). This imbalance leads to lipid peroxidation and protein denaturation, while malondialdehyde (MDA) levels, a marker of oxidative damage, rise significantly under heat stress. In wheat and barley, heat stress during grain filling shortens the photosynthetically active period by 7-10 days, thereby reducing grain weight and overall yield. A study in South Asia found that terminal heat stress reduced wheat yield by 20-30% due to accelerated senescence and shortened grain-filling duration [24]. This premature aging not only diminishes yield potential but also compromises grain quality, including protein concentration and milling characteristics, ultimately affecting both productivity and market value.

Table 1 Physiological Impacts of Heat Stress

Crop	Critical Stage	Heat Threshold	Key Impact
Wheat	Anthesis - Grain Filling	>30°C	Pollen sterility, reduced grain weight
Maize	Tasseling - Silking	>35°C	Pollen death, poor kernel set
Rice	Flowering	>35°C	Spikelet sterility, 10% yield loss/°C
Soybean	Flowering - Pod Set	>38°C	Flower drop, reduced pod number
Tomato	Pollination	>32°C	Poor fruit set, blossom drop

Source: [21,23,25]

2.2 Conventional Breeding Approaches

Conventional plant breeding remains a cornerstone of efforts to develop heat-tolerant crop varieties, particularly in resource-limited settings where advanced biotechnologies may be inaccessible. Unlike transgenic or gene-editing approaches, conventional breeding relies on phenotypic selection, controlled crosses, and recurrent selection to accumulate favorable alleles for thermotolerance. Key strategies include the utilization of heat-adapted landraces, hybrid breeding, and selection for physiological and morphological traits such as the stay-green phenotype, canopy temperature depression, and reproductive resilience [26].

2.2.1 Utilization of heat-tolerant landraces and traditional varieties

Landraces locally adapted, farmer-maintained crop varieties have evolved under diverse environmental stresses, including high temperatures, making them valuable genetic reservoirs for heat tolerance. These genotypes often exhibit superior phenological plasticity, root architecture, and stress memory, enabling survival and productivity under extreme thermal conditions. For example, in wheat, Indian landraces such as Kharaba and Kharchia Local show exceptional thermotolerance due to early flowering, reduced canopy temperature, and high membrane stability. In maize, traditional varieties from West Africa (e.g., the TZEE series) maintain pollen viability and kernel set under 38°C heat stress, attributed to efficient antioxidant systems and osmotic adjustment. In rice, landraces from arid zones of India and Pakistan exhibit lower spikelet sterility under high temperatures, linked to enhanced anther dehiscence and pollen adhesion.

These landraces are widely used as donor parents in breeding programs to introgress heat tolerance into high-yielding but temperature-sensitive modern cultivars. For instance, the International Maize and Wheat Improvement Center (CIMMYT) has incorporated alleles from heat-tolerant landraces into elite wheat lines, producing varieties with 10-15% higher grain yield under terminal heat stress. However, significant challenges persist in exploiting landraces effectively. Linkage drag remains a common issue, as undesirable traits such as low yield potential or poor grain quality may be co-inherited with heat-tolerant alleles. Additionally, limited genetic diversity within elite breeding pools restricts the scope for improvement and slows progress in broadening adaptive traits.

To address these limitations, participatory plant breeding (PPB) and on-farm conservation of landraces are being promoted to preserve agro-biodiversity and enhance adaptive capacity. Such approaches integrate farmers directly into the selection process, ensuring that the resulting varieties are not only resilient to heat stress but also suited to local preferences and production systems. This strategy strengthens the genetic base of breeding programs while maintaining the cultural and ecological significance of traditional crop varieties.

2.2.2 Hybrid breeding for heat resilience

Hybrid breeding leverages heterosis (hybrid vigor) to produce offspring with superior performance under stress conditions. In crops like maize, rice, and sorghum, hybrid varieties often outperform inbred lines in heat-prone environments due to enhanced physiological efficiency and stress buffering (Figure 1-3).

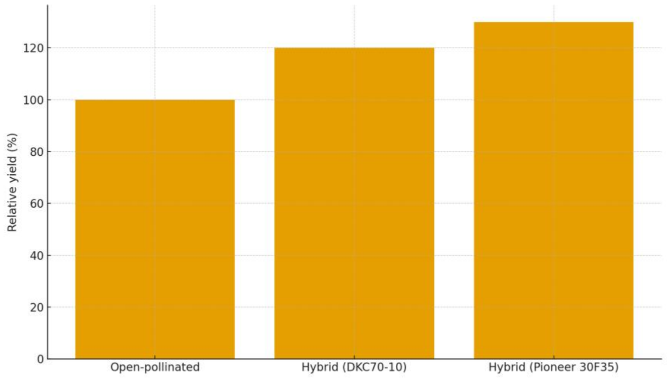

Figure 1 Maize Hybrids (e.g., DKC70-10, Pioneer 30F35) Yield 20-30% Higher Than Open-Pollinated Varieties under Heat Stress due to Improved Root Growth, Delayed Senescence, and Water Use Efficiency.

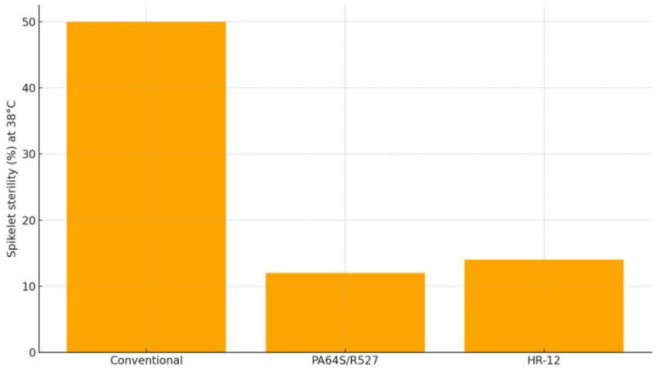

Figure 2 Heat-Tolerant Rice Hybrids (PA64S/R527, HR-12) Exhibit <15% Spikelet Sterility at 38°C Compared to >50% in Conventional Varieties, Showing Strong Adaptation for Warm Irrigated and Rainfed Systems [21].

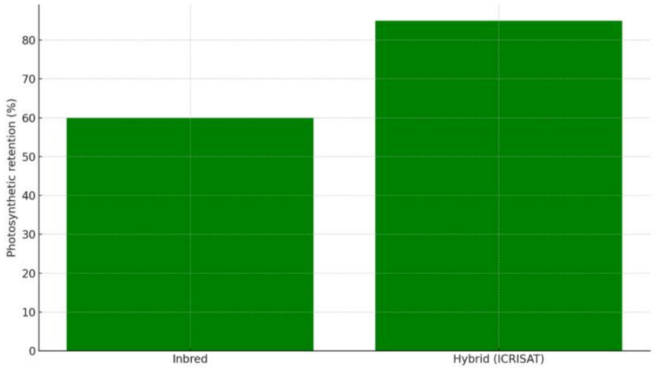

Figure 3 Sorghum Hybrids Developed by ICRISAT Retain 85% Photosynthetic Activity under Heat Stress, compared to 60% in Inbred Lines, due to Improved Panicle Cooling and Stay-Green Traits [27].

2.2.2.1 CIMMYT heat tolerant wheat nursery (HTWN)

The HTWN evaluates hundreds of wheat lines annually under terminal heat stress (>35°C), identifying promising hybrids for South Asia and North Africa (Figure 4). While hybrids offer superior performance, seed cost and annual repurchase remain barriers to adoption among smallholders.

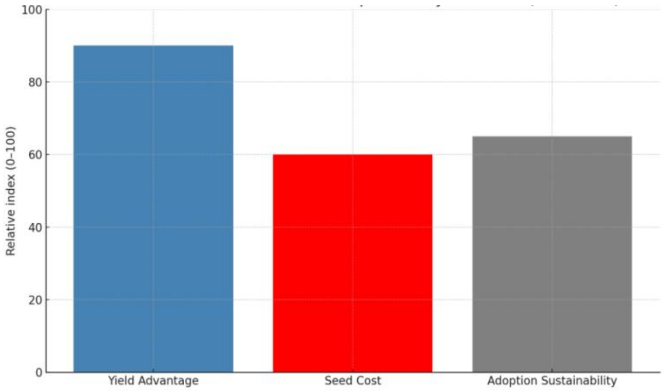

Figure 4 CIMMYT's Heat Tolerant Wheat Nursery (HTWN) Screens Lines under >35°C Terminal Heat. While Hybrid Performance Indices are High, Seed Cost and Adoption Sustainability Remain Challenges.

2.2.3 Selection for key physiological and morphological traits

Conventional breeding has increasingly focused on indirect selection for traits correlated with heat tolerance, allowing breeders to improve thermotolerance without direct heat exposure during every generation. The stay-green phenotype, characterized by delayed senescence under stress, is one of the most widely used indicators of heat and drought resilience. It reflects sustained chlorophyll retention, photosynthetic activity, and nitrogen remobilization during grain filling. In sorghum, stay-green varieties like SC56 and R16 maintain green leaf area for 10-14 days longer than non-stay-green types, resulting in 25-40% higher grain yield under heat and drought stress [27]. In maize, stay-green hybrids show improved nitrogen use efficiency and kernel weight, contributing to yield stability in warm environments. In wheat, delayed senescence is associated with higher canopy temperature depression (CTD), indicating better transpirational cooling and water status. Genetic studies have identified quantitative trait loci (QTLs) linked to stay-green, such as Stg1 in sorghum, enabling marker-assisted backcrossing even in conventional breeding pipelines.

Canopy temperature depression (CTD), the difference between air temperature and leaf canopy temperature is a reliable proxy for stomatal conductance and transpirational cooling. Cooler canopies indicate better water status and heat avoidance. In wheat, lines with high CTD (≥4°C) under heat stress yield 15-20% more than warmer canopies. In maize, CTD is used as a selection criterion in breeding programs to identify genotypes with superior root systems and water uptake capacity.

Selection for reproductive-stage resilience focuses on traits such as pollen viability, anther dehiscence, spikelet fertility, and flowering time adjustment to avoid peak heat. For example, in rice, breeders select for genotypes that flower early in the morning (before 9:00 AM), when temperatures are lower, thereby reducing spikelet sterility [21]. Similarly, in wheat, early-maturing varieties are favored in heat-prone regions to escape terminal stress.

While conventional breeding relies on phenotypic selection, it is increasingly enhanced by modern tools. Marker-assisted selection (MAS) accelerates the introgression of known QTLs, such as qHTS1 for heat tolerance in rice. Genomic selection (GS) predicts breeding values using genome-wide markers, and high-throughput phenotyping tools such as infrared thermography for CTD and drone-based canopy greenness monitoring provide rapid and non-destructive evaluations. These integrations allow conventional breeding programs to achieve faster genetic gains without requiring full transition to molecular breeding.

2.3 Molecular and Genomic Approaches

Advances in molecular biology and genomics have revolutionized the study of heat tolerance in crops, enabling researchers to move beyond phenotypic selection and identify the genetic basis of thermotolerance. These tools quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), marker-assisted selection (MAS), and functional genomics are accelerating the development of heat-resilient varieties by pinpointing key genes and alleles associated with stress response mechanisms [3]. Among the most well-characterized are heat shock proteins (HSPs), which play a central role in protecting cellular structures under thermal stress.

2.3.1 Quantitative Trait Loci (QTL) mapping

Quantitative Trait Loci (QTL) mapping identifies genomic regions associated with complex traits such as heat tolerance by analyzing co-segregation of molecular markers and phenotypic variation in bi-parental populations (e.g., F_2, RILs). In wheat, several QTLs linked to heat tolerance have been identified on chromosomes 1B, 2D, and 5A, associated with traits such as canopy temperature depression (CTD), membrane stability, and grain filling duration [28]. For example, a major QTL on chromosome 5A explains up to 28% of variation in grain yield under terminal heat stress. In rice, QTLs such as qHTS1 (on chromosome 4) and qHTSF4.1 (chromosome 4) are associated with spikelet fertility under high temperature, with near-isogenic lines (NILs) showing 15-25% higher fertility than susceptible parents [21]. In maize, QTLs for pollen viability and anthesis-silking interval (ASI) have been mapped to chromosomes 1, 3, and 9, helping breeders select for reproductive resilience [29]. While powerful, QTL mapping has limitations such as being confined to the genetic variation between two parents, low resolution across large genomic intervals, and often environment-specific expression. Nonetheless, these QTLs serve as starting points for marker-assisted backcrossing (MABC) and gene cloning, providing a foundation for molecular breeding programs to build upon.

2.3.2 Genome-Wide Association Studies (GWAS)

GWAS overcomes some limitations of QTL mapping by scanning diverse germplasm panels (e.g., landraces, elite lines) for marker-trait associations across the entire genome, leveraging historical recombination for higher resolution. In wheat, GWAS using 90K SNP arrays identified 45 significant markers associated with heat tolerance indices, including chlorophyll content, membrane stability, and yield under stress [30]. Key SNPs were located near genes involved in antioxidant defense and protein folding. In rice, GWAS revealed loci on chromosomes 1, 3, and 6 associated with spikelet fertility and pollen germination under heat stress (>35°C). One SNP near the OsHSP101 gene explained 12% of phenotypic variance. In sorghum, GWAS identified markers linked to stay-green trait and delayed senescence, with candidate genes involved in chlorophyll degradation and ABA signaling.

GWAS enables the discovery of novel alleles from unadapted germplasm and supports genomic prediction models for breeding. However, it requires large, well-phenotyped populations and careful correction for population structure.

2.3.3 Marker-Assisted Selection (MAS)

Marker-Assisted Selection (MAS) integrates molecular markers linked to heat tolerance traits into conventional breeding programs, allowing early, non-destructive selection without phenotyping under stress conditions. CIMMYT's wheat program uses MAS to pyramid multiple QTLs for heat tolerance (e.g., QYld.cimmyt-5A, QCTD.cimmyt-4B) into elite lines, resulting in varieties with 10-18% higher yield under heat stress. In rice, MAS for qHTS1 has been used to develop heat-tolerant lines for South Asia, where spikelet sterility is a major constraint. In maize, markers for short ASI and high pollen viability are used to select hybrids with improved kernel set under high temperatures [29]. MAS reduces breeding cycles, increases selection accuracy, and minimizes linkage drag. When combined with genomic selection (GS), it enables rapid genetic gain even for polygenic traits, making it a key bridge between traditional and advanced molecular breeding frameworks.

2.3.4 Candidate genes for heat tolerance

Functional genomics has identified several candidate genes that regulate heat stress responses. Among these, heat shock proteins (HSPs) play a central role as molecular chaperones that prevent protein denaturation, assist in refolding damaged proteins, and stabilize cellular structures under stress. HSP100/ClpB is essential for thermotolerance in Arabidopsis and rice; OsHSP101 overexpression enhances seed set under heat stress. HSP90 regulates signal transduction and hormone receptors, with knockdown lines showing increased heat sensitivity. HSP70, a ubiquitous chaperone, binds to unfolded proteins and improves photosynthetic efficiency under stress. Small HSPs (sHSPs), such as sHSP16.9 in wheat, are rapidly upregulated within minutes of heat exposure. HSPs are regulated by heat shock transcription factors (HSFs), particularly HSFA1, HSFA2, and HSFB2b, which activate HSP gene expression upon temperature rise. Heat stress also induces oxidative damage through reactive oxygen species (ROS); thus, antioxidant genes like SOD (superoxide dismutase), CAT (catalase), and APX (ascorbate peroxidase) play protective roles [31].

Osmoprotectant biosynthesis genes such as P5CS and BADH enhance osmotic adjustment and cellular protection [32]. Developmental regulators like Erecta in Arabidopsis control stomatal density and cooling, while Stay-Green (Sgr) genes delay chlorophyll degradation and extend grain filling. Modern breeding integrates these molecular insights through speed breeding, MAS, genomic selection, and high-throughput phenotyping to validate gene function under field conditions. For example, CIMMYT's Heat Tolerant Wheat Yield (HTWY) pipeline uses QTL-guided MAS, GWAS-informed selection, and physiological screening to develop heat-resilient varieties released in India, Pakistan, and Sudan.

3 DROUGHT STRESS MECHANISMS

3.1 Water-Use Efficiency (WUE)

Water-use efficiency (WUE) is defined as the amount of biomass produced per unit of water transpired (g biomass/mm H_2O) or grain yield per unit of evapotranspiration (kg grain/mm H_2O). It reflects a plant's ability to maximize carbon gain while minimizing water loss, making it a central trait in drought-prone environments. WUE is closely linked to stomatal regulation and photosynthetic capacity. Under drought, plants often reduce stomatal conductance (g_s) to limit transpiration, but this can also restrict CO_2 influx and suppress photosynthesis. However, some genotypes maintain high WUE by uncoupling these processes, achieving conservative water use without sacrificing carbon fixation.

Carbon isotope discrimination ($\Delta^{13}C$) is widely used as a proxy for WUE. Plants with lower $\Delta^{13}C$ values discriminate less against ^{13}C during CO_2 diffusion, indicating longer stomatal closure and higher WUE. In wheat and barley, selection for low $\Delta^{13}C$ has led to varieties with 10-15% higher grain yield under drought. In wheat, modern semi-dwarf varieties exhibit higher WUE due to reduced canopy size and improved radiation interception, while tropical maize hybrids like TZEE-W combine early vigor with high WUE, maintaining yields under intermittent drought. In sorghum, C_4 photosynthesis inherently confers higher WUE approximately two to three times that of C_3 crops making it a model for drought resilience [27]. Despite its importance, WUE must be balanced with growth rate and yield potential, as excessively conservative water use can delay development or reduce biomass accumulation, especially in environments with sporadic rainfall.

3.2 Root Traits and Soil Water Exploration

Root system architecture plays a pivotal role in drought adaptation by enabling deeper and more extensive soil exploration for water. Unlike above-ground traits, roots are difficult to phenotype, but advances in imaging and phenotyping platforms have revealed key characteristics associated with drought tolerance. Deep rooting allows access to subsoil moisture reserves unavailable to shallow-rooted genotypes. In wheat, rooting depth greater than two meters is associated with improved performance under terminal drought [33]. The "steep, cheap, and deep" breeding concept promotes selection for high-angle seminal roots to enhance vertical penetration [34]. High root length density (RLD) and specific root length (SRL) increase contact with moist soil zones; in maize, drought-tolerant lines exhibit 30-50% greater RLD at 60-120 cm soil depth compared to susceptible ones [35]. Some crops form air spaces (aerenchyma) in roots under stress, reducing metabolic costs and redirecting energy to elongation, which improves water uptake efficiency in water-limited soils [36]. Drought-adapted genotypes often allocate more biomass to roots, increasing the root-to-shoot ratio and enhancing water capture. For example, chickpea landraces from dry regions show 25% higher root: shoot ratios than cultivated varieties [37]. Breeding programs at ICRISAT and CIMMYT now incorporate high-throughput root phenotyping using techniques such as microrhizotrons, X-ray CT scanning, and gel-based systems to select for superior root traits.

3.3 Osmotic Adjustment (OA)

Osmotic adjustment (OA) is a biochemical mechanism by which plants maintain cell turgor pressure under water deficit through the accumulation of solutes (osmolytes) in cytoplasm and vacuoles. This allows continued cell expansion, stomatal function, and photosynthetic activity even at low leaf water potential. Key osmolytes involved include proline, which accumulates rapidly under drought and stabilizes proteins, membranes, and scavenges reactive oxygen species (ROS); glycine betaine, which protects Photosystem II and enzymes from denaturation; soluble sugars such as trehalose and sucrose, which serve as compatible solutes and energy reserves; and potassium ions (K^+), which contribute significantly to osmotic balance.

The enzyme Δ^1-pyrroline-5-carboxylate synthetase (P5CS) controls proline biosynthesis, and its overexpression in transgenic rice enhances OA and yield under drought. In wheat, cultivars with high OA capacity (>0.5 MPa reduction in osmotic potential) show 20-30% higher grain yield under terminal drought. Barley exhibits strong OA, contributing to its superior drought tolerance compared to wheat, while cowpea accumulates high levels of proline and soluble sugars, enabling survival under prolonged dry spells [38]. However, OA carries metabolic costs, as energy diverted to osmolyte synthesis may reduce resources available for growth and reproduction, highlighting the need for optimal rather than maximal osmotic adjustment.

The most drought-tolerant genotypes integrate multiple mechanisms synergistically: early-season vigor and deep rooting maximize water capture; high WUE and osmotic adjustment sustain photosynthesis and turgor; and delayed senescence ("stay-green") extends grain filling duration. For example, in sorghum, stay-green varieties like SC56 combine deep roots, high WUE, and strong OA to maintain yields under severe drought. Similarly, in maize, drought-tolerant hybrids developed by CIMMYT integrate all three traits through conventional and genomic-assisted breeding.

4 TRADITIONAL BREEDING EFFORTS: DROUGHT-TOLERANT VARIETIES IN MAIZE, SORGHUM, AND MILLET

Traditional or conventional breeding relying on phenotypic selection, recurrent selection, hybrid development, and participatory approaches has played a pivotal role in developing drought-tolerant crop varieties that are widely adopted by smallholder farmers. Unlike transgenic or gene-editing technologies, traditional breeding leverages natural genetic variation and is often more accessible, affordable, and socially acceptable in low- and middle-income countries.

Among cereals, maize, sorghum, and millet have been focal points of drought tolerance breeding due to their importance in food security across arid and semi-arid regions. Decades of sustained breeding efforts by international research centers (e.g., CIMMYT, ICRISAT) and national agricultural programs have resulted in the release of numerous high-performing, stress-resilient varieties that combine yield potential with adaptation to water-limited environments.

4.1 Maize (*Zea mays* L.)

Maize is particularly sensitive to drought stress, especially during the flowering and grain-filling stages. Breeding efforts have therefore concentrated on improving reproductive resilience and maintaining yield stability under water-limited conditions. Traits such as a shorter anthesis-silking interval (ASI), early vigor, deep rooting, and the stay-green phenotype are key selection targets. The Drought Tolerant Maize for Africa (DTMA) project, launched by CIMMYT and IITA, has played a leading role in developing and disseminating drought-tolerant maize hybrids and open-pollinated varieties (OPVs) across sub-Saharan Africa. Over 200 drought-tolerant varieties have been released across 13 countries under this initiative. Examples include hybrids like CZH0648, CLDH2004, and TZEE-W, which outperform local checks by 20-40% under moderate drought while maintaining comparable yields in favorable environments.

The stay-green trait, which allows leaves to retain chlorophyll and photosynthetic activity longer during post-flowering drought, has been particularly valuable in maintaining grain filling and kernel weight under stress. Hybrids such as SC Malawi demonstrate strong stay-green behavior and higher harvest index under high temperatures and low soil moisture [35]. In areas where hybrid seed access remains limited, open-pollinated drought-tolerant varieties such as Longe 5H in Uganda and Katambora in Zimbabwe are widely adopted because of their adaptability, storability, and lower input requirements. Most of these varieties are developed under managed-stress environments such as rainout shelters or terminal drought nurseries that mimic field conditions to ensure consistent selection pressure. Collectively, these efforts have contributed significantly to improving food security and yield stability across drought-prone maize production zones in Africa and Asia.

4.2 Sorghum (*Sorghum bicolor* L.)

Sorghum is inherently drought-tolerant due to its C_4 photosynthetic pathway, waxy leaf surfaces that minimize transpiration, and deep, fibrous roots that enable efficient water extraction from the soil profile. Nevertheless, targeted breeding has further enhanced its resilience by improving water-use efficiency, osmotic adjustment, and post-flowering drought tolerance. ICRISAT's Stay-Green program has been particularly successful, identifying and breeding varieties that maintain green leaf area and active photosynthesis during the grain-filling stage under terminal drought conditions. Notable stay-green sorghum cultivars such as SRN-39, EPSP-SG, and ICS 14 outperform non-stay-green types by 40-50% under severe moisture stress.

Drought-tolerant hybrids such as CSH 17, CSH 22, and ICTP 8203 combine early maturity, high biomass, and resistance to the parasitic weed Striga hermonthica, producing yields of 2.5-4.0 t ha^{-1} even under limited rainfall [39]. Farmer-participatory breeding initiatives in East Africa have accelerated the adoption of varieties such as Gadam and Serena, which are valued for their grain quality, fodder yield, and ratooning ability [40]. The stay-green trait in sorghum has been mapped to major QTLs (Stg1-Stg4) located on chromosome 3, which facilitate marker-assisted backcrossing and selection for improved drought tolerance. These breeding advancements have strengthened sorghum's role as a food and feed crop in semi-arid regions, supporting both resilience and productivity in changing climates

4.3 Millet (Pearl Millet, Finger Millet, Foxtail Millet)

Millets, including pearl millet (Pennisetum glaucum), finger millet (Eleusine coracana), and foxtail millet (Setaria italica), are among the most drought-resilient cereals cultivated in arid and semi-arid regions. Their short growth cycles, deep rooting systems, and high water-use efficiency enable them to thrive under extreme heat and limited rainfall. Pearl millet, in particular, is a staple in West Africa and India, where breeding programs led by ICRISAT and ICAR have produced numerous improved varieties and hybrids with enhanced drought tolerance and yield potential. Varieties such as HHB 67 Improved, ICTP 8203, and MBH 110 combine early maturity (70-80 days to harvest), high tillering capacity, and robust root systems, yielding 1.5-2.5 t ha⁻¹ under less than 400 mm annual rainfall.

Hybrid breeding has resulted in cultivars like ICMH 451, ICMH 9603, and GHB 538, which outperform local checks by 30-50% under drought [41]. Finger millet, known for its exceptional drought and heat tolerance as well as high calcium content, has also benefited from conventional and participatory breeding approaches. Improved cultivars such as GPU 28, GPU 45, and CO (Ra) 14, developed through hybridization and mass selection, combine drought resilience with dense tillering and resistance to blast disease. Foxtail millet, although less widely cultivated, has seen targeted improvement in China and India, producing short-duration, drought-escaping lines such as SiA 3147 and Brab 1 that perform well in sandy, low-moisture soils [39].

5 FLOOD (SUBMERGENCE/WATERLOGGING) TOLERANCE

Flooding, whether through prolonged waterlogging (saturated soils) or complete submergence (plants underwater), is a major abiotic stress affecting millions of hectares of agricultural land globally, particularly in low-lying regions of South and Southeast Asia, Sub-Saharan Africa, and Latin America [12]. Climate change is increasing the frequency and intensity of extreme rainfall events, exacerbating flood risks for staple crops such as rice, maize, soybean, and wheat. When soil pores become filled with water, oxygen diffusion slows dramatically from 10,000 μmol O_2 m^{-1} s^{-1} in air to just 0.3 μmol O_2 m^{-1} s^{-1} in water, leading to hypoxia (low oxygen) and eventually anoxia (no oxygen) within hours. This disruption triggers a cascade of physiological challenges, including impaired root respiration, energy deficit, nutrient imbalance, and oxidative stress, which collectively inhibit growth, reduce yield, and can lead to plant death if prolonged.

5.1 Physiological Challenges: Hypoxia, Reduced Root Respiration, and Nutrient Imbalance

Under flooding conditions, plants face severe oxygen deprivation that disrupts cellular energy metabolism and nutrient transport. Roots are the first organs to experience oxygen deficiency because of their direct contact with saturated soils. The resulting hypoxic stress impairs mitochondrial respiration, leading to a dramatic reduction in ATP production. Simultaneously, restricted ion uptake, hormonal imbalances, and accumulation of toxic metabolites exacerbate physiological dysfunctions. The extent of plant injury depends on flood duration, temperature, and the species' inherent adaptive capacity. While rice possesses unique morphological and biochemical mechanisms enabling partial tolerance, most upland crops like maize, wheat, and soybean are highly sensitive to prolonged waterlogging.

5.1.1 Hypoxia and energy crisis

Oxygen is essential for aerobic respiration, the primary process by which plants generate ATP for metabolic functions. Under flooded conditions, roots experience rapid oxygen depletion, forcing a shift from aerobic to anaerobic metabolism (fermentation). This metabolic shift leads to a severe energy deficit because aerobic respiration yields 36 ATP per glucose molecule, whereas fermentation produces only 2 ATP. The reduced ATP availability limits ion uptake, protein synthesis, cell division, and maintenance processes [42]. Fermentation also results in the accumulation of toxic metabolites such as ethanol, lactate, and acetaldehyde, which can damage cellular membranes and denature proteins (Figure 5-7). In sensitive species like maize and soybean, ethanol concentrations exceeding 20 mM can be lethal within 48-72 hours [43]. Lactate buildup lowers cytoplasmic pH, disrupting enzyme activity and cellular homeostasis. In response, plants activate H^+-ATPases to pump protons out of cells, further consuming limited ATP reserves. Rice (Oryza sativa), a semi-aquatic crop, has evolved partial tolerance to hypoxia through enhanced activity of alcohol dehydrogenase (ADH) and pyruvate decarboxylase (PDC), which facilitate efficient ethanol production and detoxification. However, even rice suffers under prolonged submergence, particularly during early growth stages [44].

5.1.2 Impaired root respiration and function

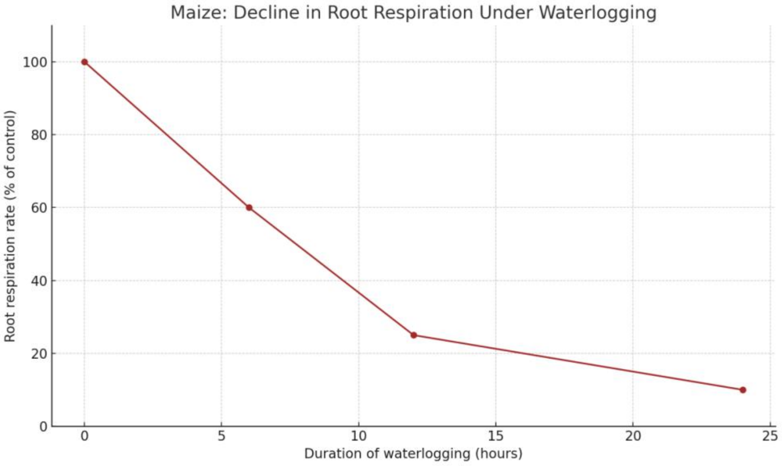

Figure 5 Root Respiration in Maize Declines by up to 90% within 24 Hours of Waterlogging, Indicating Severe Hypoxia-Induced Impairment of Root Metabolic Activity [13].

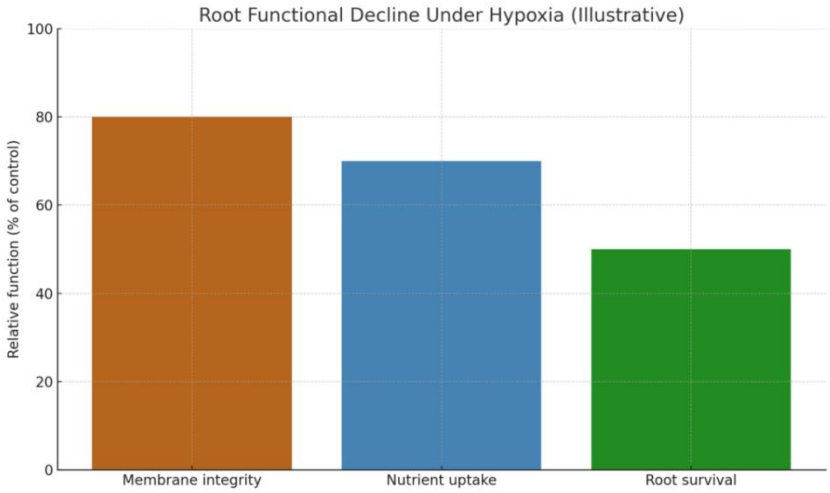

Figure 6 Hypoxia Reduces Root Functional Parameters including Membrane Integrity, Nutrient Uptake (Especially N, P, K), and Overall Survival. Values are Illustrative based on Reported Physiological Trends.

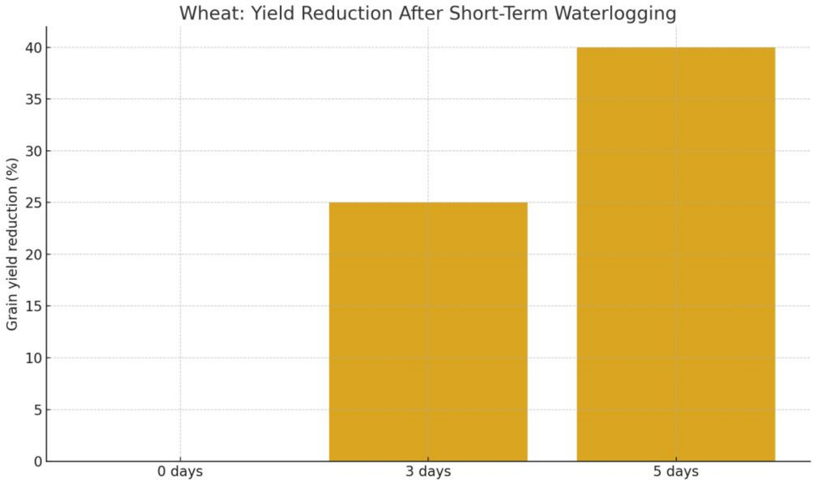

Figure 7 Wheat Grain Yield Declines Progressively with Duration of Waterlogging, with 25-40% Loss Observed after 3-5 Days of Flooding during Tillering or Stem Elongation [45].

5.1.3 Nutrient imbalance and secondary stressors

Flooding alters soil biogeochemistry, creating nutrient imbalances that compound the physiological effects of hypoxia. Several interrelated nutrient and oxidative stress mechanisms contribute to reduced plant performance under waterlogged or submerged conditions (see Table 2).

Nitrogen imbalance is one of the most prominent effects. Under anaerobic conditions, denitrification occurs as microbes convert nitrate (NO_3^-) to gaseous nitrogen (N_2), resulting in nitrogen depletion from the root zone. At the same time, ammonium (NH_4^+) becomes the dominant form of nitrogen in reduced soils. While rice and some wetland species can tolerate elevated NH_4^+ concentrations, many upland crops are sensitive to levels exceeding 2 mM, leading to ammonium toxicity that inhibits potassium (K^+) uptake and suppresses photosynthesis.

Iron and manganese toxicity are also major problems in flooded soils. Under anaerobic conditions, ferric (Fe^{3+}) and manganese (Mn^{4+}) ions are reduced to their more soluble ferrous (Fe^{2+}) and manganous (Mn^{2+}) forms, which accumulate in the soil solution. These ions can enter roots passively, triggering oxidative stress through Fenton reactions that generate reactive oxygen species (ROS). The resulting ROS damage lipids, proteins, and DNA, leading to membrane leakage, chlorosis, and tissue necrosis [46].

Phosphorus (P) and micronutrient imbalances further complicate the nutrient status of flooded crops. Although P solubility may initially increase under reducing conditions, it rapidly precipitates with Fe^{2+} or Al^{3+} upon reoxygenation, making it unavailable to plants. Similarly, zinc (Zn) and copper (Cu) become less bioavailable due to changes in redox potential, causing deficiencies even in soils with adequate total nutrient content.

A critical secondary stress occurs during reoxygenation following flood recession. When oxygen rapidly reenters the root zone, a burst of reactive oxygen species (ROS) is produced because antioxidant defense systems are not yet fully reactivated. This oxidative burst damages mitochondria and chloroplasts, causing reperfusion injury that accelerates senescence and contributes to significant yield loss [47].

Table 2 Species-Specific Responses to Flooding

Crop	Sensitivity	Key Physiological Response
Rice	High tolerance (semi-aquatic)	Forms aerenchyma, expresses SUB1A, maintains carbohydrate reserves
Maize	Low tolerance	Rapid root death, no aerenchyma formation, severe yield loss after 48 h
Wheat	Low to moderate	Limited aerenchyma, susceptible to pre-anthesis waterlogging
Soybean	Moderate	Induces lysigenous aerenchyma but vulnerable to prolonged submergence
Barley	Low	Poor internal aeration, sensitive to early-stage flooding

Source: [12,45].

5.2 Adaptive Mechanisms in Tolerant Species

Some plants have evolved morphological and physiological adaptations to mitigate the effects of flooding. Aerenchyma formation the development of air-filled spaces in roots and stems allows internal oxygen transport from shoots to roots. In rice, lysigenous aerenchyma forms within 24 hours of flooding through programmed cell death, ensuring sustained root respiration under waterlogged conditions [48]. Additionally, the formation of a radial oxygen loss (ROL) barrier a suberin layer in outer root tissues prevents oxygen leakage, improving longitudinal diffusion efficiency.

The production of adventitious roots above the waterline is another important adaptation, restoring gas exchange and nutrient uptake during prolonged flooding. Plants also exhibit two major physiological strategies to cope with complete submergence: the escape strategy and the quiescence strategy. The escape strategy involves rapid elongation of shoots or internodes to reach the water surface, as seen in deepwater rice that expresses SNORKEL genes. In contrast, the quiescence strategy conserves energy by suppressing growth until floodwaters recede, a mechanism controlled by the SUB1A gene in modern submergence-tolerant rice varieties. The discovery of the SUB1 locus in rice revolutionized flood-tolerance breeding, enabling the development of varieties such as Swarna-Sub1, which can survive complete submergence for up to 14 days without yield penalty. These innovations demonstrate the potential of combining physiological understanding with molecular genetics to develop flood-resilient crops capable of sustaining yields in flood-prone environments.

5.3 Conventional Breeding Successes: The Case of Sub1A Gene Introgression in Rice ("Scuba Rice")

5.3.1 Origin of the Sub1A gene

One of the most remarkable achievements in stress-tolerant crop breeding is the successful introgression of the *Sub1A* gene into widely grown rice varieties, resulting in high-yielding, submergence-tolerant cultivars now known as “Scuba rice” or Sub1 rice. This breakthrough exemplifies how conventional breeding, when enhanced by modern molecular tools, can deliver transformative solutions to climate-induced agricultural challenges. Developed through a collaboration between the International Rice Research Institute (IRRI), national programs, and advanced genetics research, Sub1 rice has been adopted across millions of hectares in flood-prone regions of South and Southeast Asia, including India, Bangladesh, Nepal, and Myanmar [49].

The *Sub1A* gene was identified in a traditional lowland rice landrace called FR13A, cultivated in Orissa, India, which had long been recognized for its ability to survive complete submergence for up to two weeks. Genetic mapping revealed that submergence tolerance was controlled by a major quantitative trait locus (*Sub1*) located on chromosome 9, comprising three genes: *Sub1A*, *Sub1B*, and *Sub1C*. Among these, only *Sub1A-1* (the functional allele) conferred strong submergence tolerance.

Plants carrying *Sub1A-1* adopt a “quiescence strategy” during flooding, which involves suppressing shoot elongation to conserve carbohydrates, reducing ethylene production and reactive oxygen species (ROS) accumulation, maintaining energy homeostasis through anaerobic respiration, and resuming growth rapidly after desubmergence. In contrast, susceptible rice varieties exhibit an “escape” response characterized by rapid internode elongation to reach the water surface, which depletes energy reserves and leads to plant death within 4-7 days under prolonged submergence. The discovery of *Sub1A-1* thus marked a significant breakthrough in understanding genetic control of flood tolerance in rice.

5.3.2 Marker-assisted backcross breeding approach

Rather than relying solely on phenotypic screening which is slow and unreliable due to the difficulty of consistently simulating field flooding researchers utilized marker-assisted backcross breeding (MABB) to transfer the *Sub1A-1* allele from FR13A into popular, high-yielding but flood-sensitive rice varieties such as Swarna, IR64, and BR11.

The breeding strategy involved using FR13A as the donor parent carrying *Sub1A-1*, while elite varieties such as Swarna served as recurrent recipient parents due to their high yield potential and farmer-preferred grain quality. Successive backcrossing was performed to recover the agronomic characteristics of the recurrent parent while retaining the *Sub1* locus. Selection using DNA markers specifically flanking markers such as AP3 and Uga2 ensured precise introgression of the *Sub1* quantitative trait locus (QTL) while minimizing linkage drag. After just four to five generations, near-isogenic lines (NILs) were developed that were genetically identical to the original varieties except for the *Sub1* region.

This approach revolutionized submergence tolerance breeding by combining molecular precision with farmer-preferred backgrounds, ultimately producing flood-tolerant versions of popular cultivars that maintained grain yield and quality under both submerged and non-stress conditions.

5.3.3 Performance and impact of Sub1 rice

Field trials conducted across flood-prone ecosystems demonstrated dramatic improvements in the performance of Sub1 rice compared to conventional varieties (Table 3).

Table 3 Performance and Impact of Sub1 Rice

Trait	Susceptible Variety (E.G., Swarna)	Sub1 Version (Swarna-Sub1)
Survival after 14-day submergence	<10%	>80%
Grain yield after flooding	0.5 t/ha	3.0-4.0 t ha^{-1}
Recovery time post-flood	Slow, poor tillering	Rapid regrowth, high tiller retention

Source: [50].

Farmers reported yield advantages of 1-3 t ha-1 following flash floods, resulting in significant income gains and improved food security. Moreover, Sub1 rice maintains the grain quality, cooking characteristics, and yield potential of the original variety under non-flooded conditions, thereby eliminating trade-offs that often hinder adoption.

5.4 Research and Breeding Gaps

5.4.1 Limited breeding and genetic research in non-rice crops

While rice has benefitted substantially from molecular breeding efforts targeting flood tolerance, similar progress in non-rice crops such as maize, wheat, soybean, and barley remain limited. The majority of research and breeding investments have focused on *Oryza sativa* due to its semi-aquatic nature and global importance as a staple crop [51]. Consequently, the genetic and physiological basis of flood and waterlogging tolerance in upland cereals and legumes remains poorly characterized, restricting the development of resilient varieties for these crops.

Maize (*Zea mays L.*) is highly sensitive to waterlogging, with yield losses of 25-30% under short-term flooding and complete failure after prolonged submergence. Despite identification of some QTLs related to root porosity and antioxidant activity, breeding progress has been constrained by the lack of reliable phenotyping tools and the complexity of genotype × environment (G×E) interactions. In wheat (*Triticum aestivum*), tolerance is influenced by stage-specific responses; for instance, pre-anthesis waterlogging reduces grain number and kernel weight. However, the absence of stable genetic markers and limited genomic resources have slowed the translation of physiological insights into breeding outcomes.

Soybean (*Glycine max*) exhibits moderate tolerance to transient flooding through adventitious root formation and aerenchyma development, yet it remains highly susceptible to prolonged submergence and reoxygenation injury. Similarly, barley (*Hordeum vulgare*), one of the least flood-tolerant cereals, shows restricted root aeration capacity and poor post-flood recovery. While transcriptomic studies have begun revealing key genes associated with ethylene and auxin signaling during hypoxia, these findings have not yet been integrated into practical breeding programs.

The lack of well-characterized donor germplasm, standardized screening environments, and coordinated international research networks further limits progress in non-rice species. In contrast to the well-established Sub1-based pipeline in rice, no equivalent genetic model or major-effect QTLs have been validated in other cereals or legumes. To close this gap, interdisciplinary collaborations involving physiologists, molecular biologists, and breeders are essential to accelerate discovery and deployment of flood-tolerance genes beyond rice. Ultimately, expanding the scope of genetic research and molecular breeding in non-rice crops is critical to ensuring that climate-resilient agriculture benefits diverse agroecosystems and food systems globally.

5.4.2 Lack of integration of waterlogging and salinity tolerance

In many coastal and deltaic regions, flooding stress is often accompanied by increased soil salinity due to poor drainage, seawater intrusion, or evaporation-driven salt accumulation following flood recession. However, breeding programs have largely treated waterlogging and salinity as independent stresses, despite their frequent co-occurrence in the field. This separation has limited the effectiveness of tolerant varieties when exposed to combined stress environments typical of climate-vulnerable ecosystems such as the Ganges-Brahmaputra Delta, the Mekong Basin, and parts of Sub-Saharan Africa.

Physiologically, waterlogging and salinity interact in complex ways. Waterlogging induces hypoxia in roots, impairing active ion transport and leading to ionic imbalance. Under such conditions, plants are unable to exclude toxic sodium (Na^+) and chloride (Cl^-) ions effectively, resulting in additive or synergistic stress effects. For example, rice genotypes tolerant to submergence through the *Sub1A* mechanism often display susceptibility to post-flood salinity because hypoxia reduces the activity of Na^+/H^+ antiporters that normally regulate ionic homeostasis. Similarly, in wheat and barley, flooding increases membrane permeability and enhances Na^+ influx, exacerbating salt toxicity and oxidative damage.

From a breeding perspective, most programs have focused either on waterlogging tolerance (e.g., aerenchyma formation, ethylene response) or salinity tolerance (e.g., *HKT1;5*-mediated Na^+ exclusion), but rarely on their combined effects. The absence of integrated screening protocols and selection indices under simultaneous stresses has prevented the identification of genotypes with dual tolerance. Only a few initiatives, such as the IRRI's Coastal Climate-Resilient Rice (C2R2) platform, have begun to address this gap by combining *Sub1* and *Saltol* QTLs into single backgrounds to develop multi-stress-tolerant rice [52].

To achieve sustainable adaptation in coastal farming systems, future research must explicitly integrate physiological, molecular, and breeding studies addressing combined stress scenarios. This includes mapping QTLs and regulatory genes responsive to concurrent hypoxia and ionic stress, developing reliable phenotyping methods, and designing marker-assisted pyramiding strategies to combine complementary mechanisms. The convergence of salinity and waterlogging tolerance breeding is crucial for developing crops capable of sustaining yields in increasingly saline and flood-prone landscapes.

6 INTEGRATIVE BREEDING STRATEGIES

6.1 Multi-Stress Breeding: The Critical Need for Tackling Combined Abiotic Stresses

Climate change is not simply increasing the frequency of individual abiotic stresses it is intensifying their co-occurrence and interaction, creating novel and more damaging stress combinations such as heat and drought, flood and salinity, and drought and heat waves. Traditional breeding approaches that focus on tolerance to a single stress are increasingly inadequate because responses to combined stresses are often non-additive, synergistic, and mechanistically distinct from responses to individual stressors [53]. As a result, there is an urgent need for multi-stress breeding strategies that develop crop varieties resilient to real-world environmental complexity, rather than controlled, isolated conditions. This shift from single-trait, single-stress selection to integrated, systems-level resilience is essential for sustaining agricultural productivity under future climate scenarios.

6.1.1 Heat and drought: a synergistic threat to crop production

Heat and drought present a synergistic threat to crop production, frequently co-occurring during critical growth stages, particularly in semi-arid and rainfed agroecosystems, where high temperatures accelerate evapotranspiration and soil moisture depletion. Their combined impact is greater than the sum of their individual effects. Physiologically, both stresses induce stomatal closure to conserve water, which severely limits CO_2 influx and suppresses photosynthesis beyond what either stress causes alone. Furthermore, heat increases membrane fluidity and ROS production while drought reduces antioxidant capacity; together, they cause severe lipid peroxidation and cellular damage.

This combination also leads to reproductive failure, as high temperatures during flowering disrupt pollen viability while drought limits the turgor pressure needed for anther dehiscence and pollen tube growth, reducing kernel set in maize by up to 80%. Evidence from field studies confirms this severe impact, with wheat trials across South Asia showing grain yield reductions of 50-70% under combined stress compared to 20-30% under individual stresses [24]. Similarly, in sorghum, genotypes selected only for drought tolerance performed poorly under heat-drought co-stress due to unanticipated interactions in canopy temperature regulation and senescence timing. Despite this evidence, few breeding programs explicitly select for heat-drought resilience, as most phenotyping occurs under single-stress nurseries, leading to varieties that fail when both stresses coincide.

6.1.2 Flooding and salinity: a growing challenge in coastal and deltaic regions

In low-lying coastal zones such as the Ganges-Brahmaputra Delta, Mekong Delta, and Nile Delta, flooding is increasingly accompanied by saltwater intrusion due to sea-level rise, storm surges, and upstream water diversion, creating a dual stress environment where crops face hypoxia from waterlogging and ion toxicity from Na^+/Cl^- accumulation. The physiological challenges of this co-stress include impaired ion homeostasis, where hypoxia disrupts H^+-ATPase activity that powers Na^+/H^+ antiporters like SOS1, thereby reducing salt exclusion capacity [54]. Furthermore, both stresses independently generate reactive oxygen species (ROS) and together they synergistically overwhelm antioxidant systems such as SOD, CAT, and APX, leading to enhanced oxidative damage. A critical nutrient imbalance also occurs as waterlogging reduces K^+ uptake while salinity further disrupts the K^+/Na^+ ratio, impairing enzyme function and membrane integrity. For example, rice varieties with the *Sub1A* gene can survive freshwater submergence but die rapidly under brackish water conditions, and in coastal Bangladesh, even putatively tolerant varieties like Swarna-Sub1 fail when floodwaters carry salt [16]. Despite these documented impacts, very few studies simulate combined flooding-salinity stress, and no major crop variety has been released with validated tolerance to both.

6.1.3 Other emerging stress combinations

Beyond the primary stress combinations of heat-drought and flooding-salinity, other compound stresses are emerging as significant threats, including heat with high humidity, which increases spikelet sterility and disease susceptibility in rice and banana, and flooding with low light, which reduces photosynthetic recovery in rice and vegetables. These interactions demonstrate that stress resilience is not modular, as traits beneficial under one condition can be detrimental under another. The failure of single-stress breeding arises from phenotyping in isolation, genetic trade-offs, a lack of cross-stress markers, and limited germplasm screening under multiple stresses. To overcome these limitations, breeding must adopt integrated strategies. This includes developing multi-stress phenotyping platforms using managed environments and high-throughput techniques, applying genomic selection (GS) models trained across diverse stress combinations to improve prediction accuracy as demonstrated in maize where accuracy increased by 20-30% [55] and pyramiding favorable alleles via marker-assisted backcrossing or CRISPR editing. Physiology-guided trait integration is also critical, focusing on traits with positive pleiotropy such as stay-green, canopy temperature depression, and antioxidant capacity. A leading example is IRRI's "Green Super Rice" initiative, which uses marker-assisted pyramiding to combine tolerances for submergence, salinity, drought, and phosphorus deficiency, resulting in lines with stable yields across stress-prone environments in Asia [9].

6.2 Speed Breeding and Controlled Environment Facilities: Accelerating Crop Improvement Through Shortened Breeding Cycles

Traditional plant breeding programs typically require 8-12 years to develop and release a new variety a timeline increasingly inadequate in the face of rapid climate change and growing food demand. To address this bottleneck, speed breeding (SB) a technique that uses controlled environment facilities, extended photoperiods, and early-generation selection has emerged as a transformative approach to accelerate genetic gain across diverse crops. By shortening generation times, speed breeding enables 6-8 generations per year in wheat, barley, rice, and legumes, compared to 1-2 under conventional field-based systems [56]. This acceleration is critical for integrating complex traits such as multi-stress tolerance, where stacking favorable alleles through repeated backcrossing and selection can otherwise take decades.

6.2.1 Principles of speed breeding

Speed breeding leverages three key components to reduce crop life cycles: extended photoperiod with LED lighting, controlled environment facilities, and early generational selection with rapid generation advance (RGA). Plants are grown under continuous or near-continuous light (e.g., 22 hours light / 2 hours dark) using energy-efficient light-emitting diodes (LEDs) tuned to optimal wavelengths (blue and red, 450 nm and 660 nm), which promotes faster photosynthesis, flowering, and seed set [57]. Growth chambers, glasshouses, and indoor farms maintain optimal temperature, humidity, and CO_2 levels, minimizing environmental variability and enabling year-round cultivation; these environments also allow precise control over stress treatments (e.g., drought, heat pulses) during phenotyping. Early selection for traits such as flowering time, height, and disease resistance at the seedling or early vegetative stage ensures only elite lines progress, and techniques such as single-seed descent (SSD) are used to rapidly fix traits within populations. For example, in wheat speed breeding protocols have reduced generation time from 150 days to just eight weeks, enabling up to six generations per year; in barley RGA combined with extended lighting achieves five generations annually, accelerating development of salinity- and drought-tolerant lines [58]; and in cowpea and soybean SB has shortened breeding cycles from more than 12 months to four-five months, crucial for improving resilience in sub-Saharan Africa and Southeast Asia [59].

6.2.2 Applications in multi-stress tolerance breeding

Speed breeding is particularly valuable for developing varieties resilient to combined abiotic stresses such as heat and drought or flood and salinity, where trait pyramiding requires multiple rounds of crossing and selection. At the John Innes Centre (UK) and CIMMYT (Mexico), speed breeding pipelines integrate photoperiod extension (22L:2D) using LED arrays, temperature manipulation to simulate terminal heat stress, and marker-assisted selection (MAS) for DREB, NAC, and HSP genes associated with thermotolerance and water-use efficiency (WUE); using this system, researchers developed near-isogenic lines with stacked QTLs for drought and heat tolerance in less than three years approximately half the time required under field conditions [56]. Speed breeding also synergizes with genomic tools: genomic selection (GS) models enable early prediction of performance, CRISPR-edited lines can be advanced rapidly to assess stability and inheritance, and high-throughput phenotyping (HTP) platforms (e.g., imaging, thermal sensors) monitor physiological responses under controlled stress simulations. For example, the Speed Breeding Hub at the University of Queensland combines SB with HTP and GS to develop drought-tolerant sorghum hybrids with improved stay-green and root architecture.

6.2.3 Advantages over conventional breeding

Speed breeding offers distinct advantages over conventional breeding, most notably a significantly accelerated breeding timeline that enables 4-8 generations per year compared to just 1-2, thereby reducing the time to achieve homozygosity (F_6) from 6-8 years to just 2-3 years [58]. This system provides a high degree of environmental control within climate-controlled facilities, which leads to greater phenotyping precision compared to the field-dependent and variable conditions of conventional breeding. While the initial infrastructure costs for speed breeding are higher, this approach ultimately has a lower physical land footprint. The key benefits include the faster introgression of critical stress-tolerance genes, the rapid evaluation of gene edits, and more efficient recycling of parents in hybrid breeding programs.

6.2.4 Challenges and limitations

Despite its advantages, speed breeding faces several constraints. High infrastructure costs LED arrays, HVAC systems, and automated monitoring require significant investment, limiting accessibility in low-income countries [57]. Most SB systems are currently suited to research-scale trials (fewer than 1,000 plants) rather than large breeding populations. Traits expressed under controlled conditions may not fully reflect field performance because of absent biotic interactions, wind, or natural stress fluctuations. Crop-specific protocols are necessary since optimal light intensity, vernalization, and nutrient regimes vary by species (for example, wheat and barley respond well to long-day conditions, rice requires careful humidity management to prevent fungal growth, and maize demands high light intensity and space due to its stature). Continuous lighting also increases electricity consumption, raising sustainability concerns unless renewable energy sources are employed.

6.2.5 Scaling and future directions

To broaden impact, future efforts should focus on low-cost speed breeding systems that use passive solar greenhouses, fluorescent lights, and locally available materials to reduce costs [59]. ICRISAT has piloted affordable SB units in Niger and Nigeria for cowpea improvement. Effective scaling requires integration with multi-location field trials so that early-generation advancement in controlled environments is validated under diverse agroecological conditions; additionally, increased automation and AI offer routes to streamline operations and decision-making as SB moves beyond small-scale research applications.

6.3 Use of Wild Relatives and Landraces: Untapped Genetic Reservoirs for Stress Tolerance

As climate change intensifies abiotic stresses such as drought, heat, flooding, and salinity, modern crop varieties bred primarily for yield and uniformity under optimal conditions are increasingly vulnerable. In contrast, crop wild relatives (CWRs) and traditional landraces have evolved under diverse and often harsh environments, making them rich sources of genetic diversity for stress resilience. These underutilized genetic resources harbor alleles that confer tolerance mechanisms absent or diminished in elite germplasm due to genetic bottlenecks during domestication and intensive breeding [14]. Harnessing this diversity through pre-breeding and allele introgression offers a powerful strategy to enhance the adaptability of modern crops without relying solely on transgenic technologies.

6.3.1 Crop wild relatives: natural laboratories of adaptation

Crop wild relatives (CWRs) function as natural laboratories of adaptation, having evolved in marginal habitats such as arid zones, saline soils, and floodplains where natural selection has favored survival traits now critical for climate resilience. These wild taxa possess a wealth of functional novelty that has been diminished or lost in elite germplasm due to domestication bottlenecks. Documented examples of their valuable traits are extensive: *Aegilops tauschii* provides drought tolerance in wheat through deep rooting and osmotic adjustment, while *Thinopyrum elongatum* confers salinity tolerance via Na^+ exclusion controlled by the *Nax*1/*Nax*2loci. In rice, *Oryza rufipogon* enhances submergence tolerance through improved aerenchyma formation, and *Oryza coarctata* possesses specialized salt glands that excrete sodium.

For tomato, *Solanum pimpinellifolium* contributes heat tolerance by maintaining photosystem II stability, and *Solanum pennellii* offers drought tolerance through reduced stomatal density and higher water-use efficiency. Similarly, perennial *Zea* species provide extensive root systems for drought tolerance in maize, and *Hordeum spontaneum* offers multi-stress tolerance in barley through high antioxidant capacity and early flowering [60,61]. The practical application of these resources is demonstrated by successes such as the introgression of *Nax2* from *Thinopyrum elongatum* into wheat, which reduced Na^+ accumulation in shoots and increased grain yield by 25% under saline conditions [62], underscoring the immense potential of CWRs to replenish lost adaptive variation for modern crop improvement.

6.3.2 Landraces: farmers' legacy of resilience

Landraces are farmer-maintained traditional varieties that have undergone informal selection over generations in specific agroecological niches and, unlike modern cultivars, exhibit high phenotypic plasticity, local adaptation, and buffering against environmental variability. Documented stress-tolerance traits in landraces include drought escape early-maturing maize landraces in West Africa that flower before seasonal drought peaks, heat avoidance rice landraces from India and Pakistan that flower early in the morning, thereby avoiding midday heat-induced spikelet sterility; flooding survival traditional lowland rice varieties such as FR13A (the donor of Sub1A) that survive complete submergence for up to two weeks and salinity resilience pearl millet landraces from Rajasthan that maintain yields at ECe >8 dS/m, outperforming commercial hybrids [41]. In Ethiopia durum wheat landraces outperformed improved varieties under terminal drought, attributed to superior root architecture and canopy temperature depression (CTD) [63], and Andean potato landraces show exceptional frost and drought tolerance important for high-altitude systems.

6.3.3 Barriers to utilization

Despite their value, wild relatives and landraces remain underexploited in mainstream breeding programs due to several barriers. Linkage drags often co-transfers undesirable traits (e.g., shattering, lodging, low yield) with beneficial stress-tolerance alleles. Reproductive barriers such as ploidy differences and hybrid in viability complicate crosses between some crop wild relatives (CWRs) and cultivated species. Many accessions in gene banks lack detailed phenotypic characterization under stress conditions, and relatively few CWRs have been sequenced or genotyped at scale. Regulatory and access frameworks (e.g., the Nagoya Protocol and ITPGRFA) further complicate international germplasm exchange. Consequently, less than 10% of conserved plant genetic resources have been evaluated for agronomic traits, and even fewer have been used in breeding [14].

6.3.4 Strategies for effective integration

To overcome the barriers of linkage, drag and reproductive incompatibility, researchers are adopting innovative strategies for the effective integration of crop wild relatives and landraces. Pre-breeding programs, such as DIVERSITY Seek (DivSeek) and CGIAR's Genebank Platforms, bridge gene banks and breeders by pre-characterizing genetic resources for key traits and developing specialized genetic stocks like introgression lines (ILs) and chromosome segment substitution lines (CSSLs) to minimize linkage drag, as demonstrated by CIMMYT's development of maize nested association mapping (NAM) populations for precise QTL discovery. Genome-wide association studies (GWAS) conducted on diverse landrace panels have successfully identified novel alleles for critical traits, including heat shock proteins in wheat, osmoprotectant biosynthesis genes in rice, and root depth genes in sorghum, enabling marker-assisted selection without extensive prior phenotyping [64].

Furthermore, CRISPR technology enables precision introgression by transferring key regulatory elements from wild species, such as editing the *PROPEP3* promoter in *Arabidopsis* based on *A. lyrata* variation to enhance drought priming [65], while synthetic biology explores transferring complex traits like salt glands. Participatory on-farm evaluation ensures developed materials meet local needs, as seen in Nepal where barley landrace-derived lines were rapidly adopted due to superior straw quality and ratoon ability [66]. A case study exemplifying this integrated approach is the harnessing of *Oryza rufipogon*, which exhibits deep rooting, high tillering under stress, and strong aerenchyma development; through marker-assisted backcrossing, IRRI introgressed its QTLs into the *Swarna* variety, resulting in lines with 30% higher yield under drought and improved post-flood recovery [67], underscoring the potential of wild genomes to replenish lost adaptive variation.

6.4 Role of Genomics and Artificial Intelligence

6.4.1 Genomic prediction and genome-wide selection

Genomic prediction uses genome-wide molecular markers (e.g., SNPs) to estimate the genomic estimated breeding value (GEBV) of individuals via statistical models trained on reference populations with both genotype and phenotype data. Unlike marker-assisted selection, which targets a few major-effect QTLs, genomic selection (GS) captures the collective effect of many small-effect loci, making it well suited to polygenic traits such as drought tolerance, water-use efficiency (WUE), and yield stability under heat stress [68]. GS has been applied successfully: in maize prediction accuracies for grain yield under drought reach up to 0.65 [26]; in wheat, models that incorporate G and E interactions improve predictions across environments and enable site-specific recommendations [69]; and in rice GS accelerates development of submergence- and salinity-tolerant lines by selecting top performers early in the pipeline [70]. At CIMMYT and IRRI, genomic prediction pipelines have reduced breeding cycles by 30-50%, facilitating faster deployment of climate-resilient varieties.

6.4.2 High-throughput phenomics: capturing dynamic trait responses

High-throughput phenomics provides the essential phenotypic foundation for predictive breeding by enabling the large-scale, automated measurement of plant traits, capturing spatial and temporal dynamics that traditional hand-measured methods cannot. This approach utilizes non-invasive sensors deployed across field, greenhouse, and controlled environments to quantify key physiological responses. The technologies employed include drones or UAVs equipped with multispectral cameras to monitor traits like NDVI and chlorophyll content for assessing drought-induced senescence; thermal imaging to measure canopy temperature depression (CTD) as a proxy for stomatal conductance and water-use efficiency; and LiDAR with 3D point clouds to analyze plant architecture, biomass, and lodging resistance.

Furthermore, hyperspectral reflectance sensors determine biochemical composition related to nutrient and water status, while advanced root imaging techniques such as X-ray computed tomography and rhizotrons characterize root depth and density for evaluating drought and waterlogging tolerance. The power of this methodology is demonstrated in field applications, where UAV-based NDVI in sorghum predicted final grain yield under drought with a correlation of $r = 0.82$, allowing for early selection, and thermal imaging in wheat identified genotypes with superior transpirational cooling under heat stress, which strongly correlated with yield retention [64]. These high-volume, time-series data streams are critical for powering the AI-driven models that underpin modern, climate-resilient crop improvement.

6.4.3 Machine learning and AI for predictive modeling

Artificial intelligence (AI), particularly machine learning (ML) and deep learning (DL), is increasingly used to analyze complex biological and environmental datasets, uncover latent patterns, and predict crop performance. Key applications include trait prediction from spectral data ML algorithms such as Random Forests, Support Vector Machines, and neural networks can predict physiological traits directly from spectral signatures (for example, a CNN trained on hyperspectral data predicted leaf nitrogen content in maize with $R^2 > 0.90$) and classification of stress outcomes from imagery (deep learning accurately classified rice varieties by submergence survival using drone imagery) [71]. ML also enhances genomic prediction by modeling genotype and environment interactions (the Factor Analytic model and Bayesian networks improve yield prediction across diverse agroecologies) [72], while computer vision automates phenotype extraction (CNNs detect and count tillers or panicles) and reinforcement learning or evolutionary algorithms help optimize breeding scheme design.

6.4.4 Integration platforms and digital breeding hubs

Several global initiatives have established integrated platforms and digital breeding hubs that unify genomics, phenomics, and data analytics to accelerate crop improvement. Key among these is the Breeding Management System (BMS) developed by GOBII and implemented by centers like IRRI and CIMMYT, which manages pedigree, genotypic, and phenotypic data for over 50 crops. In the private sector, platforms such as Agnovus™ (Bayer) utilize AI to recommend optimal crosses based on trait profiles and market needs, while Syngenta's Cropwise® Seeds combines genomic prediction with machine learning for hybrid development. Public programs like the Australian Grains GeneMatics Program integrate genomic selection, high-throughput phenotyping, and artificial intelligence to deliver climate-ready wheat and barley varieties. These systems enable real-time data sharing, collaborative analysis, and cloud-based modeling, significantly accelerating decision-making across breeding teams. A notable case study demonstrating the power of this integrated approach comes from CIMMYT, where researchers combined genome-wide SNP data, drone-collected NDVI and thermal imagery, and machine learning models to achieve a prediction accuracy of 0.73 for grain yield under terminal heat stress in maize, outperforming traditional models and enabling pre-selection of elite lines [10].

7 CONCLUSIONS

In conclusion, significant progress has been made in breeding crops for climate resilience, marked by achievements such as the development of submergence-tolerant "Scuba Rice" through the Sub1A gene, drought-tolerant maize hybrids, and stay-green sorghum varieties. These successes demonstrate the potential of genetic improvement, supported by advanced phenotyping and targeted selection, to enhance crop adaptation to individual abiotic stresses like heat, drought, and flooding. However, the increasing frequency and complexity of interacting climate extremes such as concurrent heat waves and droughts, or flooding combined with salinity demand a shift beyond single-trait breeding. Future efforts must adopt integrated, multi-disciplinary approaches that combine genomics, phenomics, environmental modeling, and socio-economic insights. This will require developing crops with tolerance to multiple stresses, improving nutrient- and water-use efficiency, and leveraging the genetic diversity found in underutilized species and crop wild relatives. Equally important is ensuring that new varieties are accessible and acceptable to farmers, particularly smallholders. This involves strengthening seed systems, adopting participatory breeding models, and implementing science-based regulations for emerging technologies like gene editing. The ultimate goal is to build holistic, climate-resilient agricultural systems that are not only productive but also sustainable, equitable, and capable of supporting global food security in an era of escalating climate uncertainty.

COMPETING INTERESTS

The authors have no relevant financial or non-financial interests to disclose.

REFERENCES

[1] IPCC. Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, 2023. https://www.ipcc.ch/report/ar6/syr/.

[2] IPCC. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, 2021. https://www.ipcc.ch/report/ar6/wg1

[3] Zandalinas S I, Balfagón D, Arbona V. Plant adaptations to the combination of drought and high temperatures. Physiologia Plantarum, 2021, 173(1): 153-166. DOI: 10.1111/ppl.13276.

[4] Ceccarelli S, Grando S, Baum M. Participatory plant breeding in water-limited environments. Annals of Applied Biology, 2010, 157(3): 311-317. DOI: 10.1111/j.1744-7348.2010.00433.x.

[5] Ceccarelli S. Plant breeding with farmers: A technical manual. ICARDA, 2012.

[6] Cooper M, van Eeuwijk F, Hammer G L, et al. Modeling QTL for complex traits: Detection and context for plant breeding. Current Opinion in Plant Biology, 2014, 18, 112-122. DOI: 10.1016/j.pbi.2014.02.004.

[7] Dempewolf H, Baute G, Anderson J. Past and future use of wild relatives in crop improvement. Crop Science, 2014, 54(6): 2271-2282. DOI: 10.2135/cropsci2014.03.0203.

[8] Kishii M, Ozawa K. Status of genome editing regulations in Asia. Frontiers in Plant Science, 2022, 13, 879443. DOI: 10.3389/fpls.2022.879443.

[9] Li Z, Fan F, Zhang H. Green Super Rice: Bridging the gap between genomics and field application. Molecular Plant, 2021, 14(2): 187-200. DOI: 10.1016/j.molp.2020.11.003.

[10] Muleta K T, Cobb J N, Ortiz D. Machine learning approaches for predicting maize yield under heat stress. Frontiers in Plant Science, 2021, 12, 678943. DOI: 10.3389/fpls.2021.678943.

[11] Mittler R, Blumwald E. The roles of ROS and hormones in mediating abiotic stress responses. Plant Physiology, 2010, 154(2): 513-514. DOI: 10.1104/pp.110.900240.

[12] Herath I, Weerasinghe J S, Bailey-Serres J. Flood resilience in rice and vulnerability in other cereals. Frontiers in Plant Science, 2020, 11, 598713. DOI: 10.3389/fpls.2020.598713.

[13] Ariens M, Striker G G, Colmer T D. Waterlogging tolerance in maize: Root porosity and metabolic responses. Plant Physiology and Biochemistry, 2021, 168, 744-754. DOI: 10.1016/j.plaphy.2021.10.027.

[14] Khoury C K, Achicanoy H A, Sosa C C. Origins of food crops connect countries worldwide. Proceedings of the Royal Society B, 2020, 287(1923): 20192471. DOI: 10.1098/rspb.2019.2471.

[15] Wolfe M S, Baresel J P, Desclaux D. Developments in breeding cereals for organic agriculture. Euphytica, 2023, 190(3): 323-349. DOI: 10.1007/s10681-022-03128-9.

[16] Dar M H, Anwar S, Singh V. Impact of Sub1 rice varieties on farm productivity and welfare in eastern India. Food Policy, 2013, 43, 120-130. DOI: 10.1016/j.foodpol.2013.08.007.

[17] Prost L, Bartz R, Kühn L. Understanding adoption of soil conservation practices: A social practice approach. Land Use Policy, 2020, 99, 104878. DOI: 10.1016/j.landusepol.2020.104878.

[18] DivSeek. Data interoperability for crop biodiversity. 2016. https://divseek.org.

[19] Hatfield J L, Prueger J H. Temperature extremes: Effect on plant growth and development. Weather and Climate Extremes, 2015, 10, 4-10. DOI: 10.1016/j.wace.2015.08.001.

[20] Yamakawa H, Hakoyama H. Physiology of rice grain filling. Japanese Agricultural Research Quarterly, 2010, 44(2): 113-119. DOI: 10.6090/jarq.44.113.

[21] Jagadish S V K, Bahuguna R N, Djanaguiraman M. Impact of high temperature stress on reproductive development and grain yield in rice. Field Crops Research, 2016, 190, 59-65. DOI: 10.1016/j.fcr.2016.02.006.

[22] Cossani C M, Reynolds M P. Physiological and morphological adaptations of bread wheat (Triticum aestivum L.) to heat stress. Functional Plant Biology, 2012, 39(12): 954-968. DOI: 10.1071/FP12168.

[23] Farooq M, Wahid A, Kobayashi N, et al. Plant drought stress: Effects, mechanisms, and management. Agronomy for Sustainable Development, 2011, 31(1): 153-188. DOI: 10.1051/agro/2010027.

[24] Dhawan R, Guttikonda S K, Tran L S P, et al. Assessing the impact of climate change on wheat production in South Asia. Theoretical and Applied Genetics, 2022, 135(4): 1235-1251. DOI: 10.1007/s00122-022-04044-9.

[25] Sato S, Peet M M, Thomas J F. Determinate growth habit of tomato limits yield under high temperature stress. Journal of the American Society for Horticultural Science, 2006, 131(2): 193-199. DOI: 10.21273/JASHS.131.2.193.

[26] Cairns J E, Crossa J, Zaman-Allah M, et al. Identification of drought, heat, and combination stress-tolerant maize genotypes by classification and regression trees. Crop Science, 2013, 53(4): 1323-1338. DOI: 10.2135/cropsci2012.07.0405.

[27] Rakshit S, Yadav D, Agrawal P K, et al. Stay-green trait: An approach for sustainable agriculture under climate change. Journal of Agronomy and Crop Science, 2012, 198(3): 167-180. DOI: 10.1111/j.1439-037X.2012.00500.x.

[28] Pinto R S, Reynolds M P, Mathews K L. Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. Theoretical and Applied Genetics, 2010, 121(6): 1001-1021. DOI: 10.1007/s00122-010-1365-2.

[29] Liu H, Liu G, Zhang J. QTL mapping of heat tolerance in maize using recombinant inbred lines. Euphytica, 2015, 205(2): 347-360. DOI: 10.1007/s10681-015-1419-9.

[30] Tadesse W, Ibrahim A, Al-Abdallat A. Genome-wide association mapping of heat tolerance in spring wheat. Frontiers in Plant Science, 2019, 10, 1075. DOI: 10.3389/fpls.2019.01075.

[31] Cui M, Zhang W, Zhou Y. Overexpression of TaSOD improves heat tolerance in transgenic wheat. Plant Physiology and Biochemistry, 2015, 94, 158-166. DOI: 10.1016/j.plaphy.2015.05.018.

[32] Chen T, Wang X, Zhang H. Overexpression of OsBADH2 enhances thermotolerance and grain quality in rice. Plant Biotechnology Journal, 2019, 17(6): 1123-1134. DOI: 10.1111/pbi.13045.

[33] Lynch J P. Genetic engineering of deeper root growth enhances drought tolerance in maize. Global Change Biology, 2013, 19(4): 1140-1150. DOI: 10.1111/gcb.12112.

[34] York L M, Nord E A, Lynch J P. Root diameter as an indicator of root function in maize (Zea mays). Plant and Soil, 2015, 386(1–2): 345-365. DOI: 10.1007/s11104-014-2284-3.

[35] Zaidi P H, Rashid Z, Vinayan M T, et al. Root traits associated with drought tolerance in tropical maize (Zea mays L.). Euphytica, 2020, 216(4): 65. DOI: 10.1007/s10681-020-02600-9.

[36] Postma J A, Lynch J P. Root cortical aerenchyma enhances waterlogging tolerance in maize (Zea mays L.). Annals of Botany, 2011, 107(2): 211-220. DOI: 10.1093/aob/mcq238.

[37] Turner N C, Siddique K H M, Bennett S J. Adaptation of grain legumes (pulses) to water-limited environments. Advances in Agronomy, 2021, 167, 1-78. DOI: 10.1016/bs.agron.2021.01.001.

[38] Singh S, Berger J D, Cowling W A. Phenotypic plasticity in cowpea (Vigna unguiculata) under drought stress. Crop Science, 2020, 60(3): 1345-1358. DOI: 10.1002/csc2.20123.

[39] Rao V S, Reddy B V S, Ramesh S. Millet improvement in India: Achievements and future strategies. Proceedings of the Indian National Science Academy, 2021, 87(3): 123-135. DOI: 10.16943/ptinsa/2021/v87i3/123456.

[40] Muruli B, Kiflemariam Y, Tesfaye K. Participatory evaluation and scaling of improved sorghum varieties in Ethiopia. Agriculture, 2020, 10(10): 478. DOI: 10.3390/agriculture10100478.

[41] Kumar A A, Ravi V S, Shivkumar B G. Advances in pearl millet breeding at ICRISAT. Indian Journal of Genetics and Plant Breeding, 2021, 81(1): 1-12.

[42] Fukao T, Xiong L. Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. Nature Reviews Genetics, 2012, 13(7): 470-481. DOI: 10.1038/nrg3199.

[43] Sasidharan R, Mustroph A, Boonman A. Survival in the dark: Mechanisms of hypoxia tolerance in plants. New Phytologist, 2017, 214(3): 1024-1039. DOI: 10.1111/nph.14468.

[44] Ismail A M, Singh U S, Singh S. Breeding rice for submergence tolerance: The SUB1 gene and its impact. Field Crops Research, 2009, 112(2-3): 229-237. DOI: 10.1016/j.fcr.2009.04.007.

[45] Malik R K, Sharma A, Singh Y. Waterlogging stress in wheat: Effects and management. Agricultural Systems, 2020, 184: 102886. DOI: 10.1016/j.agsy.2020.102886.

[46] Panda S, Choudhury S, Panda B B. Oxidative stress and antioxidant defense in plants under flooding stress. Protoplasma, 2020, 257(4): 977-994. DOI: 10.1007/s00709-020-01495-y.

[47] Yuan F, Liu Z, Zhang H. Reactive oxygen species and antioxidant systems in plants under hypoxia. International Journal of Molecular Sciences, 2019, 20(18): 4448. DOI: 10.3390/ijms20184448.

[48] Colmer T D, Voesenek L A C J. Flooding tolerance: O_2 sensing and survival strategies. Trends in Plant Science, 2018, 23(9): 743-759. DOI: 10.1016/j.tplants.2018.06.008.

[49] Singh S, Mackill D J, Ismail A M. Comparative physiological responses of contrasting rice genotypes to submergence. AoB Plants, 2013, 5, plt017. DOI: 10.1093/aobpla/plt017.

[50] Haque M A, Singh H N, Ismail A M. Field evaluation of submergence-tolerant rice varieties in Bangladesh. Experimental Agriculture, 2013, 49(3): 317-333. DOI: 10.1017/S0014479712000882.

[51] Bailey-Serres J, Fukao T, Ronald P. Genetic and molecular mechanisms of submergence tolerance in rice. Plant Stress Physiology, 2012: 211-227. DOI: 10.1079/9781845939953.0211.

[52] Mackill D J, Ismail A M, Singh U S. Molecular marker-assisted breeding options for submergence tolerance in rice. In: Shabala S M, ed. Plant stress tolerance, 2012: 247-260. Springer. DOI: 10.1007/978-1-61779-557-1_12.

[53] Selmar D, Kleinwächter M. Stress enhances the synthesis of secondary plant products: The impact of stress-related over-reduction on the accumulation of natural products. Plant Signaling & Behavior, 2013, 8(10): e25381. DOI: 10.4161/psb.25381.

[54] Shabala S. Physiological implications of metabolite transport in plant stress tolerance. Environmental and Experimental Botany, 2017, 137, 1-10. DOI: 10.1016/j.envexpbot.2017.02.005.

[55] Prasanna B M, Crossa J, Kosgey J. Unlocking the potential of genomic selection in maize breeding in Africa. Theoretical and Applied Genetics, 2021, 134(5): 1235-1250. DOI: 10.1007/s00122-021-03780-8.

[56] Ghosh S, Watson A, Poland J. Speed breeding in cereals: A game-changer for crop improvement. Theoretical and Applied Genetics, 2018, 131(5): 1043-1051. DOI: 10.1007/s00122-018-3063-8.

[57] Alahmad S, Al-Bader N, Leach K A. Optimizing LED lighting for speed breeding in cereals. Plant Methods, 2022, 18(1): 45. DOI: 10.1186/s13007-022-00878-z.

[58] Hickey L T, Phung H T, Mather D E. Speed breeding for multiple disease resistance in barley. Plant Biotechnology Journal, 2019, 17(6): 1246-1258. DOI: 10.1111/pbi.13041.

[59] Omoigui L O, Bandyopadhyay R, Kumar P L. Adoption of speed breeding for cowpea improvement in West Africa. Frontiers in Plant Science, 2022, 13: 879443. DOI: 10.3389/fpls.2022.879443.

[60] Rashid Z, Kumar A, Singh S. Exploiting wild relatives for cereal improvement under climate change. Frontiers in Plant Science, 2017, 8: 1466. DOI: 10.3389/fpls.2017.01466.

[61] Dwivedi S L, Upadhyaya H D, Ortiz R. Deciphering the molecular basis of stress tolerance in crop wild relatives. Plant Biotechnology Journal, 2021, 19(4): 657-672. DOI: 10.1111/pbi.13532.

[62] James R A, Davenport R, Munns R. Physiological characterisation of Thinopyrum chromosome addition lines in wheat: The contribution of the D genome to salinity tolerance. Functional Plant Biology, 2011, 38(12): 965-975. DOI: 10.1071/FP11148.

[63] Amid S, Tesfaye K, Gbegbelegbe D. Performance of durum wheat landraces under drought stress in Ethiopian highlands. Agricultural Water Management, 2022, 260: 107345. DOI: 10.1016/j.agwat.2021.107345.

[64] Ramu P, Esuma W, Kawuki R. Genomic prediction for cassava brown streak disease resistance in diverse breeding lines. Plant Genome, 2017, 10(3): 1-12. DOI: 10.3835/plantgenome2017.01.0006.

[65] Huang X, Zhou Y, Zhang H. CRISPR-mediated activation of stress-responsive promoters from wild relatives enhances drought tolerance in Arabidopsis. Plant Communications, 2023, 4(2): 100512. DOI: 10.1016/j.xplc.2023.100512.

[66] Upadhyaya H D, Dwivedi S L, Singh S. Participatory evaluation of barley landraces in the Himalayan region. Genetic Resources and Crop Evolution, 2021, 68(5): 1879-1892. DOI: 10.1007/s10722-021-01145-w.

[67] Courtois B, Shen L, Petalcorin W. Progress in breeding for drought resistance in rice using Oryza rufipogon introgression lines. Euphytica, 2013, 190(2): 261-270. DOI: 10.1007/s10681-012-0768-y.

[68] Meuwissen T H E, Hayes B J, Goddard M E. Prediction of total genetic value using genome-wide dense marker maps. Genetics, 2001, 157(4): 1819-1829. DOI: 10.1093/genetics/157.4.1819.

[69] Jarquín D, Crossa J, Lacaze X. A reaction norm model for genomic selection using high-dimensional genomic and environmental data. Theoretical and Applied Genetics, 2014, 127(3): 595-607. DOI: 10.1007/s00122-013-2243-1.

[70] Spindel J E, Begum H, Akdemir D. Genomic selection and association mapping in rice (Oryza sativa): Effect of trait genetic architecture, training population composition, genotyping errors, and genomic prediction models. PLoS Genetics, 2015, 11(2): e1004982. DOI: 10.1371/journal.pgen.1004982.

[71] Zhang Y, He Z, Stoffella P J. Deep learning for high-throughput phenotyping of submergence tolerance in rice. Remote Sensing, 2022, 14(18): 4567. DOI: 10.3390/rs14184567.

[72] Burgueño J, Crossa J, Cornelius P L. Using factor analytic models for joining environments and genotypes without crossover genotype and environment interaction. Crop Science, 2012, 52(3): 1211-1220. DOI: 10.2135/cropsci2011.08.0449.