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RESEARCH ARTICLE

Trends in Biotechnology and Plant Sciences

Harnessing Genetic Innovations to Develop Climate-Resilient Maize

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Abstract

Maize (*Zea mays* L.) is a cornerstone of global food, feed, and industrial systems, yet its productivity is increasingly threatened by climate change, particularly through recurrent heat and drought stresses. These abiotic constraints severely impair photosynthesis, reproductive development, grain filling, and ultimately yield stability, especially in rain-fed agro-ecosystems of the tropics and subtropics. The simultaneous occurrence of heat and drought further exacerbates physiological damage, leading to oxidative stress, pollen sterility, kernel abortion, and deterioration of grain quality. Addressing these challenges requires an integrated, genetics-driven approach to develop climate-resilient maize cultivars. This review synthesizes recent advances (2020–2025) in understanding the physiological, biochemical, genetic, and molecular mechanisms underlying maize tolerance to heat and drought stresses. Key adaptive traits, including stay-green phenotype, deep root architecture, optimized transpiration efficiency, osmotic adjustment, antioxidant defense, heat shock proteins, and membrane stability, are discussed in relation to yield resilience. At the molecular level, the roles of quantitative trait loci, transcription factors, hormonal signaling pathways, epigenetic regulation, and multi-omics approaches are highlighted as critical components of stress adaptation. Furthermore, the review critically evaluates modern breeding innovations such as marker-assisted selection, genomic selection, genome-wide association studies, pan-genomics, and CRISPR/Cas-based genome editing as transformative tools for accelerating the development of climate-smart maize hybrids. The integration of physiological trait phenotyping with genomic prediction models is emphasized as a key strategy to enhance selection accuracy under complex stress environments.

KEYWORDS
Heat stress, Drought stress, Abiotic stress tolerance, Climate-resilient breeding, Genomic selection, Marker-assisted selection, CRISPR/Cas9, Multi-omics.

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1 | INTRODUCTION

Maize (Zea mays L.) is one of the most important cereal crops worldwide and is the second most important cereal after wheat on the basis of global production (Erenstein et al., 2022). It is a staple food but also a necessary livestock feed, establishing a connection between plant and animal production that is unique. The broad adaptability, short growing period and high production potential are the reasons why it has become a favored crop in a range of agro-ecological zones, from temperate to tropical region (Yadesa & Diro, 2023). Besides the direct consumption by humans, maize is also an important crop for industrial utilization starch, sweetener and biofuel production. In the United States, for instance, another significant portion of maize is made into ethanol to supply renewable energy and bolster rural economies (Assaf et al., 2024). In parts of Sub-Saharan Africa or Latin America, maize is a staple that contributes directly to household food security and can make up a significant amount of the diet in terms of energy intake. Maize is one of the most important sources of food and culture in Mexico. Both types of corn tortillas are still commonly eaten and a staple of the diet and culture of Mexico and Central America. Even now, maize porridge remains a staple in many African households. In fact, the food-feed duality of maize has led to its status as a food staple in global food systems. So was corn, in certain farm towns. As much as a food reserve, it is also a commercial cash crop for millions of smallholder farmers. More production, more income that is being sold and marketing access. This has made the consumer cash crop low-yielding one of the most valuable one in agriculture (and food security) an income issue in human socio-economics (Arumugam et al., 2022). By the degree of world dependence on maize, production can no longer be approached in a sustainability address limited only to the agricultural realm, but in nutritional, energy, trade and economic terms. This takeaway is why maize, consumed and cultivated all over the world, serves as such a linchpin on crop improvement and agricultural tech development everywhere (Vidanapathirana et al., 2022).

The observed and projected negative effects of climate change on maize production are likely to change in the quantity and quality of food produced. More extreme weather conditions may reduce the amount of food produced, Changes in temperature and precipitation may increase the incidence of pests and disease (Neupane et al., 2022). The Ecological footprint of different crops may need different environments and reduced productivity in Sub-Saharan Africa. But a warming climate, punctuated by more extreme weather, has meant that the farming landscape is changing in ways that may make it uncertain. Both heat stress and drought stress are the two most critical constraints for maize, and the two stresses usually happen simultaneously or jointly (Tang et al., 2025). Flowering and grain filling stages are affected because of heat stress this suffer from low photosynthesis, early senescence of green leaves and low viability of the pollen and the result is low seed fill. Even very short periods of the daily mean temperature being greater than 35 °C can result in irrecoverable loss of final yield (Mehmood et al., 2025). Drought stress brings about a decline in soil water content, upon which maize plants close their stomata and the entry of CO_2 is also limited, resulting in a decline in photosynthesis (Deribe, 2025). The consequence is small plants, later silking, and low kernel set. The double blow of heat and drought is even worse than either alone. Maize in fact, experiences these stresses collectively, particularly in the rain fed South Asia region when at its most critical reproductive phase. This correlation was associated with an increased oxidative burst, source-sink translocation of shunted and affination-reduced yield stability (Boddupalli M Prasanna et al., 2021). Maize consumption for this period of population growth and dietary change is projected to at least double by 2050. But models of what the climate is likely to do also tell us that unless we all pull our socks right up, we are also going to have to face a 10-25% loss of our global maize harvest in the tropical and subtropical parts of the planet (Paliwal & Smith, 2024). This will pave the way for a widening chasm between explosive demand and climate endanger supplies. Science-led game changing solutions that prepare maize to survive in a climate-changing environment will be needed to address these challenges. Climate-resilient breeding is one such, longer-term strategy to help ensure food sovereignty under these altered conditions.

The small repetitive variation in the sensitivity of maize to climate stress is an issue of key challenge in developing resilient maize varieties. In this study, resilience in maize is defined as the ability to maintain yield under contrasting and sometimes harsh environmental conditions (i.e., heat and drought) (Boddupalli M. Prasanna et al., 2021). The successful development of such tolerance would, however, ultimately be contingent on an inclusive strategy integrating the physiological, biochemical and molecular tools into breeding programs. Conventional agriculture and irrigation practices are inadequate to deal with the challenge, especially in rain fed agriculture-based zones. Small-scale farmers in low input farming systems often lack access to large scale irrigation facilities, synthetic fertilizer and pest control and stress tolerant cultivars may be the best bet for stability in yield (Jayaraman et al., 2021). Root features with adequate length and number, stay-green characteristics, high water-use efficiency and thermo-tolerance at the flowering time are necessary for the drought tolerance of resistant maize hybrid. Equally important as the behavior under stress of genotypes is the capacity of them to conserve the quality of grain, because the quality in nutrient concentration for yield counts at least as much (Waqas et al., 2021). Besides improving food security, the climate-resilient maize supports environmentally sustainable farming with less reliance on chemicals and irrigation. This is both environmentally and producer cost beneficial (Srivastav et al., 2021). The tolerant maize provides the smallholder farmers in the marginal areas with a higher degree of livelihood security by reducing the risk of crop failure. Therefore, the dissemination of climate-resilient maize is not just a science issue, but a global concern that has direct connection to issue ranging from hunger and food security, better life of human being and the coping with climate change (Srivastav et al., 2021).

Genetically creative solutions for climate-resilient maize. Unlike traditional breeding tactics which rely on phenotypic selection, the new genetic tools allow for direct targeting of the plant stress response genes and pathways, enabling the rapid creation of stress-resistant crops (Singh et al., 2021). Stress tolerance can be identified via MAS, and selection can now be proven to be much more precise and rapid. Genome Selection takes it one-step further and relies heavily on whole-genome information to concurrently improve desirable traits such as heat and drought adaption effectively coordinated these traits those closely using phenotypic predictions and directly breed for increasing more precisely several complex traits. Opportunities arise through biotechnology and genome editing. It has also been enhanced by the technology of transgenic with genes that assisted osmoprotection and detoxification of ROS or enhancing photosynthetic capacity and had produced tolerance in plants to salt. Integration of multi-omics such as genomics, transcriptomics, proteomics, and metabolomics, helps in identifying the mechanisms of stress tolerance at different biological levels. They make candidate genes, regulatory networks and metabolic and proteomic pathways associated with resilience accessible and complement the toolbox for breeders (Roychowdhury et al., 2023). By tapping into these genetic gains, breeders should be able to accelerate the breeding cycle, increase precision and develop climate-smart maize varieties that are perfectly matched to any environment. Such transition from classical hybridization to knowledge-guided technologies is a major milestone to address the impact of climate change on maize yield (Li et al., 2025).

In this review, we have summarized the existing knowledge on genetics, physiology and molecular mechanisms of heat and drought stress in maize, along with recent breeding strategies for making climate resilient. It thus emphasizes on genetic innovation relevant to abiotic stress from MAS and Genome Selection, but we would like to add, also genome editing. The review also added that genetic efforts had to be accompanied by climate-smart agricultural approaches, as breeding alone may not be sufficient to face the entire challenge. Those and other actions have a possibility to strengthen it with a somewhat subordinated value to precision water management, digital agriculture, smaller-holder breeding, influence marketing apparatus etc are absolutely essential to get to the impact levels on the ground. The tools that allow us to take results from laboratory and field into a breeding animal are included in the package. This will require trait/genetic resource discovery and new breeding strategies for new stress tolerant hybrids for the farmers. The other focus has much more to do with the big public questions surrounding hard maize: food security, sustainable farming, country lives. The climate resilient maize provides improved grain quality and security (food and income) for the most vulnerable populations of the drought stressed areas. Finally, this essay stresses the importance of interdisciplinary integrative perspectives as well. It aims to enable the science community, breeders, and agro-policy makers to provide climate-resilient maize systems in the future for global food security.

2 Climate Challenges faced by Maize

Maize (Zea mays L.) is a crop with a wide range of adaptation, and it is also confronted with more challenges than ever in a changing climate world. Increasingly, there are mismatches between the genotypes we have and the environments in which they are growing. As the linchpin of the world's food-feed-industrial systems, the enhanced susceptibility of maize to extreme environments poses a threat to global food security and the income of rural people all over the world (Tang et al., 2025). Among the array of climate-induced stressors, rising temperatures, erratic rainfall, and frequent droughts stand out as the most detrimental, particularly because they occur during sensitive growth stages such as flowering and grain filling (Kaplan et al., 2024). Unlike controlled agricultural environments, most maize in developing regions is cultivated under rainfed conditions, making it highly exposed to climatic fluctuations. These challenges are not isolated but interactive, with heat and drought stress often coinciding to create compounded impacts that surpass the effect of each stress alone (Du & Xiong, 2024). Understanding projected climate trends and their implications for maize-growing regions is therefore critical to designing resilient cropping systems and breeding strategies that can safeguard maize production in the decades ahead.

3 Projected Climate Trends and their effect on Maize

One of the most consistent projections of climate models is the steady increase in global mean temperature, with an estimated rise of 1.5–2.0 °C by mid-century under moderate emission scenarios. For maize, which thrives best between 25–33 °C, this change poses direct threats to productivity. Even short periods of extreme heat (>35 °C) during the reproductive phase can decrease pollen viability, accelerate leaf senescence, and shorten grain-filling duration. Maize-growing regions in Sub-Saharan Africa, South Asia, and Central America are especially vulnerable, as baseline temperatures in these areas already approach the crop's tolerance limit (Mehmood et al., 2025). Future warming trends are likely to turn once-optimal growing seasons into periods of ongoing heat stress, significantly reducing yield potential. Rainfall variability is another key feature of climate predictions. In maize-dependent regions such as Eastern and Southern Africa, rainfall is expected to become more unpredictable, with longer dry spells interrupted by heavy rainfall events (Z. Wang et al., 2025). This pattern hampers maize production in two main ways: prolonged dry periods reduce soil moisture during critical growth stages, while excessive rainfall causes flooding, nutrient leaching, and soil erosion. Drought stress, particularly during tasseling and silking, can lead to yield losses of up to 50%. Climate models forecast that drought frequency and severity will increase in semi-arid areas of Africa and South Asia, putting millions of smallholder farmers at greater risk of crop failure (Naseer et al., 2023).

Perhaps the most alarming projection is the simultaneous occurrence of heat and drought stress. These stresses not only overlap in many maize-growing environments but also exacerbate each other's impacts. High temperatures accelerate soil moisture depletion, while limited water availability reduces the plant's capacity for transpirational cooling, leading to elevated canopy temperatures (Li & Tian, 2024). The interaction results in severe oxidative stress, disrupted pollination, and significant kernel abortion. Climate scenarios indicate that such compound stress events will become more frequent in rainfed regions of Africa and South Asia, with yield losses surpassing those caused by either stress in isolation (Zhao et al., 2023). Another major impact of projected climate change is the geographical shift of suitable maize-growing areas. In some temperate regions, warming may expand maize cultivation into previously cooler zones, such as northern Europe, Canada, and parts of Russia. In contrast, low-latitude tropical and subtropical regions currently contributing to a large part of world maize production are projected to become less suitable because of heat and water stress (Shekhar & Singh, 2022). For instance, in models, large areas of Southern Africa could become marginal for maize production by 2050 resulting in substitution with other crops such as sorghum or importation of maize. Those spatial displacements will not only reconfigure production geographies, they will dislocate food systems and economies closer to home (Mumo et al., 2021).

Under a potential climate change the uniformity both in space and time of the total maize yield for every year might be decreased. In these climatically highly inter-annual regions (e.g., Indo-Gangetic Plains and Sahel), farmers stand to lose much and gain almost nothing by the change to a chaotic boom-bust system (Yasin et al., 2022). Even greater climate variability will intensify these yield fluctuations, and farmers will have almost no control over when to sow and harvest, where and how to market their crops, or whether their family will have enough to eat. Yield instability has a ripple effect on animal-feed supply, ethanol production and global maize trade, which could drive up food prices and worsen poverty and undernutrition in areas and communities made vulnerable (Erenstein et al., 2022). In addition to yields, risks on maize grain quality are also foreseen according to the climatic predictions. Aflatoxin producing environmental conditions the blistering hot, drought-stressed are excellent conditions for fungal pathogens (Aspergillus species in particular) to produce avenalin, which in the end produce aflatoxins that is a feral food safety issue (Commey et al., 2024). Furthermore, there is a shortage of starch accumulation and unbalanced protein profile due to lower starch accumulation caused by the heat and drought stress to grain fill. These modifications diminished the feeding value and industrial utility of maize for human consumption and animal-feed purposes (Sadhukhan et al., 2024).

Yield of grain in the past has improved by increasing, like other food crops, but adaptation to these problems (potentially also problems of climate change) will be an integral part of being resilient in the future, however more of the better and best grain is a counter-trend response to the climate changes that we will start to see producing larger and better-quality grain, soon (Naseer et al., 2023). The projected impacts due to climate variables on maize are not only on biophysical factors, but they also penetrate deeply to socio-economic dimensions. But rainfed production systems and limited reach of adaptation technologies are exposing the smallholder farmers who form the backbone of maize production in Africa, Asia and Latin America to greater risk (Guo et al., 2021). A smaller harvest of maize does result in less rural income, which increases reliance on outside food aid, so all of that signs do show that it does cause the national food and Insecurity to fall , even if slowly. Reduced crop yields could also be a tipping point for social and political stresses in areas like Kenya, or Mexico, where maize represents something of a cultural totem, and so make it that much harder to adapt. It paints a bleak picture of the future when it comes to maize production, all these climate projections combined. This would hasten a re-patterning of global maize systems, in which rising temperature, more-variable rainfall, and growing multi-stress force majeure events would conspire to re-cast the geography, productivity, and stability of maize systems (Ahmad et al., 2024). Whole countries dependent on corn (or whole other continents, the more) we will increasingly be exposed to food insecurity, economic instability, and ultimately political instability unless we start to tackle these issues. And that is a powerful case for investing in climate-ready solutions, especially those that use genetic innovation. By anticipating what can be anticipated and then modifying both breeding and management in response, maize can remain a stable pillar of global food systems under climate change.

3 Heat Stress in Maize

Heat stress is one of the most severe abiotic stresses affecting maize (Zea mays) production, especially in the tropical and subtropical regions where this crop is frequently sown near its maximal thermal limits. Since maize likes 25 -33 °C and is damaged by temperatures less than 16 °C and higher than 35 °C, the week of hot day (>35 °C) and dry and shiny days during flowering could be enough to cut maize production (Ahmad et al., 2024). The extent of damage isn't just a function of how hot and for how long, but also of when and how long the insult occurs. Sensitive periods such as tasseling, anthesis and grain filling are particularly sensitive. The physiological events most influenced by heat stress are photosynthesis, pollen development and fertility, and the duration of grain fill. Suppressing the photosynthesis is one of the earliest and the most fundamental effects of heat stress (Ahmad et al., 2024). High temperatures also cause the collapse of the ultrastructure and activity of chloroplast proteins, especially those found in photosystem II (PSII). The thylakoid membranes of chloroplasts under heat stress are destabilized resulting in dysfunction of the electron transport and photochemical reaction. Furthermore, the enzyme rubisco activase (which activates rubisco during fixation of CO_2) is extremely sensitive to high temperatures. Under high temperature, it is inhibited so that the rate of CO_2 assimilation decreases (Zhang et al., 2023). The stomatal closure at high temperature would decrease excess CO_2 absorption, exacerbating the situation. This significantly reduces the source capacity of the plant (its capacity to produce assimilates for growth and reproduction) under heat stress (Tarafdar et al., 2022).

Heat also induces the generation of reactive oxygen species (ROS) in chloroplasts and mitochondria, ultimately resulting in oxidative stress. Excessive production of ROS is toxic, causing damage to proteins, lipids, and DNA, and leads to a decline of the photosynthetic apparatus (Medina et al., 2021). Maize plants have antioxidant defense mechanism including SOD, CAT and APX, but frequently the prolonged/strong heat condition leads to it become inadequate. The imbalance of ROS generation and scavenging would promote leaf senescence that fades the age of leaves (effective photosynthesis) (Rajput et al., 2021). This premature loss of photosynthetically active tissue in turn inhibits the supply of assimilates in all the important reproductive phases and has adverse impacts on yield potential. Beyond photosynthesis, heat stress directly affects the male reproductive process, particularly pollen development and viability. Pollen grains are highly sensitive to elevated temperatures, and exposure to heat during anthesis can lead to pollen sterility (Resentini et al., 2023). High temperatures impair microsporogenesis, disrupt tapetum function, and reduce pollen hydration, resulting in malformed or non-viable pollen grains. Even when pollen is produced, its germination capacity and pollen tube growth are often compromised under heat. Since successful fertilization depends on synchrony between viable pollen and receptive silks, any disruption in pollen viability drastically reduces kernel set and overall yield (Mehmood et al., 2025).

Female reproductive organs are also negatively affected by heat stress, though to a slightly lesser extent compared to pollen. High temperatures during silking delay silk emergence, reduce silk elongation, and shorten the window of receptivity. This creates an asynchrony between pollen shed and silk availability, commonly referred to as an extended anthesis-silking interval (ASI). A longer ASI is strongly correlated with a poor kernel set under stress conditions. Thus, heat stress impacts both sides of the reproductive process, compounding its negative effect on yield formation. Grain filling, another critical phase, is significantly shortened under heat stress (H. Wang, J. Sun, B. Zhao, Y. Li, Z. Zhang, A. Khan, J. Zhang, Y. Chen, et al., 2025). Elevated temperatures accelerate leaf senescence and hasten the remobilization of assimilates to developing kernels. While this may initially appear beneficial, the net effect is a reduced duration of grain filling, which results in lighter kernels with less starch accumulation. The starch synthesis enzymes, including ADP-glucose pyro phosphorylase, are especially heat sensitive, hence the incomplete starch deposition. As a result, smaller, shrunken kernels of less weight develop, which causes losses in yield (Du et al., 2022). This abbreviated grain filling is a particular concern for hybrids developed for high yield potential because they depend on an extended duration supply of assimilates for maximum kernel growth.

The grain composition reduction is not only the result of decreased kernel weight in response to heat stress. Reductions in starch and sometimes increase in kernel protein content under high temperature have been observed. However, the change from the grain portion of such a composition is disadvantageous, in that it leads to a grain usually less digestible, of less processability quality (C. Wu et al., 2022). Meanwhile, heat stress can also induce defective endosperm development leading to reduction in nutritional quality of endosperm for human diet and processing quality for industries. Heat stress affecting both yield components, quality and quantity and combined between them, is an obstacle for producing maize. The combined effects of photosynthesis suppression, pollen abortion and shorter grain-filling period significantly decrease maize productivity (Wang et al., 2023). The yield reductions that are incurred under extreme heat stress during the reproductive period may surpass 50% and may be even higher when exposure is concurrent with flowering. More importantly, these responses are not consistent among genotypes, other maize germplasm expresses improved tolerance characterized by traits as heat-stable photosynthetic enzymes, enhanced antioxidant capacity, and higher levels of pollen thermotolerance (Fatma et al.). Detection and utilization of such traits in breeding programs is, therefore, an important strategy to counteract the negative consequences of heat stress.

4 Drought Stress

Drought stress is one of the most pervasive and damaging abiotic stresses affecting maize production worldwide. Because more than 60% of maize is cultivated under rainfed conditions, its productivity is directly dependent on the availability and distribution of rainfall. When soil moisture becomes insufficient to meet plant demand, maize experiences water deficit stress that triggers a cascade of physiological, biochemical, and developmental responses (Sheoran et al., 2022). The severity of drought impacts depends not only on the intensity and duration of stress but also on the growth stage at which it occurs. Stress during vegetative growth restricts plant height and biomass accumulation, while stress during reproductive stages particularly tasseling and grain filling causes dramatic yield reductions (Seleiman et al., 2021). The stomatal closure of maize also represents one of the first responses to drought in order to reduce water loss through transpiration. Stomata are open and close under the control of digital guard cells, and water deficit induces the guard cells to close via ABA. Though this saves water, it limits the movement of CO_2 into the leaf mesophyll and there is a compromise between saving water and taking up CO_2 (Liu et al., 2025). Long-term stomatal closure results in a decreased intercellular CO_2 concentration, which will reduce photosynthesis. This balance provides an explanation for why maize, a C_4 species being inherently efficient in water use, has a significant productivity loss under water stress (Tian et al., 2024).

The suppression of photosynthesis by drought is complex, involving more than stomatal control. Low CO_2 availability restricts Rubisco carboxylation, whereas water stress directly affects chloroplast ultrastructure and photosystem integrity. The thylakoid profile in particular becomes disordered and the efficiency of electron transport drops. The situation may be well aggravated by drought- provoking the oxidative stress, when reactive oxygen species (ROS) accumulate in chloroplasts and mitochondria, which results in the damage of proteins, lipids, and nucleic acids (Bhattacharya, 2022). There are also stress-related responses such as the activation of an antioxidant system consisting of a series of enzymes such as superoxide dismutase, catalase, and peroxidases which can only offer partial protection, the long-term drought often exceeds this defense mechanism (Engwa et al., 2022). This imbalance leads to faster leaf aging and decreases the photosynthetic area of the leaves to support plant growth and reproduction. Drought also limits the absorption and translocation of nutrients in maize. The diffusion and mass flow of nutrients, including N, P, and K, to the root surface are reduced by low soil moisture content. At the same time, there is a lower transpiration flow, it restricts the transport of nutrients from the roots to the shoots. This feeding imbalance adds to the decline in photosynthesis since chlorophyll biosynthesis and enzyme activity are affected. Leaves under severe conditions also become chlorotic, rolled, and senesce prematurely, limiting the potential of the crop to produce assimilates for the development of the grain (Kumari et al., 2022). As a result, drought stress generates a double lock of carbon and nutrient loss in maize plants.

The reproductive phase is particularly sensitive to drought, with tasseling and silking stresses resulting in some of the most severe yield penalties. Among the most distinctive responses to these stress conditions is increase in anthesis-silking interval (ASI). Under drought, tassels may drop pollen as usual, but silk elongation is delayed because of a lack of turgor and the timing of availability of pollen versus receptivity of silks are not synchronized. This asynchrony substantially reduces fertilization and results in poor kernel set. Kernel abortion is also common under drought even when fertilization occurs, as the restricted photosynthate is inadequate to support development of all grains (Tang et al., 2025). Therefore, ears frequently exhibit partial rows of kernel and a generalized poor kernel set which is characteristic of drought injury at the reproductive phase. Beside ASI elongation, pollen viability per se is frequently impaired by drought. Water stress negatively affects microsporogenesis and reduces pollen hydration, generating shriveled pollen grains or nonviable ones. Pollen tube penetration through the silk is slowed, thereby reducing the success of fertilization (Guo et al., 2021; H. Wang, J. Sun, B. Zhao, Y. Li, Z. Zhang, A. Khan, J. Zhang, Y. Chen, et al., 2025). On the female side, plants silks under drought condition may be desiccated to lose the receptivity of pollen grains. These multiple impaired reproductive functions justify that even short durations of drought during flowering results in 40 to 60% yield loss depending on the intensity. Drought shortened the duration of grain filling, similar to high temperature effects. Reduced photosynthetic rate and early leaf senescence are responsible for poor source in developing kernels. Maize plants can attempt to compensate by remobilizing stored carbohydrates from stems and leaves, yet this is often not enough to support grain filling (Ghalib et al., 2025). Hence, kernels are small and underfilled due to low starch accumulation and test weight. A decreased period of grain filling occurs which causes quantifiable losses in yield per ear, and under extreme conditions barren cobs.

The effect of drought is not limited only on shoot yield, but it also influences grain quality. Starch and protein are also affected in drought-stressed maize plants. Although percent protein in kernel may increase, various levels of essential amino acids such as lysine, and tryptophane are frequently changed (H. Wang, J. Sun, B. Zhao, Y. Li, Z. Zhang, A. Khan, J. Zhang, Y. Chen, et al., 2025). Furthermore, drought also causes the occurrence of fungus causing infections like Aspergillus spp. and with Fusarium spp. the producers of aflatoxins and fumonisins, respectively. The dominant grain storage pests that lead to the increase in numbers of insects and the raise in grain moisture content are not only harmful to grain product quality but also have a huge effect on human and animal life, increasing the heavy load under which farmers reside caused by drought (Akello et al., 2021). The biggest social and economic problem is a shortage of corn, due to a drought. Tens of millions of poor farmers in Sub-Saharan Africa, South Asia and Latin America are losing access to variety of seed and irrigation that was crucial to their cultures (Orimoloye et al., 2022). And just one dry season can tip families into acute food insecurity and poverty. At global level, sudden and large national-level production deficit (because of reasons such as drought) can sometimes force to put an upward pressure of markets' prices and over foreign exchange reserves (for importing food items). All of this has pushed up the price of food around the world, squeezing both producers and consumers (Karume et al., 2024).

5 Synergistic Effect of Combined Heat and Drought Stress

Under field conditions, it is uncommon that maize is subjected to one abiotic stress alone as heat and drought collectively influence maize growth, especially in the tropical and subtropical regions. The interaction of these stresses when combined do not summate effectively but instead interact synergistically with an impact on plant physiology, growth and yield that is greater than either of the stresses applied singly (Zandalinas & Mittler, 2022). This link between the two occurs because heat speeds up soil water loss and a drought shuts down the plant's cooling process due to transpiration. Therefore, temperatures within canopies increase dramatically, triggering a sequence of detrimental events. Given the potential for higher likelihoods of co-occurrence of heat waves with drought events with climate change, it is important to know effects of this interaction on maize under these conditions to develop resistant cropping systems (Bamboriya et al., 2022). Physiologically, combined heat and drought impose great inhibition on photosynthesis. At high temperatures, chloroplast membranes become destabilized, and the activity of the stromal enzyme Rubisco activase is reduced, and drought-induced stomatal closure limits the entry of CO_2 into mesophyll cells (Abdelhakim et al., 2022). Combined, these limitations far exceed the reduction in carbon assimilation under each stress separately. Moreover, dual stress produces excess ROS, resulting in oxidative stress and destroying the structure, protein, and DNA of chloroplast. The antioxidant defense mechanisms quickly become saturated, which leads to early leaf senescence and extreme loss of photosynthetic area. The rapid depletion of source tissue caused by CPH, deprives developing ear and kernels assimilation (Langer, 2024; Li & Kim, 2022).

Water relations are similarly severely affected under combined stress. Drought decreases the availability of soil moisture, while heat increases evaporative demand. This leads to a rapid decrease in leaf water potential and cell turgor (Qiu et al., 2023). Under such conditions, the leaves of maize plant show excessive rolling, wilting, and scorching. The hydraulic network of tissues (including xylem conduits) of the plant is more susceptible to cavitation and embolism, and water efficiency is consequently even lower. This combined water stress prevents plants from maintaining sufficient transpiration and promoting an even higher canopy temperature, and the process continues in a downward spiral. The reproductive stage of maize is susceptible to multiple combined stresses (Li et al., 2023). Heat stress lowers pollen viability and drought delays silk emergence, resulting in an increased anthesis-silking interval (ASI). When these stressors act in concert, reproductive deficiencies occur in both sexes. The few pollen grains that do survive heat exposure on silks that have dried from drought rarely hydrate adequately (Wang et al., 2025). Even if fertilization does occur, a shortage of assimilates, the result of reduced photosynthesis, results in a high proportion of kernel abortion. The result is ears with few and incomplete kernel rows, a typical symptom of combination injury in maize (Song et al., 2021). The kernel development and grain filling are all inhibited seriously. Heat specifically reduces the duration of grain-filling, while drought limits the availability of assimilate via inhibition of photosynthesis and accelerating leaf senescence (Ma et al., 2023). Combined, these stresses substantially shorten and reduce the efficiency of grain fill. Starch synthesis, an enzymatic process, already heat-sensitive is even more sensitive in response to drought caused oxidative stress. As a result, kernels are light, shrunken, and low in starch. The compounded stress also enhances the remobilization of stem reserves to supply the kernels development, however, this is frequently insufficient resulting in additional yield loss (Naseer et al., 2023).

Under combined stresses the quality of grain decreases significantly. Large canopy temperatures and water deficits destroy the balance between Starch-Protein of kernels, resulting in the poor quality of protein. Simultaneously, the conditions of the stress combination are conducive to fungal infections, especially caused by Aspergillus which forms aflatoxins (Bhattacharya, 2022; Wang et al., 2022). Mycotoxin contaminated maize constitutes a great risk to food safety, especially in developing countries with poor post-harvest storage facilities. For this reason, the effect of combined stress is not only on yield, but on its safety and marketability as a grain in maize (Wekesa, 2022). The socio-economic consequences of combined heat and drought stress are often higher than of the single stresses. Yield reductions under simultaneous stress often surpass 60%, well above the average yield losses under drought or heat alone. For the poor and resource-scarce small holders of the African rain-fed savannah system (South Asia and Latin America), these losses are often devastating leading to short-term acute food shortage, income loss, and external dependency (Cohen et al., 2021; Tuhin et al., 2025). At the global scale, large-scale, simultaneous crop failures due to combined stresses can weaken maize chains and result in higher food prices and increased vulnerability to food deprivation among the poor (Khatri et al., 2024).

Acclimation to the combined stress is even more difficult, since mechanisms for coping with one stress may not be fully effective against the other .e.g., they could provide insulation from drought through having a stay-green trait or through a deep-rooting strategy, but not for heat-induced pollen sterility (Jiang et al., 2025). Heats table enzymes are likely to be treated similarly, as they could not balance the assimilate shortage incurred by water limitation. Thus, the plant breeding programs are now also focusing on identifying genotypes with additional tolerance features such as improved antioxidant capacity, stable photosynthesis even in stress condition and reproductive potential in high temperature (Dos Santos et al., 2022). Necessary to combine stress trials under controlled conditions across diverse environments to identify hybrids capable of withstanding the gamut of these different factors. At the molecular level, combined stress induces general reprogramming of the signaling network that is both unique to, and significantly different from, heat or drought stress alone (Smith et al., 2021). Crosstalk between ABA, ethylene and HSPs under abiotic stresses. Some unique expressed genes and metabolites in response to the combined stresses are identified between both transcription levels and metabolite levels, which may possibly be the candidate of genetic engineering. And now, in an age of genome-editing techniques like CRISPR/Cas9, the maize germplasm with precisely these mutations in precisely these pathways that so powerfully fortify resilience can be created (Li et al., 2025; Müller, 2021).

Stressful environments of heat and drought simultaneously are among the most harmful abiotic stresses to maize production with respect to low maize yield under climatic changes. Its aggregation of effects cause photosynthesis, water relations, outgrowth, grain filling and suckling (Waqas et al., 2021). Also, extent of these yield losses amplified with the stress on socio-economic aspects call for a clear reversal- the use of genetic solutions and new genetic toolkits, modern day breeding approaches and operationalizing the streaming mechanism for the adoption of the climate smart agronomic practices (Biswal et al., 2022). Without more resilient adaptation, zones dependent on maize will experience increasingly unpredictable production fortunes, and food for people throughout the world could be imperiled. There may still be a way to avoid the consequences of joint stresses, with targeted research in selective breeding, and with the genetic raw material available to modify food systems at their base in the future, to make maize a sustainable food system to build upon (Ameen et al., 2023).

6 Physiological and Biochemical Underpinnings of Resilience

Maize tolerance to this abiotic stress (e.g., high temperature, drought S deficiency etc.) is complex interaction of diverse physiological characters and biochemical pathways participating in normal growth, reproduction, and maintenance of the yield stability in the stress environment (Peer et al., 2024). As an asexual crop that is slow or nearly impossible to propagate into new fruit bearing trees, this delicious perennial crop takes time, and inbreeding depression is hard to get rid of after the problem has rooted itself in the gene pool. The crops are in the range of tolerance physiology traits that includes water use efficiency, stay-green types, root system configuration, and the capacity to conduct photosynthesis under a variety of circumstances (Meena et al., 2025). Biochemically, resistance is accomplished by osmotic adjustment, synthesis of antioxidant defense and protective proteins that protect cellular integrity and function. Together, the two pathways represent the front line of maize in defense to environmental stress (Mishra et al., 2023). The stability of the water saving and photosynthetic carbon gain under stress are other import traits in the choice of drought tolerant maize genotypes. In plants that have not yet been stunted for growth, results of physiological modifications to the leave water state (reduced stomatal conductance, deeper rooting plants, salved transpiration) have been revealed as allowing plants to achieve the leave water state needed (Peer et al., 2024). Meanwhile, the traits of stay green types are anti-senescent and actually extend the photoperiod of a day's photosynthesis even while under stress. These characteristics are responsible for a constant assimilates supply to the sink of the leaves in order to enable kernel set under conditions pressure, including water stress and heat stress (Skowron et al., 2025).

Nevertheless, besides these physiological modifications, the maize plants also use bio-chemical mechanisms to alleviate the cellular damage induced by the stress. Drought and high temperature often cause an osmotic unbalance and oxidative stress that can be counteracted by the accumulation of compatible solutes (proline, glycine betaine, sugars) which protect proteins and the membrane (Tang et al., 2025). Conversely, reactive oxygen species (ROS) generated during stress are scavenged by an interplay of enzymatic antioxidants, such as superoxide dismutase, catalase, and peroxidases, and nonenzymic antioxidants, such as ascorbate and glutathione (Skowron et al., 2025). These biochemical-physiological mechanisms contribute to decrease of a cell injury by preservation of a photochemical apparatus and its operation in pathological conditions. Another key factor in biochemical tolerance is stress related protein (SPROT protein HSP and LEA protein) responses. Molecular chaperones maintain the stability and facilitate protein refolding under nonpermissive conditions and thereby protect them from aggregation (Lal et al., 2022). Similarly, hormone secondary messenger networks, like those modulated by abscisic acid (ABA), are central to control of stomatal closure, root growth and gene expression under stress. These physiological and biochemical alternations presented here collectively pave the way for the formation of a coordinated defense mechanism to help maize respond to stress and sustain productivity under stress (Singh & Roychoudhury, 2023).

7 Physiological Traits

Stay green is an important physiological mechanism that permits maize to retain the green leaf area function from flowering to grain filling period when exposed to stress conditions. Under both high temperature and water stress conditions, maize generally exhibits accelerated senescence after anthesis. This early leaf senescence leads to a decrease in the leaf area available for photosynthesis and, consequently, in the supply of assimilates to the growing kernels. Stay-greens genotypes are characterized by delaying senescence, maintaining chlorophyll contents and photosynthetic activities for longer periods which helps to increase the available carbohydrates for grain filling (Chibane et al., 2021; Du et al., 2022). This is one of the reasons of improved yield stability over wide agro-climatic conditions. On the mechanistic level, stay-green plants have a reduced degradation of photosynthetic proteins, including Rubisco and chlorophyll-binding proteins. Oxidative stress caused by drought or heat often results in the accelerated senescence but stay-green lines are equipped with more robust antioxidant defense systems, which contributes to the decrease in damage to chloroplasts and to delaying leaf death (Rahman & Ullah, 2023). Such maintained photosynthetic competency is very important under terminal drought stress conditions with kernel abortion being a key yield-limiting factor. Stay-green screens plants for kernel set and capacity of the source to fill kernels. Hormonal control may also be an important factor for stay green. Senescence is induced by ethylene and abscisic acid and delayed by cytokinin (Guo et al., 2021; Sun et al., 2025). Stay-green maize genotypes have been found to be less sensitive to ethylene and to have more cytokinin activity for increased leaf longevity during stress. This hormonal balance might be advantageous with respect to the resistance as reproductive and grain-filling stages are provided with assimilates when they are most needed (Bhattacharya, 2022).

Another physiological feature that significantly contributes to presence is the deep root system. Root system architecture (RSA) is exploited by maize (Zea mays L.) to access water and nutrients in soil profiles, particularly under water stress (Yadesa & Diro, 2023). Genotypes with deeper roots with deeper root systems (i.e. greater vertical depth) may be able to access subsoil water that may still be extractable during topsoil drying. This characteristic is particularly important at flowering because this is when a crop is running on its highest water levels, it's when it really cannot afford not to reproduce successfully by silk and pollen not attaining turgor (Nakhforoosh et al., 2021). Thus, they are relatively spared from the higher magnitude of deficit response yields under prolonged drought stress. It is not only the depth of root traits that matters, but plasticity also counts. Drought tolerant genotypes can regulate root growth according to soil moisture status by a greater deep and or abundant roots in the moist layers and by a higher density of fine roots. This flexibility increases the efficiency of water foraging in the face of unpredictable rainfall (Tan et al., 2023). Deep rooting also facilitates nutrient uptake, particularly nitrogen and phosphorus in many cases beyond the original rooting zone. Roots therefore contribute to both hydrological and nutritional resilience (Tariq et al., 2024).

Transpiration efficiency (TE) is another base trait for the resilience in maize. Although maize is a C4 crop with relatively higher water use efficiency than C3 species, there is great genotypic variation in maize in WUE. Multifoliolate plants likely have an ideal genotype with a high level of stomatal regulation achieved to reduce water loss in the leaves, with little impact on CO_2 assimilation (Togawa-Urakoshi & Ueno, 2022). These traits include reduced stoma sizes, optimizing stoma densities, and leaf rolling that enable plants retained the cooling ability without water loss potential at high temperature environment. But too much conserving can also prove counterproductive in the heat. If stomata close tightly, evaporative cooling will decrease, causing canopy temperature to increase and photosynthesis and reproductive tissue to be compromised (Tian et al., 2024). The most drought tolerant maize genotypes consequently appear to compromise between water conservation under moderate water stress and continuing to transpire for cooling under high temperature (Tan et al., 2023). Through the use of stay-green, deep roots and optimized TE characteristics, a physiological portfolio is constructed that allows the plant to perform well across a broad range of stress environments.

8 Biochemical Mechanism

Maize suffers from osmotic imbalance and oxidative damage in response to stress, but accumulated osmolytes function as adaptive buffer (Hossain et al., 2021). Osmolytes like proline, glycine betaine, trehalose and soluble sugars are the compatible solutes, that is more diffusive and take part in stabilization process of protein, membrane and enzyme but do not involve in metabolic reaction (Afzal et al., 2021). Under water stress conditions osmolytes decrease osmotic potential of cells facilitating turgor maintenance under low water availability. Such osmotic adjustment is crucial for the maintenance of stomatal openness, leaf expansion and silk and thus for reproductive success under drought stress (Seleiman et al., 2021). Proline accumulation is deemed to be more critical to corn under stressed conditions. In addition to osmotic adjustment, proline is a molecular chaperone, which stabilizes protein, membranes and scavenges ROS. GB can inhibit PSII photoinhibition under drought and high temperature, stabilize the electron transfer, and facilitate the normal development of photosynthetic course activities (Wei et al., 2022). And these osmolytes are more than just stress-soakers. They are biological GINSU knives, cutting cellular damage down to size. An additional stress-related adaptation is detoxification of reactive oxygen species. Not only heat, but even drought stress can induce the production of ROS further in chloroplasts, mitochondria, and peroxisomes (Zhao et al., 2023).

And excessive ROS might provoke lipid, protein, and nucleic acid damage in other oxidative stress. Deterioration test against abiotic degradation is responded by maize with enzymatic detoxifying systems such as detoxifying, scavenging, dismutation and neutralizing the reactive species (Raza et al., 2021). Superoxide dismutase dismutase superoxide radicals into hydrogen peroxide, which is further disarmed by catalase and ascorbate peroxidase. These enzymes together constitute the initial level of ROS defense, sustained ROS homeostasis under stress. In addition to this enzymatic protection, there is support from non-enzymatic antioxidants (Liu et al., 2022). Compounds including ascorbate, glutathione, carotenoids, and flavonoids directly scavenge radicals and reactivate oxidized enzymes. This would essentially act like a redox tone maintaining sleeping metabolism under chronic stress (Tumilaar et al., 2024). The equilibrium between the generation of ROS and the action of the antioxidant system mainly determines the level of injury to the cells of maize during climate extremes.

9 Heat Shock Proteins and Membrane Stability

Molecular chaperones like HSP (heat shock proteins) are known to play a role in maintaining, refolding denatured proteins under stressed conditions. There is a disrupted protein folding identity under the conditions of maize leaves to heat or drought stress and there probably is a protein aggregation status in cells and disrupted normal function at the cellular level (Jeyachandran et al., 2023). HSPs monitor this by surrounding unfolded proteins so that they do not clump together, and allow us to monitor this unfolding, when the calms down. They act like molecular band-aids, stabilizing and keeping proteins working when they come into life’s vicissitudes. HSP can be classified into different families such as HSP70, HSP90, small HSPs etc and they function in diversified manner in response to stress. For example, sHSPs protect against heat-induced damage of photosystem II past the anuridersibly-electron transport chain. HSP70 participates in protein renaturation and HSP90 in stress signaling (Khan et al., 2021). In this way, both responses are also maintaining the ability of maize cells to perform vital metabolic functions even in response to brief periods of high temperature.

Membrane stability is also a prominent resistance mechanism, in addition to protein stability. Membranes of cellular modified by temperature and drought, by the alteration of lipids composition and by the peroxidation rise (Rawat et al., 2021). Such analog metabolism-membrane systems should be able to produce regular ion gradients and may be used for enclosure and for inclusion of enzymes. These findings are consistent with the high proportion of SFA and MUFA present in membranes of less stress-sensitive maize genotypes, which contributes to their rigidity and help to avoid leakage of membrane compounds under stress. ROS control is also implicated in maintaining membrane stability (Carlson et al., 2024). Lipid peroxidation after oxidative stress causes membrane disruption, cell contents release and cell death. Together, they prevent such a damage by maintaining the proteins within the membrane-bound form and by scavenging ROS before they could act on the lipids. This crosstalk could govern cell architecture survival under stress (Xu et al., 2023).

Electrolyte leakage as a common methodology to estimate membrane stability in breeding. Decreased leakage of electrolyte under heat-stressed or drought condition shows positive correlation with resistance. This physiological trait has consistently been related with high yield stability and as such it becomes to be reaffirmed its practical value (Taratima et al., 2022). Finally, the induction of HSP is related to membrane stabilization. The stability of the membrane is supported to a great extent by the HSPs that help the protein function and maintain its structure. Together, they play cellular protective role in maize to withstand heat and drought (Csoboz et al., 2022).

10 Integration of novel techniques in Breeding Strategies

The physiological and biochemical characters listed above are the most effective when used in a combined package of resilience traits integrated into breeding program. No single character alone is able to confer complete protection against stress, but their combination adds to the overall plant performance in response to different, unpredictable environmental situations (Budhlakoti et al., 2022). Breeding programs are now aiming to identify QTLs for these resilience traits. For example, in maize, QTLs associated with stay-green, root architecture, and antioxidant enzyme activity are mapped. Such genetic landmarks provide more efficient discrimination of genotypes for which the stress related characteristic are targeted in the course of a MAS selection (Cooper & Messina, 2023). The identification of beneficial alleles is dramatically accelerated by the use of modern tools such as genomic selection and genome-wide association studies. Through genome-wide markers breeders can predict how hybrids will perform under stress and then in the early selection stage they can select stress resilient lines before the more expensive field trials are made (Uffelmann et al., 2021). Incorporating physiological and biochemical traits into genomic prediction models increases accuracy of ownership selection and accelerates breeding of climate resilient maize (Amin et al., 2025).

Innovative use of biotechnologies is also central. The over-expression of the stress-related genes (e.g., HSPs, antioxidant enzymes, and osmolyte biosynthetic pathways) has been found to be a potential strategy to increase the tolerance. With the availability of CRISPR/Cas9-mediated genome editing, stress regulators can now be modified more finely, for example components of ABA signaling, ROS detoxification, etc., with possibility of optimizing the stress responses without compromise (Csoboz et al., 2022; Kumar et al., 2023). Apart from genetic novelty, trait integration of resistance to multiple stresses should be evaluated in multi-environment trails under real stress combinations. Field phenotyping platforms measuring canopy temperature, chlorophyll, root depth and antioxidant activity were employed to test trait performance under field conditions to validate performance (Pozzi et al., 2025). Finally, insertion of some of these (physiological and/or biochemical) traits into the pipeline of current breeding lines would lead to hybrids resistant to multiple stresses. Such drought and heat stress tolerant hybrids also must be able to convey a crop under stress of total stress but also produce and maintain grain quality (Roychowdhury et al., 2023). The spirit of synergy and participation that embodies this integrated approach is fundamental to climate-smart maize breeding, as well as to the future of maize as a major global food crop.

11 Genomics and Genetics Implications of Genomics on Stress Tolerance

Integrating genetics and physiology to improve stress tolerance combine good genetics and physiology of maize to develop genotypes that can perform under these challenges. Both are parents of the stress-responsive genes of the transgenes or their proteins which set vertices of a graph on a body from which you can see an all-shrug plant, but which lead all the way, down to the finest register switches, ingredient by ingredient, to the large-brushed sweep of choreographing gene circuit families, scatterings of transcription factors, signaling and molecular effectors, metabolic pathways, and so on that are responsible for the dance a plant dances in being the stress it is (Malenica et al., 2021; Peer et al., 2024). Recent developments in genomics, transcriptomics, proteomics, and metabolomics have already shown that the classical drought and heat tolerance are polygenic and a quantitate trait as well as a complex adaptive trait that is governed by numerous small-effect loci (Yeaman, 2022). Central regulators, such as heat shock factors, DREB (dehydration-responsive element binding) TFs and ABA(-dependent) cell signaling cascades control them, regulating both, the expression of stress-responsive genes and metabolic reprogramming (Hussain et al., 2021). Concomitantly, epigenetic modification and non-coding RNAs also contribute to the complexity in the responses of plant terms toward repeated or combined stresses. Both genetic and molecular information likewise contribute not only to our understanding of maize adaptability, but they are also excellent genetic entry points for precision breeding, marker-assisted selection, and genome editing to aid in the further development of climate-resilient maize cultivars (Akhter et al., 2021).

Quantitative trait loci (QTLs) are segments of the genome associated with the variation of complex traits, e.g., response to abiotic stresses drought and heat tolerance in maize. These attributes are genetically controlled in a polygenic manner, so that several genes with minor or moderate effects are responsible for them and the QTL mapping is suitable for dissecting their genetic architecture (Raj & Nadarajah, 2022). For instance, the QTLs of ASI (anthesis -silking interval), which is a major trait at reproductive phase, has been identified in many chromosomes. Low ASI is strongly associated with good drought tolerance, because it increases the chance of not suffering from bad pollination and grain abortion during water stress. Solitary and root-related QTLs have been extensively studied as the architecture of the root system has a vital function for both water and nutrient uptake (Wen et al., 2024). Chromosomal loci controlling root depth, root density at lowest soil layer, and root-to-shoot ratio have been detected and validated in various maize populations. These QTLs are potential loci to be introgressed in breeding programmes designed to increase water-uptake efficiency under TDP (Siddiqui et al., 2021). Similarly stay-green, leaf rolling and transpiration efficiency-associated QTL highlight the polygenic inheritance of stress adaptation. Similarly, QTLs for pollen viability, duration of grain filling and regulation of canopy temperature were also found under heat stress (Lohani et al., 2025). Pollen sterility occurs under heat stress, but some QTLs contribute to pollen fertility and silk receptivity under high temperature. By stacking such QTL types along with those associated with drought, breeders can develop hybrids with a common tolerance to both stresses (Raj & Nadarajah, 2022).

Transcription factors (TFs) are key regulators of gene expression, many of those TF families have been reported to be related to drought and heat stress in maize. Heat shock proteins (HSPs) function as molecular chaperones to prevent the denaturation of cellular proteins, and their expression is regulated by heat shock transcription factors (HSFs) (Jeyachandran et al., 2023; Li & Howell, 2021). HSFs mediate a quick transcriptional response by binding to heat shock elements (HSEs) in promoter region so that cellular homeostasis is maintained in response to high temperature. Another main group is the DREB (dehydration-responsive element binding) family which is closely related to drought tolerance (Mushtaq et al., 2021). DREB TFs-Regulated Genes for Osmolyte Biosynthesis, Antioxidative Defense and Stomatal Movement Can Maintain Water in Plants but Prevent them from Closing Photosynthesis (Haider et al., 2022). The overexpression of the DREB genes in maize and related cereals has been proven to result in improved drought tolerance without causing severe yield penalty under the well-watered conditions (Mei et al., 2022).

Additionally, NAC transcription factors are associated with the stress response. They control senescence, cell-wall modification and root development, all important processes during long periods of drought. NACs reprogram stress responsive signaling networks to improve the growth capability of plants under nutrient stress (Jian et al., 2021). Similarly, WRKY TF genes are proved to be involved in crosstalk with the biotic and abiotic stress, that is, the ROS signaling pathway, the hormone pathway, and the secondary metabolism. MYB and TFs are involved in flavonoid biosynthesis, stomatal aperture, stress-induced metabolic reprogramming. They temper how the body responds, particularly under conditions of multiple types of stress (Wani et al., 2021). Together, these TF families generate redundant regulatory loops that provide robustness as well as evolvability to the stress response system. To reveal that stress tolerance is seldom controlled by a unique TF in maize but is determined predominantly by complex interactions among HSF, DREB, NAC, WRKY or MYB proteins (Manna et al., 2021). An understanding of this contribution would lead to interesting dreams of transgenic or without direct targets that indefinitely reprogram the stress responses in a qualitatively and quantitatively more general way.

Hormones are the chemicals that tell a plant how to respond to stress. One of them, abscisic acid (ABA) is an important regulator of drought and high-temperature tolerance in maize. Exposure to stress increases ABA levels that quickly induces stomatal closing to minimize water loss and the expression of stress-associated genes (Hussain et al., 2021). This ABA-dependent pathway depends on a variety of TFs, such as AREB/ABF factors, which are involved in the regulation of protecting proteins and osmolytes. A comparable significance of the ABA-independent path was found also (Hussain et al., 2021). In this latter case, DREBs control the expression of stress genes apart from ABA. This binary system allows them to possess a fluidity that can be applied to various levels and duration of stress (Y. Wu et al., 2022). It was also evident that ABA signaling crosstalks with ethylene, JA, SA and cytokinin extensively construct an extremely complex network of the signaling pathway.

In addition, ethylene signaling can also enhance, under some conditions, root growth and hence increase WUE may downregulate senescence under desiccating stress as well. Stay-green and more leaf elongation rich in developing and suppress untimely elongation which in many cases repression on gibberellins is useful to control over-growth as under stress (Nazir et al., 2024). This reequilibration of hormones permits maize to balance its fitness between survival and reproduction. Cross communication between hormone systems is also widespread to refine responses. For example, ABA and JA commonly crosstalk during the induction of defense genes for pathogen resistance, while ABA also antagonizes CK during senescence. Such crosstalk regulate the trade-off between growth and stress adaptation (Nawaz et al., 2023). It is difficult to accept that breeding traits, or at least hormones that regulate their action, may be subjected to manipulation, due to pleiotropic regulation, however, the identification of master regulators and/or signaling nodes opens the space for targeted intervention (Neres & Wright, 2024). Genetic manipulation strategies, e.g., in ABA biosynthesis or cytokinin stability, have indicated potential in generating stress-tolerant maize.

The genetic bases for drought and heat tolerance are complex and require systems-level approaches, and omics technologies have revolutionized our ability to examine stress responses in maize (Saleem et al., 2025). Next generation sequencing technology has facilitated the genomics study and unveiled the extraordinary level of diversity in the maize genome, and featured candidate genes for stress tolerance. Genome-wide association studies (GWAS) and genomic selection are being increasingly used to predict performance and accelerate breeding of stress-tolerant hybrids (Li et al., 2025). Dynamic view of genes that cause stress is provided by transcriptomics. Thousands of droughts and heat responsive genes have been identified for maize by RNA sequencing studies, and osmotic adjustment, ROS detoxification, and protein protection are indicated to be the pathways (Medina et al., 2021). These datasets enable the identification of new transcription and signaling factors involved in resilience. The levels of proteins are mainly regulated by PTMs, which change the stability, and/or activity of the protein. Stress is known to affect chaperone conformation, chaperone phosphorylation and chaperone expression. Through proteomics studies in heat-treated maize, heat shock proteins and metabolic enzymes have been identified as the predominant proteins implicated in maintaining cell viability (Lee et al., 2023; Storey & Storey, 2023). Metabolomics extends these to profiles of small molecules, including sugars, amino acids and secondary metabolites that build up in response to stress. These substances may function as osmoprotectants, antioxidants, or signaling molecules. Metabolomic signatures can serve as biochemical indicators of genetic diversity in the accumulation of metabolites as well as the stress tolerance (Salam et al., 2023).

Non-coding RNAs, such as miRNAs and endogenous siRNAs, represent an extra layer of control. They can silence gene expression through degradation of mRNAs or inhibition of translation on target mRNAs. Maize miRNAs may target stress responsive genes including the root growth, osmolytes accumulation and antioxidant defense related genes. Interactions of epigenetics and small RNAs contribute to flexibility (Naeli et al., 2023). For example, stress responsive small RNAs might instruct DNA methylation to generate stable but reversible modifications of gene expression. It’s not preinstalled with the stress response genes, instead, plants put it in the genome in case stress comes (Cai et al., 2025). This is the tool box by which maize responds immediately to the environment. There is some evidence that epigenetic diversity is transmissible and therefore a potential target in breeding. In an additional strategy, epigenetic marks combined with genomic approaches may help in recognizing the stress-resilient genotypes (Vogt, 2021). Further, epigenome editing approaches are pioneering technology in constructing stress memory and resilience. Hence, epigenetics and small RNAs are considered as new molecular mechanisms contributing to the phenotypic variation of maize, supplementing the existing genetic variation framework of maize and opening up new avenues for improvement of maize cultivars adapted to the challenges from our erratic climate patterns (Sun et al., 2021).

12 Breeding Innovations for Climate Resilient Maize

Most current campaigns targeted towards climate-resilient maize breeding are promoting innovations in breeding, with the premise that this will deliver longer-term responsive plant improvements under elevated levels of drought, heat wave and frequent rainfall variability. Classical breeding has come a long way in yield over the century, but it’s not fast enough, or yielding enough, or yielding in the right direction to keep up with environmental change (Raina et al., 2023). To overcome the drought stress, Physiological and the biochemical features of well-hydrated and drying (leaf) tissue of maize varieties under drought and to breed drought tolerant maize varieties the following knowledge should not only be known but also advanced molecular and cellular techniques should be implemented on creative breeding strategies (Skowron et al., 2025). By integrating trait-related selection, and molecular breeding, genomics and biotechnology, a tolerant hybrid can be produced that is productive, stable under climate extremes and cater to the requirement of global food security (Singh et al., 2025). The studies of maize stress tolerance are complicated by the fact that many genes and their interactions with the surroundings contribute to their derived phenotype.

Traditional breeding strategies including trait-based selection and hybridization under managed stress conditions have formed the basis of tolerance variety. The limitations of these techniques are that it’s time-consuming to develop a new cultivar, typically requiring 8 -10 years (Varshney et al., 2021). In order to speed up the genetic progress made in breeding, recent genomic technologies including marker-assisted selection (MAS) and genomic selection (GS), have been adopted to allow breeders to use genetic variation more efficiently. These tools minimize the reliance on phenotypic screen and enable stress resilience to be connected to DNA-based predictors and predictive models (Kumar et al., 2024). Apart from molecular breeding, biotechnology and genome editing are promising breakthrough technologies for climate-resilient maize. Transgenic technologies enable the direct transfer of stress-responsive genes, e.g., heat shock proteins, antioxidant enzymes, or osmoprotectants to improve the tolerance. More recently, CRISPR/Cas9-mediated genome editing has transformed plant breeding by editing native maize genes implicated in stress signaling, hormones and ROS detoxification (Mohapatra et al., 2024). Case studies for the biotech maize demonstrated that integration of GM added to hybridization and molecular breeding pathways resulted in hybrids tolerant to concurrent heat and water stress. Cumulatively, these breeding successes offer a multi-faceted strategy to secure maize productivity in an era of climatic uncertainty (Malenica et al., 2021).

13 Conventional Breeding Approaches

Traditional breeding has been the foundation of improvement in corn for many years through phenotypic selection and hybridization breeding programs. Properties such as stay-green, early flowering, strong root system and similar other traits have historically been sacrificed in the context of breeding for resilience (He et al., 2024). Stay-green genotypes can delay leaf senescence and maintenance of green leaves and photosynthetic activity under stress, while early flowering genotypes can escape from the terminal drought and heat at the end of crop cycle and finish the reproductive phase before the stress strengthens (Antonietta et al., 2024). Similar to drought yield effects, enhanced deep root systems and root plasticity enhance water use efficiency and therefore should be target traits for selection in water-limited environments (Kou et al., 2022).

The resilient capacity of maize is even more enhanced by the hybrid breeding under managed stress conditions. Through the controlled application of drought and heat stress to populations during reproductive development, breeders can select lines with enhanced tolerance mechanisms. This method also effectively mimics field stress resistance and assures that the chosen hybrids perform well under various stress prone conditions (Langridge & Reynolds, 2021). Managed stress trials have been key in the testing response of genotypes in breeding stations in Africa, Asia and Latin America, where climate risk is the most severe. However, traditional breeding has limitations even though it has been successful (Boddupalli M Prasanna et al., 2021). Given the polygenic nature of drought and heat tolerance, response to selection alone is limited to achieving stable improvement because of the necessity to accumulate many small-effect genes. Further, the traditional methods are tediously slow, often taking 8 to 10 years to develop and introduce new variety into the marketplace (Ma & Li, 2024). The expenses involved in carrying out multi-location trials and variations in the intensity of stress from location to location make the selection reasonably difficult.

In order to circumvent this draw back, breeders are utilizing recurrent selection programs in which desirable alleles are added into the program over the cycles of selection. This approach has been most successful for enhancing stress tolerance in open-pollinated varieties, which continue to be significant in resource-poor farming systems (Rutkoski et al., 2022). Heterosis is also valuable tool where productivity of hybrids is increased as compared to their inbred counterparts, which results from the act of combining different alleles or gene systems inherited from two parents. In classical breeding, the contribution of landraces and exotic germplasms to the breeding population is as important (Begna, 2021). Landraces of indigenous origin may have been adapted to cope with some co-adapted characteristics such as drought escape or high root production on a stress background. These traits can be introgressed into high yielding germplasm to broaden the genetic base and will not limit the breeding programme to only few progenies. Overall, conventional breeding cannot face the urgency of these challenges due to climate change, and yet these are the fundamental breeding ground. It has been fused with molecular and genomic technologies, so much that the old theories of selection now inform modern successes in breeding climate-resilient maize (Razzaq et al., 2021).

14 Marker-Assisted Selection (MAS)

MAS revolutionized the breeding value of maize by linking phenotypic traits with molecular markers with indirect selection for stress tolerance. MAS allows breeders to not rely on phenotypic traits that are often inconsistent due to changing environmental factors (Shafiq et al., 2025). Instead of these arbitrary markers, DNA markers, including SSRs and SNPs, would be valuable to facilitate the tagging of targets linked in repulsion phase with beneficial drought or heat tolerant alleles. One of the applications in maize where MAS has had the greatest impact is in introgression of QTLs associated with traits conferring stress adaptation (Kumar et al., 2024). For instance, QTLs associated with early anthesis-silking interval, deep roots, or stay-green have been genetically mapped and tagged with markers. These markers enable breeders to follow and introgress positive alleles into elite germplasm more accurately. Therefore, MAS represents a reduction in the number of numbers of breeding cycles that need to be completed in order to combine more than one tolerance trait. MAS is especially important for traits of low heritability or that are hard to measure directly (Gökçe et al., 2021). Root traits, for example, are critical in water uptake but difficult to phenotype with precision in the field. Since these markers are associated with desired root architectures, breeders can identify well performing genotypes without the need for tedious and expensive field screening. Similarly, traits associated with pollen fertility under heat stress are important for breeders to preserve reproductive ability in critical periods of growth (Maqbool et al., 2022). Secondly MAS can used to pyramid several QTL in the same variety. MAS expedites the breeding progress of multistress tolerant hybrids by pyramiding the beneficial alleles for multiple stress-related traits. This DAP for the CC is aimed at pyramiding resilience for multiple environment type where maize commonly suffers from overlapping drought and heat stress (Jha[1] et al., 2023).

15 Genomic Selection

The new approach, GS, for enhancing maize breeding programs to alleviate the limits of MAS is a revolution in the field but vectors need to be developed to deliver promising genes more efficiently. In contrast to the approach with MAS which uses markers aligned with major QTL, GS uses marker information for the entire derived genome in order to select directly for the individual breeding values (Kumar et al., 2024). It takes jointly into account the effects of thousands of loci along the entire genome and is particularly relevant in polygenic traits such as the ones conditioning drought and heat adaptations(Lovell et al., 2021). Prediction models based on a reference population of individuals with genotypic and phenotypic information form the core of GS. When trained, these models can forecast the performance of novel genotypes when given only their DNA profiles. This allows for reduced phenotyping in early generations and thus provides a much faster breeding cycle (Dekkers et al., 2021). For maize, genomic selection shortens the duration of the release of new hybrids from around nine years to a few years only. High throughput genotyping technologies, mostly snps assayed by microarray and next generation sequencing, are responsible for the increased production of data required by genomic selection (Li et al., 2022). In combination with statistical modeling and machine learning, genomic selection is being able to reliably predict stress tolerances. For example, genomic selection models have accurately estimated anthesis -silking interval, stay-green, root depth and grain yield under drought stress in multiple environments. Another advantage of genomic selection is that it can control for genotype × environment interactions (Malakondaiah et al., 2025). When multi environment trials data is included, genomic selection models with the potential for selecting genotypes which are able to perform under general stress conditions can be obtained. The above information is particularly valuable in the breeding of hybrids suitable for growing receive areas of unreliable rainfall and frequent heat waves (Resende et al., 2021).

GS also enables breeders to pre-select genotypes for breeding material, eliminating less promising lines before costly and long-duration field phenotyping. These efficiencies are resource conserving, will allow us to test larger breeding populations and increase the chance of the discovery of high yielding hybrids under stress (Civan et al., 2021). Genomic selection is very promising, but comes at a high cost of infrastructure, data storage and computing. Smaller breeding programs may face a challenge to fully utilize it. However, advances in public-private partnerships and open-access genomic databases such as Giga Science are democratizing access to genomic selection (Sinha et al., 2023). In conclusion, genomic selection is a new era of facilitating breeding towards products in a data-driven way that is scalable and ready to adapt new challenges of the climate in maize production.

17 Future Perspective

The potential for breeding for climate-resilient maize is to use the immense genetic diversity in germplasm worldwide. Wild relatives and traditional landraces of maize contain alleles for stress tolerance, commonly lost during domestication and subsequent intensive breeding for yield in modern hybrids. The genetic the above-ground organs also factor resistance is a perfect target to select for, for improving host for QTL mapping as the roots, stems and new breeding lines leaves do not affect all have shown such higher yield due to high low heritability relative levels of resistance. Breeding programs are becoming more aware of the value of pre-breeding activities for transferring such positive alleles from unadopted germplasm into high yielding varieties that should not lose any of its productivity.

Wild relatives, such as Zea diploperennis and Zea perennis, present unique sources of genetic diversity for traits such as perennially, pest resistance and abiotic stress tolerance. Concomitantly, landraces that small-holder farmers are cultivating in drought/heat and nutrient stress environments in Africa and Latin America are naturally tolerant to drought, heat and nutrient starvation. Advanced breeding programs with genomic-assisted introgression from these landraces can significantly expand the ‘resilience portfolio’ of maize germplasm. And this process also brings with it the ancillary benefits of conserving biodiversity and recycling it into a potential contributor to global food security. The advent of pan-genomic era has changed the view of the genetic architecture of maize. As opposed to single reference genomes, the pan-genomes included all the core and variable gene abundance across different maize lines. This makes it possible for breeders to recognize presence/absence variations, structural variations and new alleles associated with climate resilience that would otherwise go unnoticed. Recently, pan-genomic data have identified stress-related genes not existing in elite breeding materials, but present in landraces and thus new avenues for enhancing resilience. Recent genome editing tools such as CRISPR/Cas systems provide maize researchers and breeders with tools of never-before-seen precision to engineer maize to tolerate climate change. Rather than passively using naturally variable genes, breeders can manipulate stress-related genes either by fine-tuning their expression or simply modifying their functional properties. For example, modifying genes involved in stomatal closure and ABA signaling can improve tolerance to combined drought and heat stress, while also maintaining yield. Unlike transgenic methods, however, technological edits mimicking these natural mutations can in principle be done with CRISPR, potentially resulting in more easily approved changes that farmers might also be less reluctant to adopt.

The new era of maize breeding would further direct multi-stress resistance, due to the fact that field stress conditions are seldom observed alone. Heat × drought × nutrient stress combinations are especially prevalent in rainfed smallholder systems. Selection for single-stress tolerance is often successful in such environments, but the mechanism of tolerance to one stress may lead to susceptibility to another. For instance, too much stomatal closure is water-conservative under drought, but it increases leaf temperature and exacerbates heat stress. Breeding crops for tolerance to multi-stress situations involves the integration of physiological, biochemical and molecular knowledge to enable the design of genotypes with a good balance among trade-offs and consistent behavior under complex stress matrices. Multi-stress breeding will be primarily driven by high-throughput phenotyping platforms. Drone multi-spectral imaging, root phenotyping and climatic chambers are allowing for high throughput and accurate phenotyping of thousands of genotypes under combined stress conditions. The application of such sort of applications in combination with genomic prediction models will enable breeders to speed up the production of hybrids tolerating multiple stresses and simultaneously more stable to climate fluctuation.

The policies and the seed systems that contribute to their success will be equally important. Surely, hybrid seeds can bring resilience, but that is not that if there is no access, affordability and farmer confidence. The hump to scale up the production and dissemination of CSA practices more widely will be the seed delivery system, quality control and support to the small seed companies. Public and private partnerships could help fill gaps between knowledge and adoption and TI, particularly in highly fragmented seed systems. Climate resilient maize will also be developed through international cooperation. Climate change is not something that’s won or lost like a ballgame: It’s a global threat, and we know already (from early successes of cooperative institutions like CIMMYT) that germplasm, tools and ideas can be passed among countries. In some or other form the DIRTS that are developed by the farmers should be tested by other farmers in the project in socially comparable conditions in countries from which we know that they are (nearly) representative for other similar regions in the country A common source of funding will make the innovations for farmers and women to be used on a regional level in the world.

A few are aiming to create incentives for investing in breeding and/or adoption for climate resilience in policy environments. Policymakers can also help promote innovation by funding research, streamlining biosafety for gene-edited crops and subsidizing the deployment of climate-smart seed. At the same, time climate insurance schemes and input vouchers may promote new climate risks and technology adoption respectively and hence push towards the different climate risks and spread of resilient maize varieties. Another important issue is how the maize breeding can be included in sustainability programs. Such climate-resilient hybrids will not only need to tolerant abiotic stress situation like low rainfall and high-temperature stress, but should be ecofriendly input -savvy with regard to fertilizer saving and increases in nutrient-use efficiency, build up soil health also. Breeding for Resilience is not breeding for sustainability It's just like the future of the agrosystem of maize: the agrosystem of future maize will be part of the all to go for to achieve food security and ecologic stability.

Third, going forward we need to start looking at inclusivity as well. Many of these are smallholder farmers, women and other disadvantaged groups who are among the most climate-stressed but also collectively responsible for a large portion of the maize grown in the developing world. The bedrock for climate resilient maize to serve those who need it most and to become a reality of the poor is participatory breeding, smallholder seed systems and farmer innovation networks. Community Innovation is increasingly shown to be a generative journey. Finally, the future of climate resilient maize is inextricably linked with the capture of genetic diversity, deployment of cutting-edge molecular tools and the emphasis on multi-stress efficacy in order to ‘mainstream’ these gains through conducive policies, seed systems and partnerships. It asserts that there needs to be greater triangulation among science, technology, policy and farmer engagement such that a breeding maize can help to address the twin challenge of climate variability and food security in order to keep the crop as a global staple food for coming generations.

18 | Conclusion

While maize is the foundation of our world's food, feed, and industrial systems, maize production is threatened by environmental stresses associated with climate change. The challenge never minds the stark gender disparities; the girls are the wilted lotuses in a parched pond of a barren Indian arid land it would have been next to impossible not to get attracted. The susceptibility of maize, especially when susceptible at critical reproductive sites, raises the point that new strategies, not just for yield maximization, but for stability, robustness, and sustainability have become a pressing need. The issues raised in review indicate that pursuit of climate resilient maize cannot be one-dimensional but should graduate from genetic/narrow genetic and molecular, and agronomic and socio-economic strategies to climate-resilient maize as a single framework. The genomic revolution is behind this transformation. The stay-green, deep rooting and increased transpiration efficiency were the elementary physiological traits which were constitutively expressed for seed filling while, the basal osmolyte, ROS detoxification and antioxidant enzymatic defenses provide minimal resilience to the organization. Making use of the molecular tools and recent molecular studies at transcription factor level, hormonal cascades, QTL mapping, genes and stress responsive pathways has helped to understand better the mechanisms for tolerance and therefore design better strategies by breeders. Advancements in biotechnology, especially CRISPR/Cas9 gene editing and omics-guided discovery, allow for precision tooling to edit maize genomes for stress resilience at an even faster and more precise rate than ever before. Nevertheless, this science advancement needs to be successfully incorporated into breeding pipelines to transfer knowledge into outcomes.

From traditional trait-driven selection to so-called marker-assisted selection (MAS), genomic selection (GS) or even transgenic/genome-editing techniques, all these tools represent a continuity in form and aim to accelerate variety development. Classical methods are built upon for the identification and validation of resilience traits, MAS for targeted introgression, GS to improve accuracy for polygenic traits, and biotechnological methodologies for accuracy and efficiency. All of these developments can be combined to reduce the length of breeding cycles, enhance genetic diversity, and facilitate the development of hybrids adapted to multi-stress environments. But their success is largely dependent on aligning genetic gains with climate-smart agronomic management, comprising conservation agriculture, precision irrigation and nutrient smart management, by which the resilience traits are realized at farm level. Use of digital tools is another frontier in climate resilient maize. Airborne, robotics and field ground-based sensors, AI-based phenotyping and environmental forecasting provide in season, high resolution information on plant performance and environmental variability. Not only do such digital solutions bolster breeding pipelines by conducting high-throughput phenotyping and predictive modeling, but they also empower decision-making of farmers by minimizing risk and maximizing resource utilization. Similarly, farmer involvement in breeding programs and farmer led programmes, make scientific interventions nuanced in the basis of local particularities expressed on community preferences and cultural practices that also enhance the rate of adoption. This is because resilience is not just inherited but is an emergent property of those systems which are a combination of science, technology, and farmer’s knowledge.

In the future, the improvement of maize will necessarily be based more on the exploitation of germplasm diversity, pan-genome resources, and stress-resilient alleles derived from wild relatives and landraces. “Multistress” breeding, that combines heat and drought and nutrient stress, will be very important for developing hybrids that can fit into the complexity of real farming systems. Policies, good seed systems and international collaborations will be crucial, to guarantee equitable access to resilient material and to enable the sharing at world level of germplasm, data and innovations. Without such enabling system provisions even the most advanced scientific developments can become confined to the laboratory and not reach then livelihoods of those that need them most.

In sum, the pathway to climate-resilient maize is an interdisciplinary one that transcends the frontiers of conventional breeding. It calls for this is the alignment of genetic innovations with agronomy, their embedding in digital and participatory spaces, and shaping policy and institutional environments. In addition, such integration will not only ensure maize production against climate stress, but will also promote efficient use of resources, maintain biodiversity, and enhance the sustainability of food systems. And in the way it has played out, maize is no longer just a crop but an exemplar of resilience, demonstrating how science-based, farmer-friendly and globally coordinated solutions can help to drive climate change and food security synergistically forward. In conclusion, the time to use genetic innovation for climate-resilient maize is not some distant dream but an urgent need. And this, combined with the bringing together of physiological, molecular, agronomic and policy dimensions in a coherent set of values, will ensure the global community continues to have maize as a life source for billions and will keep farming systems resilient enough to succeed despite the uncertainties of climate. The outcome of those efforts is likely to not only dictate the future of maize but the security of the global food supply in the 21st century.

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