Building Climate-Resilient Crops: Genetic, Environmental, and Technological Strategies for Heat and Drought Stress Tolerance

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Highlight

The primary objective of this review is to examine the environmental and genetic factors that contribute to heat and drought stress tolerance in crops. It also assesses the limitations of current breeding programs and models, and discusses emerging technologies and interdisciplinary approaches for developing climate-resilient crops. These innovations aim to sustain agricultural productivity amid increasing extreme weather conditions.

Abstract

Global crop production faces increasing threats from the rise in frequency, duration, and intensity of drought and heat stress events due to climate change. Most staple food crops, including wheat, rice, soybean, and corn that provide over half of the world's caloric intake, are not well-adapted to withstand heat or drought. Efforts to breed or engineer stress-tolerant crops have had limited success due to the complexity of tolerance mechanisms and the variability of agricultural environments. Effective solutions require a shift towards fundamental research that incorporates realistic agricultural settings and focuses on practical outcomes for farmers. This review explores the genetic and environmental factors affecting heat and drought tolerance in major crops, examines the physiological and molecular mechanisms underlying these stress responses, and evaluates the limitations of current breeding programs and models. It also discusses emerging technologies and approaches that could enhance crop resilience, such as synthetic biology, advanced breeding techniques, and high-throughput phenotyping. Finally, this review emphasizes the need for interdisciplinary research and collaboration with stakeholders to translate fundamental research into practical agricultural solutions.

Keywords
abiotic stress tolerance, agricultural productivity, climate change, climate-resilient crops, drought stress, field-to-lab-to-field, genetic engineering, heat stress, high-throughput phenotyping, plant breeding

Introduction

Global crop production is increasingly threatened by worsening drought and heat stress events (Lengnick, 2015). Since the 1960's, heat waves have dramatically increased in frequency, duration, and intensity in the US (United States Environmental protection Agency) (**Fig 1A**). Further, drought and heat waves often occur together and the combination of both is the third most costly event in the US out of 7 disaster types (Smith, 2020) (**Fig 1B**). The IPCC predicts that heat and drought waves will occur more frequently with increases in both duration and intensity this century ('IPCC WGI Interactive Atlas') (**Fig 1C**).

Billions of the world's population continue to experience hunger (Cooper *et al.*, 2021) and remain vulnerable to climate-related crop failures and decreasing food affordability (Caparas *et al.*, 2021). Most of our current food crops (Awika, 2011) are not adapted to heat (Zhao *et al.*, 2017) and drought (Santini *et al.*, 2022) (**Fig 1D**), which can be detrimental to sustaining agricultural yield with increasing extremes in weather. Most current crops are vulnerable to temperatures above 35 ºC (Hatfield *et al.*, 2011; Hatfield and Prueger, 2015), a temperature threshold expected to be crossed more frequently in the future ('IPCC WGI Interactive Atlas') (**Fig 1D**). Even sorghum, a crop originally domesticated in Africa and considered to be relatively heat tolerant, decreases its biomass and seed yield at temperatures beyond 40 ºC (Prasad *et al.*, 2006).

Efforts to breed or engineer stress-tolerant crops have had limited success in both commercial and research contexts. This is largely due to the complexity and diversity of tolerance mechanisms and variation in agricultural production systems. Genetically modified plants with improved resilience in lab settings often fall short when tested in multi-location field trials (Braun *et al.*, 2010). Further, field-based selection of advantageous genes or alleles do not always prove effective when moved from model to crop plants or from reference genotypes to elite germplasm. This discrepancy is thought to come from limitations of field approaches that cannot test all the possible combinations of growing conditions and varieties within a specific area (Anten and Vermeulen, 2016; Casadebaig *et al.*, 2016).

To increase robustness of agricultural productivity under drought and heat, it is crucial to understand how crops experience stress and incorporate realistic features of agricultural systems into plant research. This approach will necessitate a paradigm shift towards conducting fundamental research in field settings or having the results of applied research in the field drive directions of fundamental research in the lab. To be successful, this shift will require greater emphasis on projects with results that can be implemented by farmers.

In this review, we examine the complexity of molecular mechanisms in plants under heat and drought stress. We also cover limitations of current models and breeding programs in translating lab findings to field conditions. Finally, we discuss technologies and approaches that could help usher in a 'field to lab to field' research paradigm in studying plant resilience against adverse climate conditions.

How heat and drought stresses are experienced in today's agricultural systems

Heat and drought stress risk varies by geography ('IPCC WGI Interactive Atlas') and crop production system. Societies will adapt to the stresses imposed by climate change by shifting production to new locations and modifying their agricultural system practices. Widely-used crop production systems today include large-scale, high-input field-based farms (Glossary), high-input greenhouse systems (Glossary), vertical multi-layer farming systems (Glossary), and small-holder farming operations (Glossary) (Dimitri and Effland, 2020). Farmers operating in each of these systems face unique challenges with regards to managing heat and drought stress experienced by their crops (Cohn *et al.*, 2017; Elias *et al.*, 2019; Ghani *et al.*, 2019; Ghoulem *et al.*, 2019; Hein *et al.*, 2021; van Delden *et al.*, 2021) **(Fig 2)**.

In rain-fed (non-irrigated) systems, which are the dominant farm type globally, summer heat and mis-timed rainfall present a perennial challenge. The magnitude of crop stress experienced will be impacted by management decisions. Beyond a crop's genotype, soil texture, quality, and chemistry can affect rooting intensity (Nunes *et al.*, 2021). These soil features affect transpiration and evaporation rates, which alter crop temperature (Nagel *et al.*, 2009). Because soil features influence rooting depth and rooting intensity (Glossary), they affect access to soil water and the risk of drought stress. In moisture-limiting environments, improvements in various rooting-associated phenotypes are expected to provide the greatest benefit (Maqbool *et al.*, 2022). Various management choices, including planting date, planting depth, the type and amount of fertilizers applied, and the rate and chemistry of herbicides used, also will influence rooting depth, intensity, and initial shoot growth.

In irrigated systems, heat and drought stress can be partially mitigated by watering, but the quality, timing, placement, and rate of watering will determine the amount of heat and drought stress experienced and whether soil quality would be affected over time (e.g. through salinization) (Yang *et al.*, 2023). In contrast, controlled-environment agriculture, i.e. greenhouses and vertical farms, aims to mitigate stress through precise environmental control to reduce or eliminate the frequency and intensity of abiotic stress such as drought and heat. In an indoor production setting, plants are limited by their inherent temperature range rather than by their environment. Currently, vertical farm operators use crop cultivars bred for the field and greenhouse due to limited germplasms bred or engineered to be optimal for indoor production (SarathKumar et al., 2020). For example, crops with varying temperature requirements are grown in a fixed-temperature environment, leading to inefficient yield maximization. For water resources, breeding new cultivars with improved water and nutrient use efficiency without negative impact on yield is needed for both indoor and outdoor production. This may require specific traits such as improved root and shoot architecture, anatomy, metabolism, and physiology. These improvements could enhance the cost-effectiveness of crop production, as water and energy for irrigation are major expenses, particularly in indoor farming.

Complexity of physiological, cellular, and molecular responses to heat and drought stress

Few stress-tolerant crop varieties have been commercially developed due to the complex nature of heat and drought stress and the challenges of integrating effective resilience traits. Drought conditions reduce water availability, which leads to turgor loss, cellular dehydration and membrane destabilization (Yang *et al.*, 2021). Heat stress disrupts protein stability through denaturation (Jarzab *et al.*, 2020), which impairs enzyme function and subsequently leads to metabolic imbalances (Mittler *et al.*, 2012; Xu and Fu, 2022). Heat stress also affects membrane fluidity and permeability by altering lipid composition or the interactions between lipids and membrane proteins. (Niu and Xiang, 2018). Under both stresses, carbon fixation is impaired and elevated levels of reactive oxygen species (ROS) are produced (Sato *et al.*, 2024). Both stresses can also induce structural changes in chromatin and DNA methylation (Probst and Mittelsten Scheid, 2015) leading to transcriptional changes in stress-responsive genes (Kim *et al.*, 2015). Active histone marks are enriched on many drought-responsive genes (Kim *et al.*, 2015) and histone modification such as acetylation and sumoylation are involved in thermal stress response (Kim *et al.*, 2015). Modification in DNA methylation also plays an important role in the transcriptional regulation of drought and heat-responsive genes (Talarico *et al.*, 2024). Plants are particularly susceptible at the reproductive stage (Cohen *et al.*, 2021) where heat and drought stress irreversibly reduce flower number, increase ovule and seed abortion, disrupt pollen formation, and reduce grain filling (Giorno *et al.*, 2013; Sage *et al.*, 2015; Djanaguiraman *et al.*, 2018; Wang *et al.*, 2019; Lamin-Samu *et al.*, 2021; Santiago *et al.*, 2021; Sinha *et al.*, 2021).

Plants employ a suite of strategies at the tissue, cellular and molecular levels to mitigate negative impacts of heat or drought stress and repair damages caused by these stresses. A suite of signaling cascades initiate tolerance mechanisms, involving abscisic acid (ABA) (Kim, 2014), calcium (Shao *et al.*, 2008), reactive oxygen species (ROS) (Furlan *et al.*, 2016), Mitogen-Activated Protein Kinases (MAPKs) (Chen *et al.*, 2021), phospholipids (Liang *et al.*, 2023), the Unfolded Protein Response in the endoplasmic reticulum (Manghwar and Li, 2022), and epigenetic regulations (Chang *et al.*, 2020). A suite of hormones, including auxin, cytokinin, gibberellin, ethylene, salicylate, brassinosteroids, and jasmonate, also regulate and fine-tune plant responses to drought and heat stress (Burgess and Huang, 2016; Li *et al.*, 2021). Heat Shock Factors (HSFs) are a group of evolutionarily conserved proteins in all eukaryotes with complex regulatory networks and are central regulators of heat stress responses (Haider *et al.*, 2022). Heat Shock Factors increase the expression of Heat Shock Proteins (HSPs) and chaperones that protect other proteins against denaturation under high temperatures (Khan and Shahwar, 2020; Mondal *et al.*, 2023). Targeting HSFs and HSPs by genetic engineering improved thermotolerance in several plant species (Fragkostefanakis *et al.*, 2015).

Following the transduction of heat and drought stress signals, plants synthesize osmoprotectants (Zulfiqar *et al.*, 2020), specialized (secondary) metabolites (Akula and Ravishankar, 2011), and proteins such as Late Embryogenesis Abundant (LEA) proteins (Chen *et al.*, 2019) and Dehydrins (Tiwari and Chakrabarty, 2021; Smith and Graether, 2022). To limit oxidative damage, ROS-scavenging compounds are generated and antioxidant enzymes are activated (Chen *et al.*, 2017; Zhao *et al.*, 2018; Hasanuzzaman *et al.*, 2019). These mechanisms enable plants to recover faster and with less damage during the vegetative stage compared to the reproductive stage, particularly if the stress is moderate and short-lived (Mahalingam and Bregitzer, 2019; Ruehr *et al.*, 2019; Cohen *et al.*, 2021). Moreover, during vegetative growth, moderate stress followed by a recovery can prime the plants to promote subsequent tolerance to stress (Wang and Huang, 2004; Bruce *et al.*, 2007; Jacques *et al.*, 2021).

The combination of heat and drought stress is more damaging than either stress alone, yet the molecular responses to combined stresses and their effects on agronomic traits remain understudied (Lawas *et al.*, 2018; Cohen *et al.*, 2021; Sato *et al.*, 2024). Heat and drought frequently occur together, triggering overlapping and sometimes contradictory responses. For example, stomata close to conserve water during drought but open for evaporative cooling under heat stress. This contradiction highlights the challenges of developing enhanced tolerance to both heat and drought simultaneously (Zandalinas and Mittler, 2022).

How drought and heat stress responses are modeled

Models can serve as useful tools for predicting effects of climate change on crop productivity and identifying engineering and breeding strategies to improve growth. Crop models that simulate entire fields, such as Agricultural Production Systems sIMulator (APSIM) (Glossary) or Functional Structural Plant Models (FSPM) (Glossary), predict crop yield under heat and drought stress (Eyshi Rezaei *et al.*, 2015; Ndour *et al.*, 2017; Ababaei and Chenu, 2020; Braghiere *et al.*, 2020).

Crop models simulate heat and drought stress by adjusting the rates of processes like photosynthesis, biomass partitioning, grain filling, respiration, and senescence in response to temperature and water availability (Messina *et al.*, 2015; Feng *et al.*, 2019; De Swaef *et al.*, 2022). Stress response functions scale the rates of these processes based on optimal condition thresholds (Ewert *et al.*, 2015; Zhao *et al.*, 2019) (**Fig 3)**. For instance, cumulative mean daily temperature drives the rate of development and time to maturity in the CERES-WHEAT and SIMPLE crop models such that higher temperatures will accelerate development (Jones *et al.*, 1983; Zhao *et al.*, 2019). In the context of drought, the ARID index is used to calculate the level of drought stress using values for evapotranspiration, precipitation, soil surface runoff, and drainage (Woli *et al.*, 2012; Feng *et al.*, 2019; Zhao *et al.*, 2019). These stress response functions are derived from constant heat or drought stress experiments (Seidel *et al.*, 2018; Horie, 2019; Wallach *et al.*, 2021) and not across a range of stress durations or severities. Moreover, drought and heat stress sensitivity varies across developmental stages, necessitating stress response functions that can dynamically simulate erratic heat waves and droughts across a crop's entire lifespan. For example, modeling heat stress as a function of cumulative mean daily temperature can under-represent short term extreme heat stress in crop models (Sun *et al.*, 2021). A recent study compared the heat stress response functions used in 14 different rice crop models that differ in how heat affects grain filling and setting (Sun *et al.*, 2021). They found that current rice crop models underestimate the effect of short term heat stress after flowering at the early grain filling stage and proposed an updated heat stress response function which improved yield predictions. This study highlights the need for more comparative research to assess the effectiveness of stress response functions that account for dynamic stress events.

To improve stress response functions, Machine Learning (ML) algorithms and statistical models are being incorporated into crop models (Jin *et al.*, 2016) and are becoming increasingly popular for predicting crop yield under stress (Crane-Droesch, 2018; Cai *et al.*, 2019; Leng and Hall, 2020; Shahhosseini *et al.*, 2020; Lischeid *et al.*, 2022; Newman and Furbank, 2022). For instance, an ML algorithm (Droutsas *et al.*, 2022) was added into a crop model to predict variables such as radiation use efficiency and harvest index based on weather data, eliminating the need for stress functions described above. In addition, combining statistical models with crop models improved prediction accuracy by 20% (Everingham *et al.*, 2016; Pagani *et al.*, 2017; Shahhosseini *et al.*, 2021). Moreover, a study that combined a popular crop model, APSIM, with a random forest model (Glossary) improved accuracy by 33% in predicting wheat yield during extreme climate events in South Eastern Australia (Feng *et al.*, 2019). The authors predicted that crop models may be underestimating yield losses during extreme climate events by up to 10%, highlighting the need to improve stress response functions in crop models (Feng *et al.*, 2019). These studies exemplify how combining multiple models can further improve yield predictions under extreme stresses.

Current challenges and opportunities

Breeding new crop cultivars that are more resilient to heat and drought stress will be essential to meet our food, fiber, and energy needs. To rapidly meet the demand, plant research must effectively address the following challenges and capitalize on the opportunities that new technologies offer to expand our understanding and accelerate translation.

A gap between fundamental and translational research

Despite extensive fundamental research into the mechanisms of plant stress tolerance to heat and drought, developing commercial crops with superior traits remains challenging (Mittler and Blumwald, 2010; Van Montagu, 2011; Gilliham *et al.*, 2017; Purugganan and Jackson, 2021).

Synthetic biology, a bioengineering approach that designs, redesigns, and assembles biological elements to develop novel functions, offers new perspectives for large-scale protein engineering (Engqvist and Rabe, 2019) and crop improvement (Sargent *et al.*, 2022). For instance, CRISPR/Cas technology can be used for targeted genome modification to generate novel desirable variations (Scheben *et al.*, 2017). Directed protein evolution, which involves the generation of a large set of diverse protein sequences that are screened for desirable properties, is another promising and powerful approach for crop improvement (Engqvist and Rabe, 2019). Directed protein evolution

(Mueller-Cajar and Whitney, 2008; Carmo-Silva *et al.*, 2015), synthetic biology (Kubis and Bar-Even, 2019), and CRISPR-based genome editing (Sami *et al.*, 2021) were attempted to engineer plants with superior heat or drought resilience capabilities. In addition, strategies involving agronomic practices such as application of compatible solutes (Wang *et al.*, 2014), plant growth promoting rhizobacteria (Ahluwalia *et al.*, 2021), and mycorrhizal fungi (Wu and Zou, 2017) were also attempted. However, studies showing successes in engineering heat or drought resilient traits are scarce. Most efforts to commercialize transgenic lines with superior drought tolerance have focused mainly on maize, resulting in eighteen lines. Very few such lines exist for other crops. There are two lines in soybean, three in sugarcane, and one in wheat ('ISAAA's GM Approval Database'). To our knowledge, no heat-tolerant commercial lines are available.

This limited success in translating fundamental research to the field may be due to the differences between lab-controlled conditions and actual field environments. Fundamental research performed in growth chambers or greenhouses is often not tested subsequently under field conditions. Yet, real life scenarios involve crop exposure to variable environmental conditions (e.g. of light, temperature, moisture) throughout the day and the life cycle of the plant, and interactions with other organisms (Mittler and Blumwald, 2010; Poorter *et al.*, 2016; Langstroff *et al.*, 2022). A significant bias arises from the choice of soil and pots used in greenhouses, which differ significantly from most field environments (Heinze *et al.*, 2016; Forero *et al.*, 2019). Greenhouse soil mixes used in controlled environments may not accurately represent field soils. Additionally, growth chamber experiments conducted in pots can have different ventilation and water holding characteristics from field soils resulting in different root architecture. The size of the pots used in growth chamber or greenhouse experiments also have an effect on plant growth. Therefore, phenotypes observed in such contexts may not translate well to field conditions.

Another reason for the slow pace of progress may be the complexity of response mechanisms to drought and heat stress. Plants respond to stress differently based on their age, as well as the duration and severity of the stress. Responding to these stresses involves many genes, some of which may have antagonistic effects when stresses are combined, complicating the breeding selection process (Snowdon *et al.*, 2021). In addition, the polygenic nature of these traits makes it challenging to identify the causal genetic determinants. Furthermore, trade-offs between growth and stress tolerance (Zhang *et al.*, 2020), as well as between moderate and severe stresses (Kusmec *et al.*, 2023), can complicate the development and selection of ideal traits. Tolerance to abiotic stresses can be associated with reduced growth (Darychuk *et al.*, 2012) or a reduced resistance against biotic stresses (Silva *et al.*, 2019). Similarly, increased tolerance to moderate heat stress in maize hybrid lines was associated with reduced tolerance to severe heat stress (Kusmec *et al.*, 2023). Such trade-offs present significant challenges to breeding crops that can withstand variable climates.

Limitations in using genomic selection

Genomic Selection (GS) accelerates the breeding cycle by using predictive models, offering a faster and more cost-effective alternative to traditional breeding programs (Heffner *et al.*, 2010; Crossa *et al.*, 2017). Moreover, recent studies have demonstrated that GS can predict complex traits with a high degree of accuracy (Merrick and Carter, 2021). However, GS requires extensive genotypic and phenotypic data to feed into the training models to obtain a higher level of prediction of the estimated breeding value (Glossary). Additionally, GS's accuracy depends on the availability of molecular markers, statistical models, field management, breeding schemes, and size and quality of testing and training populations (Rabier *et al.*, 2016; Xu *et al.*, 2020). In breeding programs of field-grown crops, the availability of large data sets is still limited, resulting in only moderate prediction accuracy. Furthermore, GS for indoor production is currently not feasible due to the lack of data from indoor-grown populations. Ultimately, the quantity and quality of training and testing populations are critical for achieving higher GS prediction accuracy (Rabier *et al.*, 2016).

Limitations of models

The biggest limitation to modeling heat and drought stress in plants is the lack of availability of data for model input and validation. FSPMs can be used to aid researchers in identifying important phenotypic traits for resilience, which can be parameterized to a specific genotype (Hammer *et al.*, 2006; Yin and Struik, 2010; De Swaef *et al.*, 2022). However, their biggest challenge is finding the data required for parameterization, such as measurements of organ width, length, thickness, and angles (Wang *et al.*, 2020). Moreover, when the mechanisms responsible for a biological process are uncertain, modeling it becomes challenging. Uncertainties in parameters, as well as the timing and impact of stresses on growth and related processes, lead to the inclusion of assumptions in models. Parameter uncertainty is difficult to avoid due to the complex biological networks that underlie plant growth.

In addition, because crop models are highly parameterized, they are prone to overfitting and can be difficult to generalize. Translating predictions across different crop species and production regions is challenging due to variations in factors such as light, precipitation, altitude, soil quality, and microbiomes. Species and location specificity limit the ability to compare models, hindering efforts to improve prediction accuracy. Furthermore, crop models incorporate simplified equations to represent complex processes such as grain setting, soil water potential, biomass partitioning, and sensitivity to heat and drought stress (Feng *et al.*, 2019; Sun *et al.*, 2021). These simplifications may fail to capture short-term or extreme climate events accurately. Simulating a broader range of environmental perturbations is essential for testing the robustness and generalizability of the models.

Breeding limitations of cumulative and combined stresses

Conventional plant breeding is a widely used methodology where crops are selected over generations based on desired traits. Unfortunately, this approach can take years to achieve a stable climate-resilient variety. Modern technologies such as gene editing, genomic selection, marker assisted selection, and high-throughput phenotyping reduce the time required to release new varieties, but increase the cost (Lamichhane and Thapa, 2022). In addition, modern breeding approaches have not effectively addressed cumulative stress conditions that have notably increased in frequency and intensity (Choudhary *et al.*, 2022; Lamichhane and Thapa, 2022). Major limitations include the genetic erosion (loss of genetic diversity) that diminishes variation and ability to adapt to multiple stresses and the limited ability for breeders to monitor critical traits for tolerance to stress combinations in a short period (Hein *et al.*, 2021; Khoury *et al.*, 2022).

Breeding limitations for indoor farming

New developments in climate control, lighting, and automation enabled the growth of the Controlled Environment Agriculture (CEA) (Glossary) industry or indoor farming. However, crops well suited to greenhouse and vertical farms are limited. Field-bred cultivars are commonly used in indoor farming due to the limited availability or lack of cultivars specifically developed for indoor production (SharathKumar *et al.*, 2020). In a well-designed climate-controlled indoor farm, environmental fluctuations seen outdoors are almost non-existent. The climate stability of indoor farming opens up a new niche of plant breeding focusing on desirable traits for indoor production including small plant architecture and stature, rapid development, improved aroma, flavor and texture, and robust temperature range. Breeding programs for indoor farming should prioritize traits that align with the specific conditions and limitations of CEA infrastructure, while also enhancing crop quality. For example, robust temperature ranges of crops like basil and spinach, which require high and low temperatures respectively, would allow co-cultivation in a single growing area without compromising yield potential of each crop. For a thorough review of breeding new CEA cultivars for plant architecture and compounds, see (Folta, 2019).

Promising strategies to enhance heat and drought tolerance in crops

Developing heat and drought resilient plants poses numerous complex challenges, as outlined above. We propose strategies to address these challenges and accelerate finding solutions through innovations from fundamental research, emerging technologies, and societal paradigm shifts (**Fig 4**).

Improving crop tolerance through fundamental plant resilience research

Engineering and breeding programs have had limited success in creating heat and drought tolerant crops for field conditions (**Fig 5A**). Innovative strategies are needed to bridge the gap between lab results and field performance and to accelerate the translation of research into practical applications.

Understanding plant responses in the natural environments where they evolved may provide valuable insights. Wild relatives of domesticated crops (Tanksley and McCouch, 1997) and naturally resilient plant lineages such as extremophiles (Eshel *et al.*, 2021; Alwutayd *et al.*, 2023; Prado *et al.*, 2023) offer a rich reservoir of genetic resources and novel mechanisms for heat and drought tolerance. One approach of leveraging these genetic resources is to identify and transfer desirable traits and genes from wild relatives or extremophiles to non-adapted crops. This approach has been most commonly used to breed biotic stress tolerance into crops, though drought tolerance was introduced for barley and rice cultivars from their wild relatives (Hajjar and Hodgkin, 2007). Several crops, including tomato, alfalfa, cowpea, and groundnut, have close relatives that exhibit drought and heat tolerance (Kapazoglou *et al.*, 2023), making them promising targets for this approach. An alternative strategy is to re-domesticate heat and drought resilient wild relatives by introducing known domestication genes into the wild species (Lemmon *et al.*, 2018; Zsögön *et al.*, 2018; Gasparini *et al.*, 2021). These strategies highlight the potential of harnessing wild relatives and naturally resilient lineages to enhance crop adaptation to heat and drought stress, offering a sustainable path forward in addressing the challenges posed by climate change.

Another strategy to accelerate the development of drought- and heat-adapted plants is to identify traits associated with heat and drought tolerance from field observations. This strategy requires high-throughput, multi-modal measurements in the field but does not necessitate a complete understanding of the underlying molecular processes (Richards, 2006). For example, plant phenotyping under field conditions identified root and shoot traits that could be important to confer drought tolerance in soybean (Fenta *et al.*, 2014) and potato (Wishart *et al.*, 2014), as well as heat tolerance in cotton (Karademir *et al.*, 2012) and maize (Liu *et al.*, 2022). This approach allows for the rapid identification of critical traits that can be directly targeted for breeding. Since results from controlled conditions may not always apply to the field, more studies should include field evaluations to identify the most reliable traits for drought and heat tolerance. Chlorophyll fluorescence, membrane integrity, and enzyme activity may serve as reliable traits for heat tolerance in both controlled and field environments for cotton and tomato (Cottee *et al.*, 2010; Wu *et al.*, 2014; Poudyal *et al.*, 2018). Field trials across different locations and seasons with varying heat and drought stress events should be routinely incorporated into evaluations. This approach was applied to wheat, which showed that green leaf area retention after heat stress in a controlled environment may be a valuable predictor of heat tolerance in the field (Telfer *et al.*, 2018). Screening at the seed and seedling stages may also be a reliable strategy to predict drought tolerant rice lines in the field (Fatima *et al.*, 2024). Integrating controlled and field evaluations, alongside multi-stage screening, provides a comprehensive strategy for identifying reliable traits that can enhance the development of heat- and drought-tolerant crops.

A significant knowledge gap exists in understanding how gene functions drive phenotype and fitness under natural, fluctuating conditions (Purugganan and Jackson, 2021). There is still a lack of complete insight into how agronomically important traits develop at the molecular level (Bailey-Serres *et al.*, 2019; Purugganan and Jackson, 2021). As a result, genes or alleles identified as advantageous in model plants and reference genotypes do not always perform effectively in crops and elite germplasm under field conditions. To address these limitations, phenomics (Glossary) may serve as a key area of development (Chen *et al.*, 2014; Tardieu *et al.*, 2017). Dissecting gene function and its regulation of phenotypes in response to heat and drought stress will require understanding mechanisms across different organizational scales (plant, organ, cell levels) and developmental stages, as well as integrating the effects of environmental fluctuations inherent in a natural environment (Purugganan and Jackson, 2021). Fundamental plant resilience research has made significant progress in uncovering molecular and physiological mechanisms to support molecular breeding and genetic engineering strategies for improving heat and drought tolerance. However, these strategies risk reaching a plateau without parallel advances in technology.

Emerging technologies and combinatorial approaches

Technological advances have become essential to comprehensively assess the impact of heat and drought in the field and estimate genetic gain. Tools like remote sensing, machine learning, modeling, and large-scale semi-field facilities, as well as their combined application, hold great potential for accelerating progress in crop improvement.

High-throughput plant phenotyping technologies, along with sensor and imaging systems, have recently made significant strides for a wide range of traits at the whole plant level (Araus *et al.*, 2018; Chawade *et al.*, 2019; Hein *et al.*, 2021), as well as at the organ and cellular levels non-invasively (Cobb *et al.*, 2013; Tardieu *et al.*, 2017; Jain *et al.*, 2021; Tanaka *et al.*, 2021). Nanotechnology-based sensors that translate plant chemical signals into stress responses offer high spatial and temporal resolution (Giraldo *et al.*, 2019). Do-it-yourself methodologies using Raspberry Pi technologies offer flexible, robust, and low cost alternatives (Dobrescu *et al.*, 2017; Cho and Yang, 2023; Ginzburg *et al.*, 2024). High-throughput phenotyping facilities that integrate automation, robotics, high-speed computing, and imaging are available in greenhouses or growth chambers (Pratap *et al.*, 2015). A complementary approach to field phenotyping has been proposed (Langstroff *et al.*, 2022), with some systems already in place under semi-field conditions such as RadiMax for the study of root growth (Svane *et al.*, 2019).

The extensive data generated by high-throughput phenotyping and imaging present a significant bottleneck in data handling and processing, hindering the translation of this information into valuable knowledge (Tardieu *et al.*, 2017). Machine learning approaches can estimate phenotypic parameters from large datasets (e.g. real-time sensors, historical trends, and omics data) and can facilitate crop yield prediction, crop planning and management, genomic crop design, breeding, and crop modeling (Mishra *et al.*, 2016; Feng *et al.*, 2019; Abdollahi-Arpanahi *et al.*, 2020; van Dijk *et al.*, 2021; Droutsas *et al.*, 2022). Models can be used to test a variety of genotypes, environments, and management strategies (Chauhan *et al.*, 2021; Hein *et al.*, 2021). Integrating crop models with machine learning methods helps disentangle the underlying mechanisms of heat and drought stress. The multi-crop model ensemble approach, which combines multiple models to enhance predictive power, has been shown to improve yield predictions compared to using individual models (Martre *et al.*, 2015; Wallach *et al.*, 2018). There is a growing demand for modeling studies that assess various engineered plant traits to determine the minimum number of gene edits required to improve yield under drought or heat stress. To improve predictions, it is crucial to increase available data for parameterization and validation (Hartig *et al.*, 2011; Wang *et al.*, 2020). It is also important to ensure model predictions are robust across a range of environmental parameters to account for the variability encountered in field conditions.

Synthetic biology is viewed as highly promising to overcome limitations of conventional breeding (Sargent et al. 2022). Valuable synthetic biology tools include gene editing such as CRISPR-Cas9, gene assembly such as Golden Gate, gene silencing such as RNAi, homing gene drives that increase the inheritance of a gene of interest, gene synthesis, and engineered promoters (Sargent *et al.*, 2022). Current synthetic biology strategies to improve drought and heat tolerance involve: 1) engineering drought inducible CAM or C4 photosynthesis in C_3 plants (Kubis and Bar-Even 2019; Yang et al. 2020; Lohani et al. 2022), 2) improving CO2 fixation, light harvesting efficiency and photoprotection systems (Kubis and Bar-Even 2019; Lohani et al. 2022), 3) engineering metabolic pathways such as carbon metabolism, starch metabolism, phenylpropanoid biosynthesis, gamma-aminobutyric acid biosynthesis (GABA), and phytohormone biosynthesis and signaling (Liu *et al.*, 2023), or 4) engineering root systems and their associated microbiota (Ragland et al. 2024) (**Fig 5B**). Despite rapid DNA assembly throughput, transformation efficiency remains a huge bottleneck in plants (Lohani *et al.*, 2022). Novel transgenesis-free functional genomics tools are under development, which are based on synthetic biology with RNA viral vectors that enable rapid screening of candidate genes (Khakhar *et al.*, 2021).

Combining approaches such as genomic selection, speed breeding (Watson *et al.*, 2018), AI, ML, synthetic biology, and metabolic engineering have the potential to substantially accelerate breeding pipelines and identify traits that can confer drought and heat tolerance (Varshney *et al.*, 2021; Liu *et al.*, 2023). A new smart breeding strategy, coined integrated Genomic-Enviromic Prediction (iGEP), used multi-omics data and AI to integrate variation in genotype and phenotype with changes in the environment (Xu *et al.*, 2022). The BREEDIT pipeline is an approach that combines gene editing and conventional breeding (Lorenzo *et al.*, 2023). This pipeline uses CRISPR constructs targeting multiple genes in a network, along with crossing, to generate different combinations of multi-gene edits in plants, producing up to 12 gene edits simultaneously. BREEDIT can be used to identify a minimum set of genes needed to alter a phenotype and has the potential to accelerate gene-editing based breeding and evaluation of multi-gene edits in the field. The integration of these cutting-edge technologies and breeding strategies could offer more efficient and precise ways to enhance resilience to climate stressors such as drought and heat.

Adoption of systems-based experimental approaches

To improve agricultural productivity in the face of increasing heat and drought stress, we need to recognize why and how crops experience stress in specific agricultural systems under investigation. To maximize relevance and utility for crop producers, it is crucial to use protocols that include key features of the chosen agricultural system (see Box 1). In addition, all factors influencing plant growth and development, which contribute to heat- and drought-related losses, should be considered within the context of the specific agricultural system. For instance, native and inoculated soil microbes, especially mycorrhizae, can contribute to drought tolerance in plants (Bahadur *et al.*, 2019). Furthermore, some inputs classified as microbial inoculants or biostimulant products may influence how plants sense and respond to abiotic stresses (Baltazar *et al.*, 2021; Martínez-Lorente *et al.*, 2024). However, the extent to which such products can supplement host responses to heat and drought stress are not yet fully understood and there is some evidence that they may not help (e.g. (Franzen *et al.*, 2023)). This may be an area worth exploring scientifically to better understand genome x environment x management interactions. Finally, a recent review on plant phenomics, emphasizing the need for a systems-based research focus to improve nutrient uptake efficiency (York *et al.*, 2022), highlights an approach that is equally relevant for mitigating heat and drought stress, considering the critical role roots play in accessing soil water.

The traditional approach of translating fundamental plant research from the laboratory and greenhouse to the field may need reconsideration. While this pathway has led to crop improvement, it has often resulted in limited progress because key factors influencing plant responses were not accurately represented in laboratory or greenhouse settings. As a result, many published findings may not be fully applicable to the real-world conditions of the agricultural systems they aim to improve, potentially slowing progress. Field studies are not inherently more difficult than greenhouse studies, but they do require interactions with producers. Collaboration with extension scientists and outreach specialists who support commercial producers can help foster stronger relationships with those producers. Although unpredictable weather and unforeseen pest and disease pressure can complicate field research, careful planning, manageable replication, and flexible scheduling can significantly contribute to achieving meaningful results. In addition, while high-throughput phenotyping is more challenging in the field than in controlled environments, recent technological advances in data analysis, sensors, robots, and computational resources can help overcome these limitations (Ninomiya, 2022).

The implications of these ideas may call for a shift in how we approach plant resilience research, with a stronger focus on studies conducted in "real-world" production environments. This could involve both controlled and natural experiments that consider one or multiple predictor and response variables. While fundamental research often begins by studying single factors in isolation, it's crucial that all other parameters and variables in the study reflect the real conditions of the agricultural system being targeted for improvement.

Collaborations among key stakeholders

To effectively sustain global food security, it is necessary to establish a research paradigm that seamlessly integrates fundamental research with translational and applied research in agriculture. For instance, advancements in plant science through genetic modification have demonstrated significant potential to increase crop yields and provide nutritional benefits. For example, a 2014 meta-analysis found that genetically modified crops, such as soybean, maize, and cotton, achieved an average yield increase of 22% (Klümper and Qaim, 2014). More recently, genome editing techniques like CRISPR have been used to develop tomatoes enriched with GABA, a compound linked to health benefits such as reduced blood pressure (Waltz, 2022). Despite such progress, our plant science research community today is generally fragmented and siloed, through co-citation, funding mechanisms, conferences and societies, and institutional structures (Henkhaus *et al.*, 2020). There are tools and resources such as team science approaches that may mitigate these trends ('Toolbox dialogue initiative – starting the dialogue'; National Research Council (U.S.); Committee on the Science of Team Science and National Research Council (U.S.); Division of Behavioral and Social Sciences and Education, 2015). Ultimately, more stakeholder collaboration will be required to ensure the results of fundamental plant science benefit society (Henkhaus *et al.*, 2020).

A successful example of collaboration among stakeholders in crop improvement is participatory plant breeding (Glossary). First proposed in the 1980s, this program was implemented in 69 countries over 36 years, covering 47 crops and involving 140 institutions, including CGIAR centers, universities, and NGOs (Ceccarelli and Grando, 2020). In participatory plant breeding, farmers, consumers, and breeders work collaboratively, making decisions together throughout the entire duration of the program. Participatory plant breeding has been successfully applied for decades in Latin America and Africa to meet the needs of underserved farmers (Bhargava and Srivastava, 2019; Colley *et al.*, 2021). This approach is especially valuable for underutilized crops, which have received less research attention and are often better understood by local farmers. This strategy is now garnering more attention in the United States, Canada, and Europe to promote knowledge sharing, crop biodiversity preservation, farmers' seed sovereignty, and organic agriculture breeding (Colley *et al.*, 2021). Participatory plant breeding expanded crop diversity (Witcombe *et al.*, 1996; Goa and Ashamo, 2017), improved farmers' access to new varieties, and increased efficiency in meeting breeding objectives (Eva Weltzien *et al.*, 2006; Goa and Ashamo, 2017). Yet, challenges remain in securing sustained funding for participating farmers and breeding program costs (Goa and Ashamo, 2017), and overcoming barriers to the commercial distribution of varieties developed through these programs (Colley *et al.*, 2021).

Adding practical experiences to fundamental plant science training

In recent years, general interest in plants and agronomy has declined (Stroud *et al.*, 2022; USDA, 2022). This decrease has led to fewer people entering plant science fields and farming. Consequently, there is a reduction in practical experience gained in commercial plant production, landscaping, greenhouse management, and farming. Now, more than ever, it is essential for fundamental plant scientists to gain first-hand experience with the agricultural systems they aim to improve. Participation in Extension and Farm Bureau field days, as well as industry and agricultural trade shows and farmer-focused conferences could help connect fundamental plant scientists with the end users of their research. Some universities operate research farms, but few students and trainees participate in their day to day management. Hands-on experience with commercial crop production systems, organized as internships with local businesses, farms, and development agencies (e.g. Peace Corp, CGIAR centers, etc.) could become a bigger part of training the next generation of plant scientists.

Although building relationships with people from different walks of life can be challenging, it is essential for true transdisciplinary research. Attending farm industry shows that cater to producers involved in the systems under study can be a valuable starting point for those who have never interacted with farmers before. University and government researchers can also connect with farm managers employed by their own institutions or attend field days organized by their departments. To make their work more relevant and impactful, it is important for fundamental plant scientists to invest time in understanding and communicating with the people they aim to serve, their practices, and the reasons behind them.

Conclusion

The increasing frequency of heat and drought events threatens global crop production and food security. While much research has explored plant responses to these stresses, applying this knowledge to agriculture remains difficult. Current crop varieties are often ill-suited to extreme conditions, and traditional breeding has had limited success. To overcome these challenges, fundamental plant research should integrate real agricultural conditions and focus on practical outcomes. Technologies such as high-throughput phenotyping and machine learning hold great promise, but they require a more comprehensive understanding of plant-environment interactions to realize their full potential. Collaboration between plant scientists, agronomists, extension scientists, and farmers is key to developing climate-resilient crops for the future.

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Conflict of interest

Brian McSpadden Gardener is the Technical Director for the Ag Spectrum Company which provides inputs and guidance on crop nutrient management with farmers. The Ag Spectrum Company also funds basic science research in crop and soil sciences at various institutions including Michigan State University. James P. Santiago is a Senior Scientist at Soli Organic, a vertical farming company that supplies USDA Organic-certified herbs to consumers nationwide. Soli Organic does not fund the research of any of the co-authors or other researchers at Michigan State University. The remaining authors declare no conflict of interest.

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Boxes

Box 1: Ten questions plant scientists should ask about experimental systems to make their heat and drought stress research more relevant to crop producers

1. What type of farming system (e.g., low input high tunnel, high input greenhouse, low input field, high input field) does the experimental set up best represent?
2. Which natural environmental features (e.g., light, air, water, soil, microbiome) of the farming system are being accurately modeled in the experiment?
3. How do farm management practices (e.g., timing, rate, and placement of fertilizers, herbicides, and irrigation) influence the frequency or severity of heat and drought stress on crops?
4. What are the typical ranges of light, heat, or water limitation experienced by the crops grown in the farming system modeled in the experiment?
5. How does the experimental system reflect diurnal fluctuations in light, heat, and drought stress typically experienced by the crop in the modeled farming system?
6. At what developmental stage(s) do plants in the modeled farming system typically experience heat and drought stress?
7. Does the developmental stage of the plants (e.g., early vegetative, rapid growth, flowering, post-pollination) influence their response to heat and drought stress in the experiment?
8. How does the plant's rooting structure impact the plants' experience of the applied stress?
9. Does the growth substrate used (e.g., hydroponic, greenhouse potting mix, field soil) affect root structure or the flow of water into the plant?
10. How does the availability of mineral nutrients before, during, and after the applied stress affect the plant's stress perception, response, and recovery?

Box 2. Glossary

- Agricultural Production Systems sIMulator (APSIM) – A crop scale model that can predict yield of several crop species under different farming management strategies
- Controlled Environment Agriculture (CEA) – A system of protected cultivation of crops with controlled environments for crop production, ranging from simple hoop houses to advanced greenhouses and indoor vertical farms, as well as plant factories with integrated climate control and robotics
- Estimated Breeding Value (EBV) – The genetic potential of inheritance of specific traits
- Functional Structural Plant Models (FSPM) – Crop growth models that combine physiology and plant architecture, using L-systems to simulate the spatial orientation of each organ and are applied to simulate an entire field

- High-input greenhouse systems – Intensive greenhouse crop production system of large-scale greenhouse complexes using extensive fertilizers, irrigation, and pest, pathogen, and weed management
- Large-scale, high-input field-based farms – Crop production system in the field with extensive use of fertilizers, irrigation, and pest, pathogen, and weed management
- Multi-layer farming systems – A type of vertical farming system where multiple levels of shelves are used to grow plants
- Participatory plant breeding – a program where stakeholders (usually farmers) collaborate with scientists in all steps of the breeding program
- Phenomics – the study of all phenotypes resulting from gene functions, environmental factors, and their interactions
- Random forest model – A machine learning algorithm that averages multiple decision trees to identify key variables linked to data (e.g. phenotypes linked to climatic data)
- Rooting intensity – density and distribution of roots within the soil, reflecting how vigorously a plant grows its roots in a given area
- Small-holder farming system – A farming operation that involves cultivation of crops in small land areas usually up to 5 acres and is typically owned, operated, and managed by a family unit

Figure legends

Figure 1. Increasing patterns of heat and drought stress and their impact on economics and and crop reproduction

(A) Increases in heat wave frequency (i), duration (ii), length of season (iii), and intensity (iv) since the 1960s. The data shown consists of the exact values provided by the source, plotted directly without smoothing, averaging, or further adjustments. Data accessed from (United States Environmental protection Agency). (B) Cost of combined drought and heat events relative to other major disasters (Smith, 2020). Total costs are summed over 44 years and divided by the number of years to provide an annualized estimate. (C) Average number of days with maximum temperature exceeding 35ºC in the contiguous USA. Red line represents the mean of state-level means, with a LOESS-smoothed curve. Shaded regions indicate the 95% confidence interval. Data accessed from (U.S. Federal Government, 2023). (D) Relative contribution of major staple crops to global caloric intake (D'Odorico *et al.*, 2014) and maximum temperature at which each crop results in reproductive failure (Hatfield *et al.*, 2011; Asseng *et al.*, 2014; Hatfield and Prueger, 2015). Created in BioRender. Holland, B. (2025) https://BioRender.com/s40z874.

Figure 2. Five common agricultural systems, their challenges, and the desirable features needed to support their development

Agricultural systems can be divided into field-based agriculture, including small-holder and large-scale farms, and controlled-environment agriculture, such as greenhouses and vertical farms (top panel). Each system faces unique challenges from increasing drought and heat stress (middle panel). Crop traits for improved resilience, water use efficiency, nutrient uptake, and higher yields are essential across all systems (bottom panel). Created in BioRender. Prado, K. (2025) https://BioRender.com/j36u724. Figure adapted from

Lugano, G. (2024). “Environmental Impact on Food Production” template and retrieved from https://app.biorender.com/biorender-templates/figures/all/t-65c3edcc7a87c37e94429caf-environmental-impact-on-food-production.

Figure 3. General framework of how crop models simulate yield under heat and drought stress

Environmental parameters (e.g., temperature, precipitation) are used as input for models that determine rates of key processes (white boxes). These processes contribute to biomass production in major organs (leaf, stem, root, and grain). Grain output serves as a predictor for yield. Asterisks indicate processes commonly affected by heat (red) or drought (blue) stress in crop models. Created in BioRender. Holland, B. (2025) https://BioRender.com/r00k447.

Figure 4. Promising strategies to increase drought and heat tolerance in crops and key components for each strategy

Enhancing agricultural productivity under heat and drought stress requires integration of multiple strategies (inner circle). Recommendations, example approaches, or stakeholders for each strategy are listed (outer circle). Created in BioRender. Prado, K. (2025) https://BioRender.com/o57u383. Figure adapted from Ona, S. (2024). “Crop Rotation” template and retrieved from https://app.biorender.com/biorender-templates/figures/all/t-65a6f3ec3d4c3616021f8489-crop-rotation

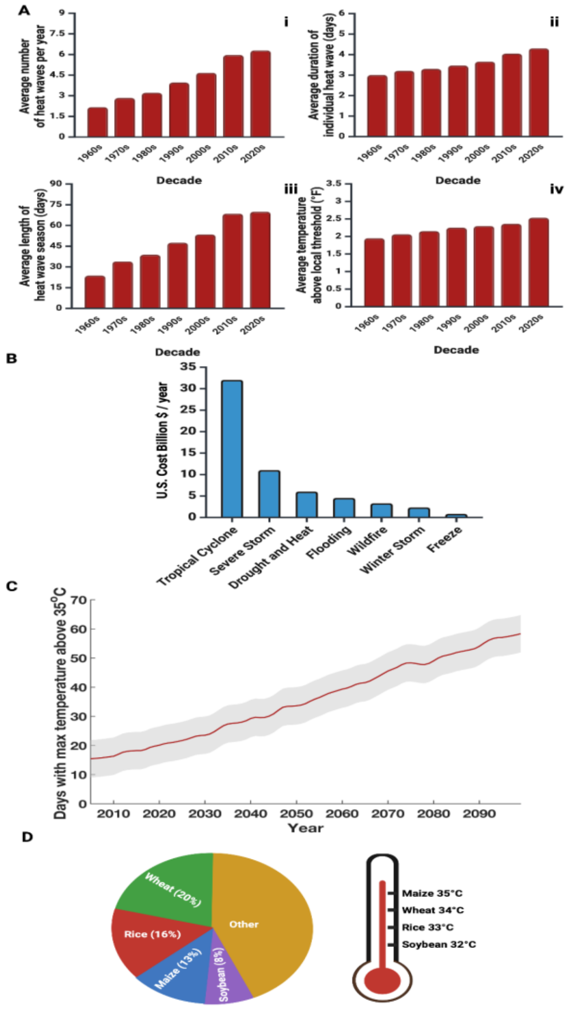
Figure 5: Engineering heat and drought tolerance traits in crops

(A) Successful genetic modifications that led to crops that are tolerant to heat and drought (top panel), heat (middle panel) or drought (bottom panel). Genetic modification was performed by overexpressing target genes if no other strategy was specified between parentheses. Text in bold and green indicates that the transgenic lines displayed higher survival rates, higher yield, or improved stress tolerance during vegetative and/or reproductive stages in economically important crops grown in the field. Abbreviations are listed in Table 1. NAC, bZIP, WRKY, RAB, MBF, MYB, HSF, AP2/ERF are transcription factors. (B) Target processes for engineering under development to produce heat and drought stress-tolerant crops. Created in BioRender. Prado, K. (2025) https://BioRender.com/y73e301 from the results reviewed in Kubis and Bar-Even, 2019; Yang *et al.*, 2020; Lohani *et al.*, 2022; Liu *et al.*, 2023; Ragland *et al.*, 2024.

Table 1. List of abbreviations in alphabetical order

ABA	Abscisic Acid
AP2/ERF	APETALA2/Ethylene-Responsive Factor
APSIM	Agricultural Production Systems sIMulator
bZIP	Basic Leucine Zipper
C2H2-EAR	Ethylene-responsive element binding-factor-associated amphiphilic repression domain found in C2H2-type zinc finger proteins
CAM	Crassulacean Acid Metabolism
CCM	Carbon-Concentrating Mechanisms
CEA	Controlled Environment Agriculture
CERES-WHEAT	Crop Environment REsource Synthesis WHEAT model
CGIAR	Consultative Group on International Agricultural Research
CRISPR	clustered regularly interspaced short palindromic repeats
DREB	Dehydration Responsive Element Binding factors
EBV	Estimated Breeding Value
FSPM	Functional Structural Plant Models
GABA	Gamma-aminobutyric acid
GS	Genomic Selection
GTP	Guanosine-5'-triphosphate
HSF	Heat Shock Factor
HSP	Heat Shock Protein
iGEP	integrated Genomic-Enviromic Prediction
LEA	Late Embryogenesis Abundant
LRR-RLK	Leucine-Rich Repeat Receptor-Like Kinases
MAPK	Mitogen-Activated Protein Kinase
MAPKKK	Mitogen-Activated Protein Kinase Kinase Kinase

MBF	Myb-related Binding Factor
ML	Machine Learning
MYB	Myeloblastosis-related
NAC	NAM (No Apical Meristem), ATAF (Arabidopsis Transcription Activation Factor), and CUC (Cup-Shaped Cotyledon)
NGO	Nongovernmental Organization
PEPKR	Phosphoenolpyruvate carboxylase kinase-related kinase
RAB	Responsive to ABA (Abscisic Acid)
RNAi	RNA interference
ROS	Reactive Oxygen Species
RuBisCO	Ribulose-1,5-bisphosphate Carboxylase/Oxygenase
RuBP	Ribulose 1,5-bisphosphate
SAM	S-adenosyl-L-methionine
WRKY	Named after the conserved WRKY domain in the DNA-binding region



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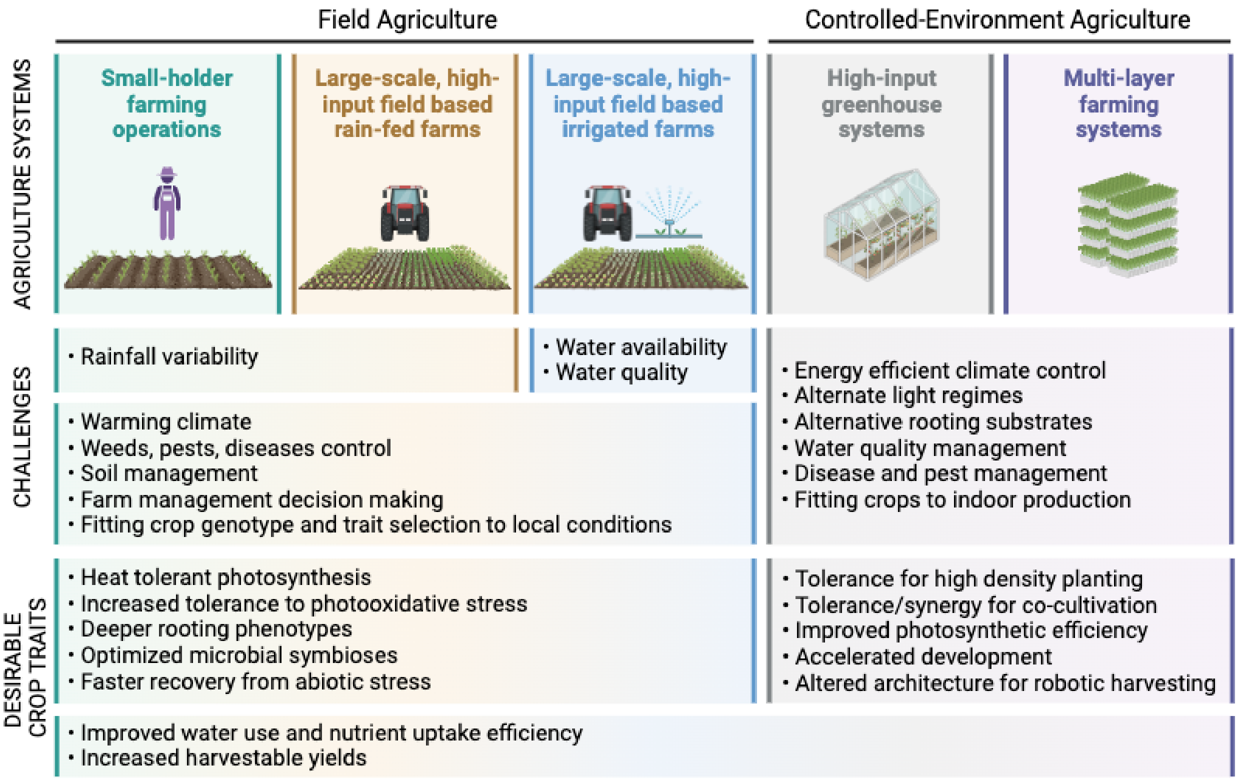

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Lugano, G. (2024). “Environmental Impact on Food Production” template and retrieved from https://app.biorender.com/biorender-templates/figures/all/t-65c3edcc7a87c37e94429caf-environmental-impact-on-food-production.

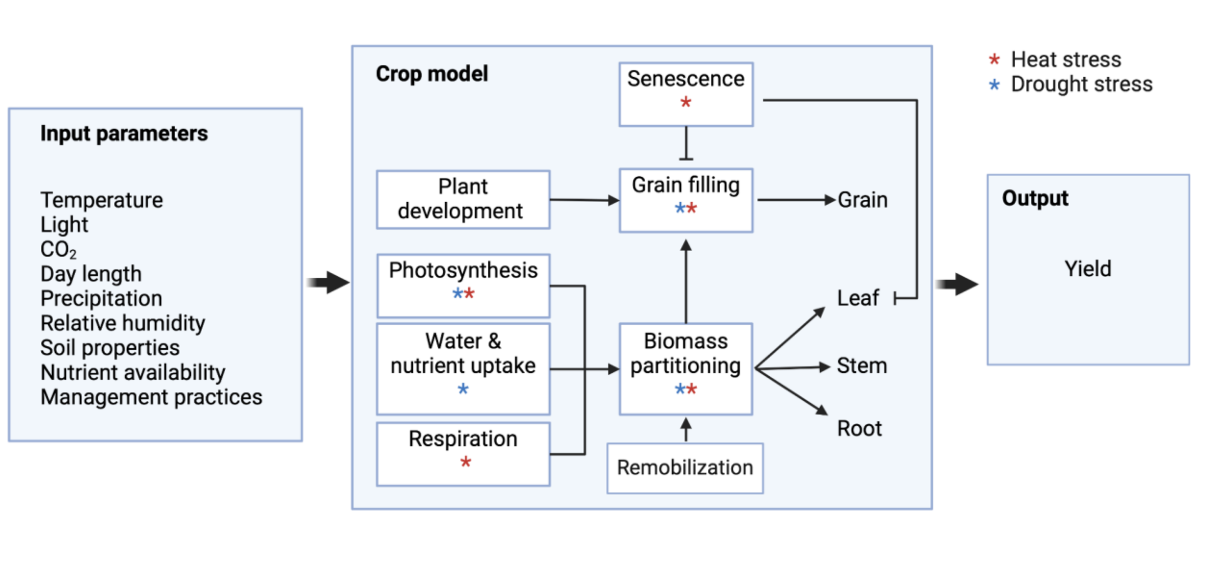

Figure 3. General framework of how crop models simulate yield under heat and drought stress Environmental parameters, (e.g. temperature, precipitation) are used as input for models that determine rates of key processes (white boxes). These processes contribute to biomass production in major organs (leaf, stem, root, and grain). Grain output serves as a predictor for yield. Asterisks indicate processes commonly affected by heat (red) or drought (blue) stress in crop models. Created in BioRender. Holland, B. (2025) https://BioRender.com/r00k447.

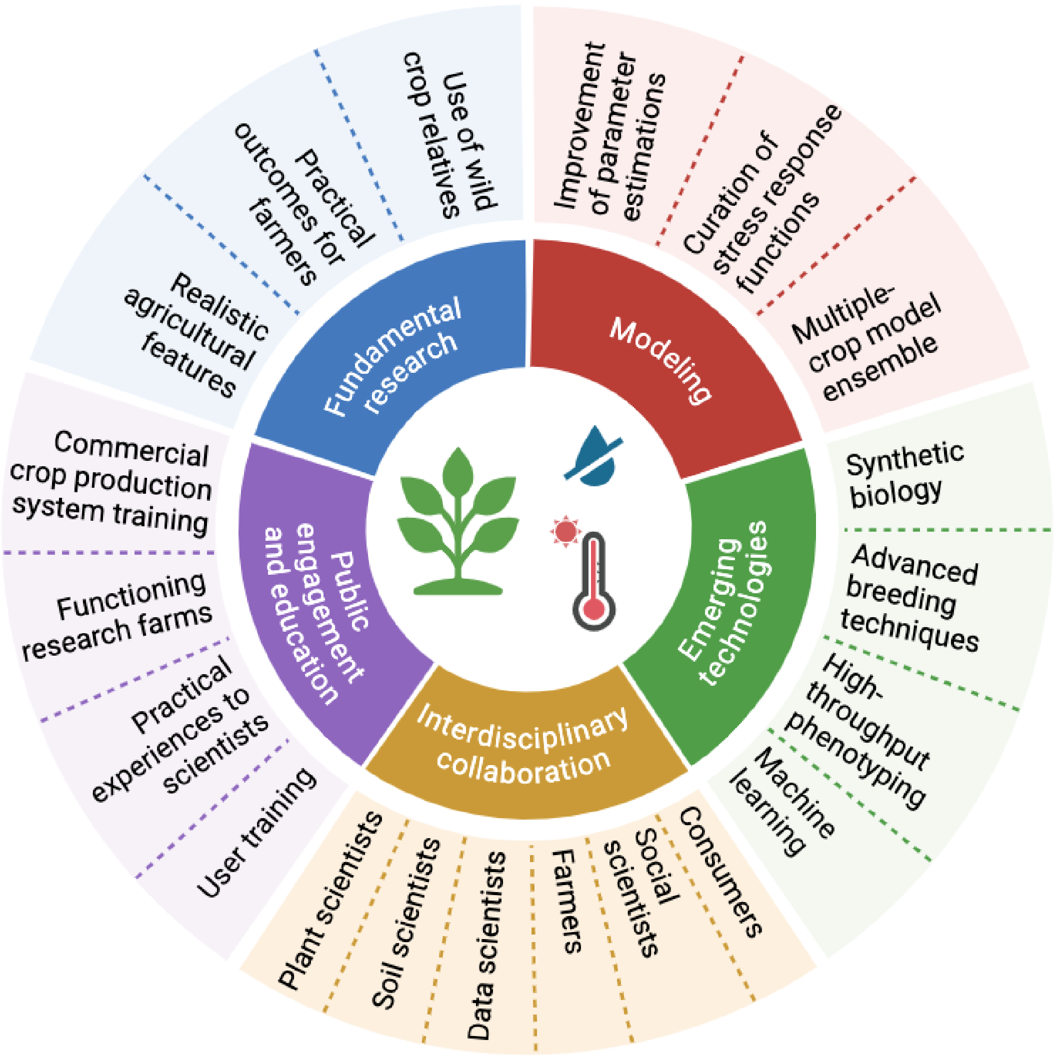

Figure 4. Promising strategies to increase drought and heat tolerance in crops and key components for each strategy

Enhancing agricultural productivity under heat and drought stress requires integration of multiple strategies (inner circle). Recommendations, example approaches, or stakeholders for each strategy are listed (outer circle). Created in BioRender. Prado, K. (2025) https://BioRender.com/o57u383. Figure adapted from Ona, S. (2024). "Crop Rotation" template and retrieved from https://app.biorender.com/biorender-templates/figures/all/t-65a6f3ec3d4c3616021f8489-crop-rotation

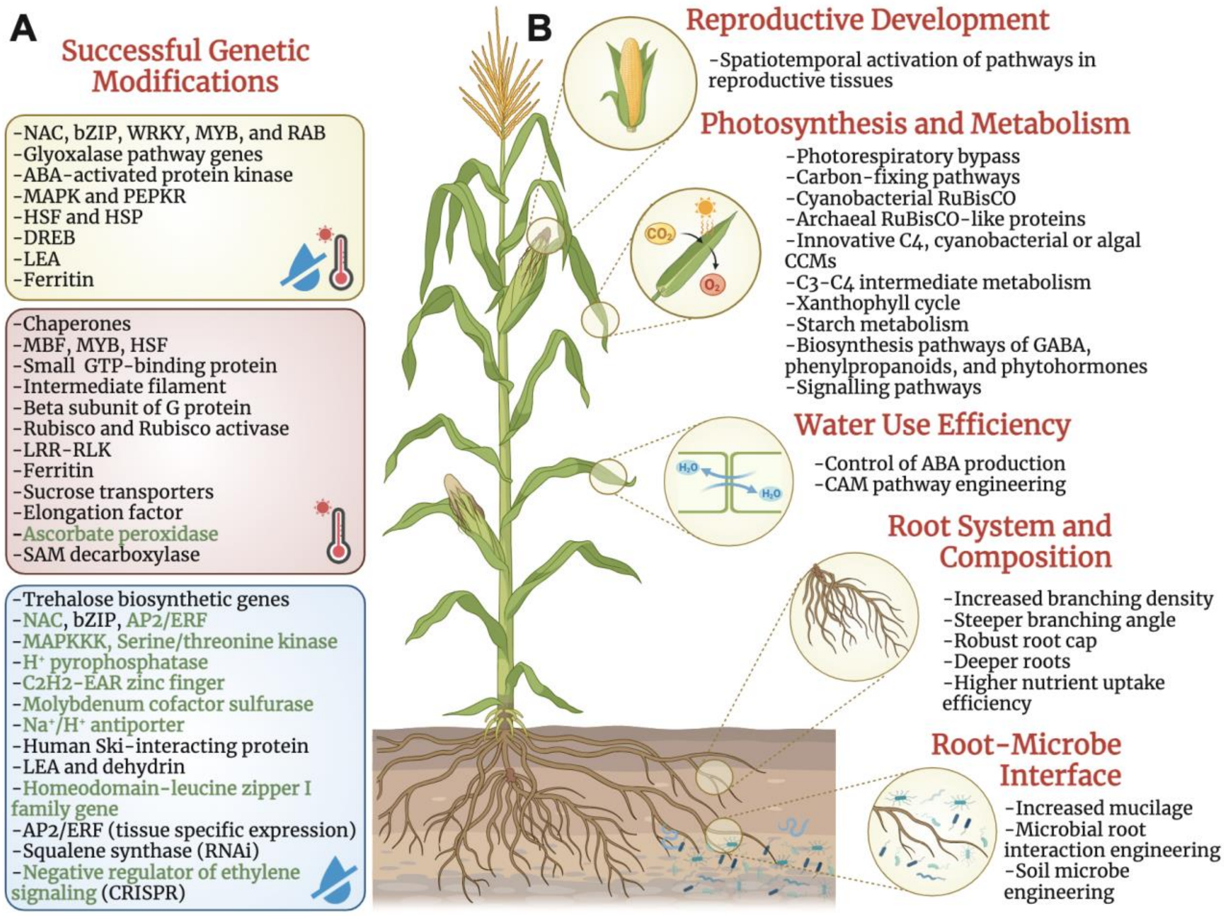

Figure 5: Engineering heat and drought tolerance traits in crops

(A) Successful genetic modifications that led to crops that are tolerant to heat and drought (top panel), heat (middle panel) or drought (bottom panel). Genetic modification was performed by overexpressing target genes if no other strategy was specified between parentheses. Text in bold and green indicates that the transgenic lines displayed higher survival rates, higher yield, or improved stress tolerance during vegetative and/or reproductive stages in economically important crops grown in the field. Abbreviations are listed in Table 1. NAC, bZIP, WRKY, RAB, MBF, MYB, HSF, AP2/ERF are transcription factors. (B) Target processes for engineering under development to produce heat and drought stress-tolerant crops. Created in BioRender. Prado, K. (2025) https://BioRender.com/y73e301 from the results reviewed in Kubis and Bar-Even, 2019; Yang *et al.*, 2020; Lohani *et al.*, 2022; Liu *et al.*, 2023; Ragland *et al.*, 2024.