

Review

Enhancing climate change resilience in agricultural crops

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SUMMARY

Climate change threatens global food and nutritional security through negative effects on crop growth and agricultural productivity. Many countries have adopted ambitious climate change mitigation and adaptation targets that will exacerbate the problem, as they require significant changes in current agri-food systems. In this review, we provide a roadmap for improved crop production that encompasses the effective transfer of current knowledge into plant breeding and crop management strategies that will underpin sustainable agriculture intensification and climate resilience. We identify the main problem areas and highlight outstanding questions and potential solutions that can be applied to mitigate the impacts of climate change on crop growth and productivity. Although translation of scientific advances into crop production lags far behind current scientific knowledge and technology, we consider that a holistic approach, combining disciplines in collaborative efforts, can drive better connections between research, policy, and the needs of society.

Introduction

There is an urgent need to increase the climate change resilience of crops, while simultaneously enhancing crop yields in a sustainable manner to ensure future food security. Climate change-associated environmental stresses, such as extreme temperatures and erratic rainfall, will compromise the ability of agriculture to meet the food demands of an increasing global population. Rapid advances in knowledge and applied crop design may provide solutions, based on state-of-the-art approaches, from genomics and gene editing to the manipulation of the soil microbiome and crop management practices. Given the magnitude of the climate change challenge, there is a need to assess current knowledge and consider how collaborative

efforts that catalyze and foster improved interactions between disciplines may be required to meet agri-food system targets.

Climate change is predicted to increase the frequency, intensity, spatial dimensions, and duration of extreme weather events^{1,2}, posing a significant threat to the production of all major crops. For example, increased incidences of heatwaves, droughts and floods adversely affect the yields of cereal crops such as wheat and maize (Figure 1A–C), which can decrease as much as 40% under drought conditions^{3,4}. The magnitude of yield losses depends on the crop, the duration and intensity of the stress and the crop developmental stage⁵. Reproduction and grain development/filling are particularly susceptible to heatwaves and drought, which decrease yields in most crops⁶.





Figure 1. Artistic depiction of the problems and mitigation strategies surrounding the impact of heatwaves and drought on food security.

(A) This painting by Besiana Sinanaj, titled 'Climate. Cultivation. Collaboration.' depicts four scientists and an indigenous leader connecting and sharing ideas in front of a scene of farmers cultivating several crops of global importance (rice, maize, tomatoes, wheat, and beans). The diverse set of onlookers are portrayed as optimistic and represent interdisciplinary collaborations to tackle the effects of drought and heat stress on agriculture. Their areas of expertise, which are reviewed in this paper, are reflected in the objects they are holding and the designs of their clothing. The scene features: (B) cracked ground and wilted plants under a scorching sun; (C) a farmer harvesting wheat; (D) stomata on the lab coat of a scientist researching plant root and shoot architecture and physiology; (E) legumes as an important element of crop management practices, including (F) intercropping; (G) interaction plots on the lab coat of a scientist researching soil and rhizosphere microbiome ecology and function; (H) grains and pulses representing crop diversity stored in seed banks; (I) a farmer harvesting gene-edited tomato varieties; and (J) the CRISPR-Cas9 diagram on the lab coat of a scientist using gene-editing technologies to develop high yielding and resilient cultivars.

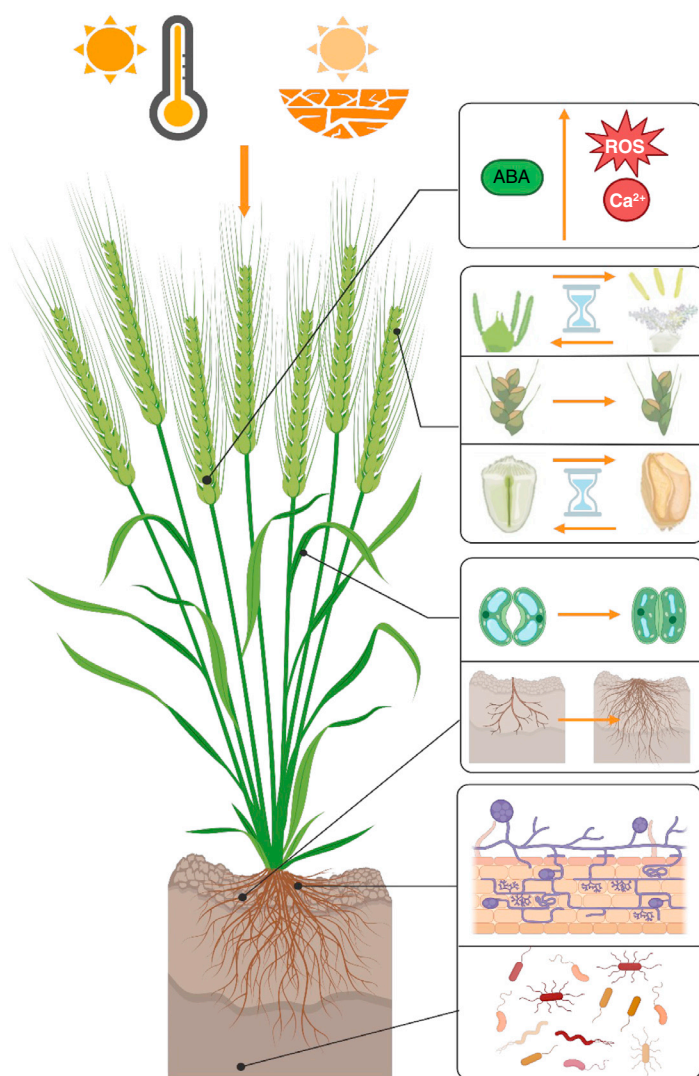
decade, thus yield decline will likely continue. Furthermore, 42% of durum wheat, 56% of barley, 41% of alfalfa and 35% of grass are currently planted in areas prone to drought (USDA Drought Monitor), exacerbating the effects of temperature changes.

Despite the constraints imposed by climate change, global agricultural production must increase by 28% over the next decade to ensure food security⁸. Approximately 828 million people globally were affected by hunger in 2021⁸. Food insecurity is predicted to worsen as the global population increases, and extreme weather events become more prevalent⁸. To achieve food security for the predicted global population of 10 billion people in 2050, the area of arable land must increase (from 1.4 to 1.5 billion hectares) while water for agriculture will decrease in availability⁹. Paradigm-shifting advances in crop breeding are required to ensure knowledge gains regarding climate resilience are effectively translated into crop improvement.

Moreover, to capitalize on modern genetic advances, these must be achieved safely, while minimizing their environmental impact and within economic constraints, with social acceptance and harmonised governance¹⁰. Within this context, we identify the main problem areas (Figure 2), highlighting outstanding questions regarding the impacts of climate

Simulations of global wheat production predict a 6% decline for each degree Celsius rise in global temperatures⁷. Cereal production in Europe was reduced in 2018 compared with the previous five-year average due to heat and drought³. Current forward projections predict a temperature increase of 0.2°C per

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Examples of crop responses to abiotic stress:

Signalling

- Increase in cytosolic Ca^{2+} and apoplastic reactive oxygen species (ROS)
- Changing levels and distribution of hormones (e.g., abscisic acid, ABA)

Floral transition, fertility and grain filling

- Altered flowering time
- Reduction in fertile florets, pollen viability and anther dehiscence
- Accelerated and shortened grain filling period

Root and shoot architecture

- Change in water use efficiency via alterations in stomata size, density and/or dynamics
- Adjustments in root length, branching and growth angle

Interaction with soil microbiome

- Changes in root association with mutualistic symbionts (such as arbuscular mycorrhizal fungi)
- Modified microbial activity and diversity (e.g., in *Actinobacteria* and *Proteobacteria* communities)

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Figure 2. Summary of plant physiological responses to abiotic stress.

A diagrammatic representation of the effects of heat and drought on crop development. Examples (cited in the main text) highlight crop signalling, floral transition, fertility and grain filling, changes in root and shoot architecture and interactions with the soil microbiome as major effects. ROS, reactive oxygen species; ABA, abscisic acid. (Image created with [BioRender.com](https://www.biorender.com/).)

change on crop growth and productivity (Box 1) and identifying potential solutions (Figure 3 and Table 1). We argue that establishing collaborative research networks, together with the application of integrated high-throughput phenotyping, genotyping, crop management and modeling approaches, as well as stakeholder engagement, are realistic solutions to the problem of climate resilience, particularly after they are tested, validated and scaled to delivery.

Molecular mechanisms regulating plant resilience to climate change

The perception and response to stress engage a range of signalling molecules, including reactive oxygen species (ROS), nitric

oxide and calcium (Ca^{2+}), which are interconnected to control plant growth, development and defence responses (Figure 2)^{11–13}. Exposure to stress induces rapid local increases in cytosolic Ca^{2+} levels that are sensed and relayed inside the cell, activating the respiratory burst oxidase homolog D (RBOHD) proteins, and generating an apoplastic ROS burst. ROS and Ca^{2+} waves provide a continuous chain of cell-to-cell signalling events that extends from the initial tissue that senses the stress (the local tissue) to the entire plant (systemic tissues) through a positive feedback loop mechanism. The systemically propagating Ca^{2+} and ROS waves allow rapid signalling in a stimulus-dependent manner to orchestrate local responses and systemic acquired acclimation (mechanism induced in

Box 1. Summary of outstanding questions/areas of research.

● **What are the molecular mechanisms underpinning crop response to climate change?**

Research is required to identify the mechanisms integrating crop responses to multiple stresses and to dissect how specificity is entrained in stress signalling. It is also important to determine which signals remain local and which are systemically transmitted and to identify the pathways regulating (at the gene, protein and structural levels) the transport and spread of stress signals. Moreover, the mechanisms to translate fundamental knowledge at the molecular level into strategies to modify crop resilience remain unclear.

● **What phenotypes/ideotypes improve crop resilience to multiple abiotic stresses?**

Research linking phenotypic/developmental traits with the variability in the stress response of different genotypes and crop species is required. Overcoming the technical challenge of assessing root traits in the field will allow breeding for optimal resource acquisition and plasticity to respond to adverse climate conditions. The importance of shoot architecture and stomata/leaf patterning has been well reported, but using this knowledge in breeding without yield reduction is still challenging.

● **Can we improve crop climate resilience by modifying management practices and the microbiome?**

Research on the effects of land and crop management practices on stress-intensity, crop development, crop yield and geographical/rhizospheric microbial distribution needs to be prioritized. It is important to uncover the effects of abiotic stress on the plant microbiome, and the role of plant root exudates and metabolites in shaping the microbiome under stress conditions, both of which directly affect plant health. Research is ongoing to optimize the use of microbial inoculants or consortia to enhance plant stress tolerance.

● **How can we exploit advances in genetics, genomics, modelling, and high-throughput technologies in breeding climate resilient crops? What are the limiting factors?**

There is limited knowledge translation from model crops to both staple and underutilised crop cultures. Indigenous knowledge of underutilised crops and semi-domesticated species is being lost or is unused in crop improvement. The use of genetic resources maintained in landrace collections, genomic technologies and big data is not efficiently exploited in tailoring crops to specific environments. It is also crucial to determine how improvements observed in the lab are maintained in the field and in the presence of multiple abiotic stresses.

Field research is also limited by the restrictions imposed on genetic modification. More research is required to identify the risks, concerns, and costs (in terms of yield, disease susceptibility, economic and social costs) of breeding crops that are more resilient to climate change. Support is lacking to develop cross-disciplinary approaches that engage policy makers, the arts, the public and other members of society.

tissues that are not yet subjected to the stress) to a range of abiotic stresses including heat and drought¹¹. The systemic cell-to-cell transmission of Ca^{2+} and ROS signals is also linked to electrical waves that involve rapid depolarization of the plasma membrane, the functions of glutamate receptor-like proteins, and plasmodesmata (channels enabling intercellular molecular transport)^{11,12}. Recent research indicates that, in response to stress, the release and diffusion of amino acids in the apoplast activates the calcium-permeable channel GLUTAMATE RECEPTOR-LIKE 3.3, leading to the transmission of Ca^{2+} waves and other downstream signalling events¹⁴.

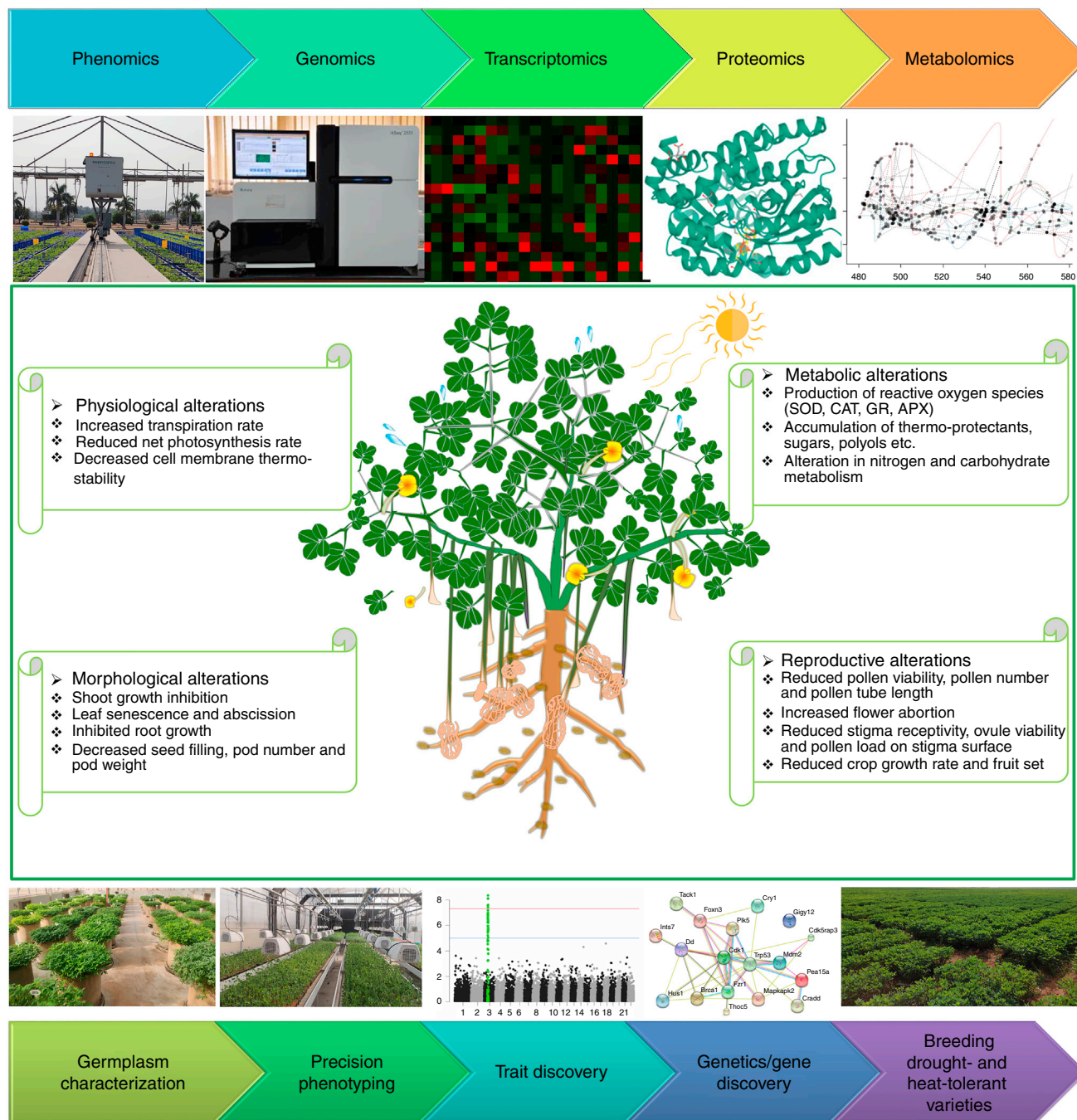
The Ca^{2+} /ROS signalling system is intrinsic to all abiotic stress responses, and thus specificity needs to be entrained in the signal to tailor these pathways^{12,13}. One way to add specificity is through controlling the relative rate of apoplastic and cytosolic H_2O_2 accumulation¹⁵. Mechanisms that integrate signals from different cellular compartments or intercellular molecular movement via the apoplast or the plasmodesmata can also define the specific nature of signal transmission¹⁶. An improved understanding of these processes will be essential, not least because the ROS, electrical and intracellular Ca^{2+} waves also transmit signals from plant to plant¹⁷.

The stress-induced changes in ROS, Ca^{2+} and electrical signals activate a complex network of downstream molecular factors such as kinases, phosphatases, chaperones, hormones, lipid molecules and transcription factors that work synergistically to modify plant responses and promote survival under the stress (Figure 2)^{12,13,18,19}. Proteins such as class A1 heat shock factors

(HSFA1) and type I MADS-box transcription factors are examples of transcriptional activators in the heat shock response. They, with other transcription factors, control acclimation and adaptation in a temperature-dependent manner^{20,21}. Floral transition and early reproductive development factors, such as *FLOWERING LOCUS T (FT)* homologues²² and the circadian clock gene *Ppd-1*^{23,24}, are highly sensitive to changes in climate. These molecular factors are therefore potential targets for manipulation that must be characterised if crop yield and quality are to be maintained under abiotic stress conditions (Box 1 and Table 1).

Phytohormone signalling integrates with ROS- and Ca^{2+} -induced mechanisms to control responses to stress^{12,13,18,25} (Figure 2). For example, accumulation of the phytohormone abscisic acid (ABA), which triggers stomatal closure to prevent excessive water loss, was described in response to drought^{26,27}. ABA activates SNF1-related protein kinase 2 (SnRK2) initiating appropriate molecular responses to drought²⁸. Interestingly, the guard cells of ferns do not respond to ABA, displaying an evolutionarily distinct passive mechanism for stomatal closure under drought conditions^{29,30}.

Changes in response to abiotic stress in crops are also observed at plasmodesmata, and specifically in callose, a β -1,3 glucan that regulates plasmodesmata aperture and symplasmic (cytoplasm-to-cytoplasm) molecular transport^{16,31}. Exposure to toxic levels of aluminium induces callose accumulation and plasmodesmata closure, impairing wheat root growth³². CALLOSE SYNTHASE 8 (CalS8), an enzyme that synthesises plasmodesmata-associated callose in response to ROS application³³, is activated in response



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Figure 3. Understanding and harnessing gene bank diversity for developing stress-tolerant varieties.

The figure represents the integration of -omics approaches with germplasm characterization, precision phenotyping, trait and gene discovery and breeding as a holistic solution to enhance climate resilience in crops. Examples using this integrated approach to breed stress-tolerant chickpea varieties are mentioned in the main text. The middle of the picture summarizes alterations in plant physiology, morphology, metabolic and reproductive development reported to occur in response to stress. SOD, superoxide dismutase; CAT, catalases; APX, ascorbate peroxidase; GR, glutathione reductase.

to heat stress, causing a reduction in symplasmic connectivity that impacts root meristem development in *Arabidopsis thaliana*³⁴. The mechanism underpinning callose accumulation and plasmodesmata closure depends on cytoplasmic Ca^{2+} levels³⁵ and the expression of the plasmodesmata-localized protein, NOVEL CYS-RICH RECEPTOR KINASE (NCRK), which interacts with

both CALMODULIN-like protein 41 (CML41, a calcium receptor) and GLUCAN SYNTHASE-LIKE 4 (GSL4, a callose synthase) in response to ROS³⁶. While multiple reports state that ROS waves induce callose deposition, in light stress, RBOHD-generated ROS increase symplasmic connectivity and the propagation/spread of the waves¹¹. Osmotic stress also triggers callose

Table 1. Proposed future solutions to improve climate change resilience in crops: summary of various novel and ongoing approaches that could be transformative in answering outstanding questions presented in Box 1.

Area of research	Novel and ongoing approaches/solutions
Manipulation of candidate genes	Improve phenotyping in the field to identify genes responsible for desirable traits and their environmental interactions. Improve understanding of signalling and molecular pathways. Establish efficiency in homology-directed repair (HDR) using CRISPR approaches to enable precise gene replacement. Use of crop modelling approaches and synthetic biology to design strategies for engineering multiple desirable traits.
Crop management practices	Improved/widespread supplementation of crop microbiota to improve tolerance to specific stresses. Intercropping with desert plants to promote novel plant growth-promoting rhizobacteria (PGPR). Reduced reliance on monocultures and associated effect on microbial biodiversity decrease. Better understanding of practices to conserve soil moisture, temperature, organic matter, and beneficial microbiota.
Use of on-farm 'insurance crops' and preservation of genetic diversity	Transition to underutilised wild and semi-domesticated crops. Progress on research of antinutrient factors. Further accessibility of genome sequencing/phenotyping data to fill the knowledge gaps in germplasm collection. Haplotype-based breeding to deploy resilient varieties/hybrids based on gene-based association analysis.
Social sciences and interdisciplinary networks	Social license and harmonised governance on GMO at a global scale. Better integration/use of new technologies to assist faster decision making and policy development. Development of pathways for translation of fundamental knowledge into plant breeding and biotechnology by collaborative interdisciplinary teams. Open access to scientific information for representatives of the political world, society and stakeholders leveraging novel approaches including the arts to facilitate engagement.

deposition (likely via Qián Shǒu kinase (QSK1) signalling), affecting symplasmic connectivity and root development^{37,38}. Transient water stress studies, conducted by exposure of small root sections to air, increased the expression of the plasmodesmata-located protein PDL3 and callose deposition, which suppresses lateral root development³⁹. Mathematical models indicate that plasmodesmata transport is important to control the flow of water across root tissues in maize and other crops⁴⁰.

An emerging field of research identifies temperature-dependent alternative splicing (TD-AS) as a mechanism regulating plant stress response⁴¹. TD-AS, predominantly occurring through the introduction of premature termination codons via a retained intron, regulates gene expression in *Arabidopsis*⁴¹ and winter sugarcane⁴². For example, the pre-mRNA of flowering repressor *MAF2* (*MADS AFFECTING FLOWERING 2*) was efficiently spliced at cold temperatures, but intron retention was observed when temperatures increased⁴³. Effectively spliced *MAF2* interacts with *MAF3* (*MADS AFFECTING FLOWERING 3*), *SVP* (*SHORT VEGETATIVE PHASE*), and *FLC* (*FLOWERING LOCUS C*), which represses the expression of *FT* and *SOC1* (*SUPPRESSOR OF OVEREXPRESSION OF CONSTANT 1*) controlling flowering. When temperature increases, *MAF2* intron-retained isoforms (unable to establish these interactions) are produced, promoting transition to flowering and reproductive growth⁴³. Parker *et al.* identified a gene encoding the *Arabidopsis* m6A methyltransferase *METTL16* orthologue, *FIONA1* (*FIO1*), associated with natural variations in flowering time across *Arabidopsis* ecotypes and regulating *MAF2* splicing in a temperature-dependent manner^{44,45}. TD-AS may also occur through temperature-labile structural changes in introns themselves, rather than through modification of the splicing machinery⁴⁶. Single nucleotide polymorphisms (SNPs) in intron 2 of the heat shock factor, *HsfA2*, are associated with variation in thermotolerance across species of tomato, and result in structural differences at the 3' splice site^{46,47}. Investigating the existence of similar mechanisms in other key crop species could provide an

elegant target for influencing the splicing patterns of temperature-response genes for agronomic benefit (Box 1 and Table 1).

To summarize, there is sparse evidence of well-defined molecular mechanisms involved in crop responses to climate change. New research fields are emerging linking developmental components and stress responses, but so far this knowledge is limited to a few model plants. Targeting molecular components to improve crop yield and climate resilience requires further efforts in dissecting the specificity, regulation and environmental interactions of these pathways in different crop species (Box 1).

Targeting plant development for climate resilience

Plant development is particularly sensitive to climate change-associated stresses, such as heat and drought (Figure 2)¹³. Stresses experienced at the early stages of reproductive development restrict yields, impairing canopy and seed development^{19,48}. Heat and drought disrupt the floral transition and fertilisation, resulting in lower numbers of fertile florets and grains^{49,50}. Stresses experienced after fertilisation primarily restrict yield by reducing grain size⁵¹. In rice, elevated night temperatures (temperatures higher than the optimum threshold during the night time) accelerate and shorten the grain filling period by impairing nutrient remobilization, translocation and processing^{52,53}. The links between plant developmental status and stress response, if better understood, could be exploited as strategies to improve climate resilience (Box 1).

Stress-induced impairment of male gametophyte (pollen) development within the anthers results in microspore abortion or sterile pollen (Figure 2)^{54–56}. This is largely due to disrupted meiosis of pollen mother cells and the premature degradation of the tapetum^{54,55}. Defects in opening the anther walls for pollen release (a process known as indehiscence⁵⁷), in pollen grain viability and in pollen tube elongation contribute to reduced fertility in stress conditions^{58,59}. Heat sensitivity during meiosis is prevalent in wheat and canola (oilseed rape), restricting plant development and yield under stress^{60,61}. The critical temperature threshold at anthesis is

25°C in spring wheat, and for every 1°C increase above this threshold, grain yields decrease by 10%, reaching a zero yield at 35°C⁶. Regulators of temperature-dependent responses in anthers and during meiosis remain under investigation⁶².

Although candidate genes for heat and drought responses have been characterized, little is known about stress perception at the whole-plant level (Figure 3). Regulation of root system architecture allows deeper root penetration^{63,64}, and is intrinsic to water and nutrient capture, but the processes underlying these responses are poorly understood and remain underexploited in agriculture^{63,65,66}. Tailoring root system architecture to improve drought avoidance could be achieved, for example, by manipulation of *DEEPER ROOTING 1* (*DRO1*), a quantitative trait locus in rice that controls the root growth angle^{67,68}. Maize roots with modified *DRO1* have steeper root growth angles, and reduced axial roots and lateral branching, potentially optimizing water uptake⁶⁹. The technical challenge of assessing root traits below-ground remains a bottleneck to plant breeders and questions remain on how root architecture affects molecular responses to combined abiotic stresses^{66,70} (Box 1).

Shoot architectural changes in response to environmental stress have been characterized (Figure 2)⁷¹. In particular, the regulation of leaf stomatal closure is critical to optimize leaf water use efficiency, which often (but not always⁷²) correlates with plant response to temperature and water availability (Figure 1D). The highly efficient shape of stomata in grasses, which rapidly change in conductance in response to light⁷³, is well-adapted to changes in climate. Regulation of stomatal size and density (SD) is also crucial to the development of crops more resilient to the effects of climate change^{74–76}. Manipulation of key developmental regulators such as maize *ZmNAC49*⁷⁷, barley *HvEPF1* (*Hordeum vulgare* epidermal patterning factor 1) and wheat *TaEPF1* can modify SD, improving gas exchange and increasing water use efficiency^{74,76}. Additionally, smaller stomata (such as those in barley) are thought to facilitate a rapid conductance response⁷⁸. In contrast, traits related to stomatal size are a good option to improve rice water use efficiency as speciation in this crop has favoured increases in stomatal density⁷⁹. Manipulation of leaf epidermal patterning can also improve resilience in crops grown on marginal land with limited water resources⁷⁶. For example, mutation in barley *HvCBP20* (cap-binding 20) gene modifies stomata patterning and increases epicuticular wax, which help to maintain leaf water content under drought^{80,81}.

To summarize, abiotic stresses experienced during plant transition to reproductive development severely affect crop growth, resource allocation and yield. Our understanding of root phenotypes for optimal resource acquisition under various drought/heat conditions is limited (Box 1). Manipulating stomatal density has shown promising results in improving water use efficiency without yield reduction. Research on other aspects of phenology by yield interaction are discussed in recent manuscripts, showing their potential as targets for improvement^{82,83}.

Building system resilience through crop management and the microbiome

Effective crop management practices, such as conservation tillage in combination with residue retention/incorporation⁸⁴, can help counteract the adverse effects of a changing climate (Table 1)^{85,86}. Irrigation scheduling based on soil moisture

monitoring and weather conditions, the use of drip irrigation and other water-saving strategies, suitable planting methods (e.g., bed sowing⁸⁷) and the choice of planting date based on agroclimatic indicators (such as total precipitation, number of dry days and average mean temperature) can improve water use efficiency and minimise the adverse effects of climate change^{88,89}. The use of integrated systems such as crop–livestock (agropastoral), livestock–forest (silvopastoral) and crop–livestock–forest (agrosilvopastoral) have advantages, such as increasing the accumulation and stock of carbon in the soil, increasing fertility, and preserving soil moisture, which influences crop tolerance to drought and high temperatures^{90,91}. However, these strategies are not available or applicable to all cultivated crops and their use can reduce productivity.

Farmers often prefer using crop rotation, cover crops and intercropping as stress management strategies. Cover crops and their residues protect the soil from erosion and can open root channels through compacted soil, allowing the cash crop to access water in deeper soil layers⁹². Some cover crops (such as clover and hairy vetch) help regulate soil temperature and moisture⁹³, reducing the stress severity. Similarly, cover crops or a living canopy cover as mulching provide shade and reduce water evapotranspiration from soil and aerial plant portions, protecting main crop seedling establishment^{94,95}.

Rotation in cropping patterns is a season-long but effective strategy to improve crop resilience to stress. Three years of wheat and legume rotation significantly reduced drought stress effects with a positive impact on crop yield⁹⁶. Crop rotation enhances organic matter through temporal litter decomposition of a diversity of crops, with positive impacts on soil hydrology^{97–99}. Rotation with crops with different water requirements is a promising strategy that mitigates adverse effects in drought-prone areas. For example, cultivating crops with a low water requirement during seasons of high-water availability could conserve soil water for the next season's crop^{98,99}.

Crop diversification and intercropping impact soil's physical properties and water storage, and can protect crop plants from heat stress^{100,101}. The benefits of plant species diversity are due to complementarity in resource use, to niche overlap, and/or to alterations in soil structure and chemistry¹⁰². However, the effects of plant interspecific interaction could be negative, depending on the species involved, the resources available, and environmental conditions^{103,104}. Crop diversification also results in phenotypic plasticity, enabling plants to capture more available resources — for example, through increases in root biomass for foraging nutrients^{105,106}.

The selection of the best suitable crop combinations in intercropping is crucial in drought-prone areas. For example, the classic cereal–legume intercropping system¹⁰⁷ (Figure 1E,F) benefits the crops through improving soil fertility, increasing soil carbon and water infiltration, and a significant gain in soil moisture during drought periods, especially in sandy soils^{108–110}. Mixing plants with deep and shallow roots (such as bean–maize, sorghum–red clover, and maize–grass pea) makes better use of the available soil moisture by enabling exploration of deep soil and subsoil¹¹¹. Such root combinations allow bio-drilling (where long tap-roots remain in the soil, providing channels for water drainage) which enhances soil structuring, increases soil organic

matter and promotes soil aggregation, thereby improving the storage and availability of soil water in the root zone^{89,112}.

Diversified cropping systems also increase soil microbial biomass and activity (and the microbial population — microbiome — in the vicinity of the plant root system), leading to better soil structure, organic matter, and improved water retention (Figure 2 and Table 1)^{113–115}. The shade provided by the canopy of diverse plantations nurtures belowground microbial activity by reducing temperature extremes, preventing the penetration of ultraviolet radiation and lowering coalescences due to less soil drying⁸⁹. High root densities, root-specific interactions with the soil microbiome and the occurrence of species-specific microbial communities in diverse plantations increase exudation and enhance soil microbial activity^{116,117}.

The microbiome exerts control over host plant metabolism and gene expression, to enhance nutrient provision and modify defences against biotic and abiotic stresses^{118–121}. Climatic conditions modify the diversity of plant microbial communities, the effects depending on plant species and developmental stage (Figures 1G and 2)^{122,123}. For example, the abundance of Actinobacteria increased two-fold and Proteobacteria decreased over 2.5-fold in soils cultivated with rice under drought conditions, and these changes persisted after alleviation of the stress¹²⁴. In sorghum, drought increased the abundance of Actinobacteria in relation to irrigated samples¹²⁵ but only when the stress was experienced pre-flowering was there a decrease in pathogenic genera (*Fusarium*, *Gibberella* and *Sarocladium*)¹²⁶. The abundance of specific rhizospheric taxa relates to plant health under abiotic stress conditions. For instance, drought-stressed sorghum plants in soils with *Arthrobacter* bacteria suffered more than those in which bacteria of the genus *Variovorax* were abundant¹²⁷. A different effect was observed in wheat plants, in which *Arthrobacter* alleviated drought-stress effects under greenhouse conditions¹²⁸. Similarly, the presence of endospheric *Streptomyces* was correlated with drought tolerance in several plant species¹²³.

Under drought, roots grown in natural- and agro-ecosystems preferentially recruit beneficial root microbiota^{129–131}, including arbuscular mycorrhizal fungi (AMF). Symbiotic fungi provide plants with macro- and micronutrients, such as phosphorus, nitrogen and selenium^{132,133}, and contribute to the stabilisation of soil aggregation by exuding soil-binding compounds through mycelial activities¹³⁴. The direct transfer of water from soil to plants through AMF mycelial networks has been demonstrated in wild oat using isotopically labelled water¹³⁵. Therefore, commercial AMF inoculants, added as a supplement to agricultural lands, have considerable potential in the alleviation of drought and nutrient deficiency in plants (Table 1)¹³⁶. However, while AMF richness increases in barley roots under drought, AMF performance (colonization and the abundance of arbuscules and vesicles) decreases, indicating antagonistic interactions¹³⁷. Little is known about how AMF symbioses is altered under other abiotic conditions or what the compatibility of different AMF strains is with crop species in different environments, as well as their interactions within plant and native microbial communities¹³⁸.

The plant microbiome response to heat stress^{138,139} differs slightly from the effects produced by drought^{140,141}. However, many plant growth-promoting microbes, including commercially available strains, increase both drought and heat tolerance in a

diverse range of plant taxa^{142,143}. The application of microbial consortia can be more efficient than single-strain inocula in enhancing stress tolerance¹⁴⁴. Desert plants may provide a valuable source of novel plant growth-promoting rhizobacteria, which are adapted to improve soil fertility in degraded regions in addition to improving plant growth and stress tolerance (Table 1)¹⁴⁵. For example, the presence of the endophytic bacterial strain *Enterobacter* sp. SA187, isolated from the desert legume *Indigofera argentea*¹⁴⁶, improved salt tolerance of model and crop plants under greenhouse conditions¹⁴⁷.

Overall, crop management practices and the application of microbiome-inspired methods are promising innovations to combat and prevent crops from stresses derived from climate change (Table 1)¹⁴⁸. More research is required to understand how specific microbial communities impact plant stress responses and how they interact in different climatic conditions (Box 1).

Exploiting genetics and genomics in breeding crop resilience

The climate resilience of agricultural crops could be improved by conventional breeding^{10,149}, but this is a relatively slow process. The integration of high-throughput technologies (such as speed breeding) and modelling approaches could accelerate and increase the precision of trait selection in plant breeding programs¹⁵⁰ (Figure 3). The declining cost of next-generation sequencing platforms has increased access to whole-genome sequence information in multiple crops, including landraces, underutilised crops and crop wild relatives, facilitating the acquisition of molecular data on large germplasm collections^{150,151}. Adoption of high-throughput precision phenotyping, speed breeding, genomic selection and gene editing, and application of digital technologies to generate high-quality data have been successful in breeding novel heat- and drought-tolerant crops^{152–155}. Enormous efforts have been invested to preserve the existing genetic diversity worldwide, including the unexplored diversity of traditional landraces and crop wild relatives (Figure 1H), for the identification of traits affected by artificial selection during domestication^{156–158}.

Underutilised crops, which are not grown and traded globally, such as sorghums¹⁵⁹ and millets¹⁶⁰, are often adapted to arid and semi-arid regions that limit the productivity for other crops, offering alternative solutions for food production during climate change^{161–164}. While underutilised crops often fulfil a valuable niche on-farm as ‘insurance crops’, they receive little attention in research, and the molecular mechanisms that confer stress tolerance in these crops remain poorly understood¹⁶⁵. Trait-linked marker genes involved in drought adaptation were identified in sorghum^{166,167} but similar research is lacking for other underutilised crops. Many such crops contain antinutrient factors, which currently limits their more widespread adoption^{159,160}. However, grain legumes, such as lablab¹⁶⁸, groundnut, chickpea, pigeon pea¹⁶⁹ and cowpea¹⁷⁰, are well adapted to tropical and subtropical environments with the added benefit of being able to grow on nutrient-poor soil due to their nitrogen-fixing capability^{171–174}.

More than 1,750 genebanks conserve about 7.4 million samples of diverse crops, including not only cultivars and landraces of major crops, but also underutilised crops and wild relatives^{157,175–178}. However, only a small proportion of the germplasm kept in these banks has been used in plant breeding programs, and even a smaller fraction has been used to develop

stress-resilient crops¹⁷⁹. Most accessions are poorly characterised, with frequent duplications within and between collections, and often incomplete passports lacking essential information such as phenotypic, physiological and agronomic data, or links to other databases compiling this information¹⁵⁷. Therefore, it is challenging for breeders to mine genebank diversity¹⁵⁶, particularly in the case of complex polygenic traits, such as abiotic stress tolerance, which are controlled by multiple non-allelic genes and show complex non-Mendelian inheritance (Table 1). Genomics, automated high-throughput phenotyping platforms, and remote monitoring of physiological traits in the field could speed up the identification of novel genetic resources and the molecular characterization of genebanks, allowing the mobilization and exploitation of genetic diversity in the identification of climate tolerance traits^{157,180} (Figure 3).

The power of breeding assisted by high-throughput technologies has led to few successes in identifying drought and heat tolerance traits in chickpea, groundnut and pigeon pea^{149,150}. A quantitative trait loci (QTL) hotspot was identified after high precision phenotyping in an intraspecific recombinant inbred line population (ICC 4958 × ICC 1882), explaining up to 58% of the phenotypic variation for a variety of drought-related traits¹⁸¹. Fine mapping identified 12 genes^{182,183} within the QTL region, including the transcription factor *CaTIFY4b*, conferring drought tolerance when expressed in *Medicago truncatula*¹⁰⁴. Marker-assisted backcrossing enabled the transfer of the QTL hotspot region from ICC 4958 into diverse genetic backgrounds, resulting in the development and release of improved chickpea varieties in India and Ethiopia¹⁸⁴. The introgression lines obtained by fast-track transfer of the QTL hotspot into JG 11 (a leading chickpea variety in India) showed greater rooting depth, better root length density and greater root dry weight as compared with both recurrent and donor parents¹⁸⁵. Transfer of the same genomic region into three elite chickpea cultivars, Pusa 372, Pusa 362 and DCP 92-3, using a similar approach¹⁸⁴ resulted in the development and release of multiple drought-tolerant lines, such as Pusa Chickpea 10216, Pusa Chickpea 4005 (BG 4005), Pusa Chickpea Shyam and IPC L4-14 (IPCMAS-1). Other collaborative efforts led to the identification of drought-tolerant varieties, such as Geletu and Girar released in Ethiopia, with 15% and 22% yield superiority over popular chickpea varieties¹⁸⁶. Similarly, advanced lines developed by the introgression of the QTL hotspot into popular varieties showed promising results in multi-location trials in Kenya, and are selected for possible release in Tanzania¹⁴⁹.

In another example, candidate gene-based association analysis using whole-genome sequencing of 292 diverse genotypes identified genes influencing seven drought-responsive component traits in pigeon pea¹⁶⁹. The most promising and superior haplotypes displayed favourable phenotypes for five component drought traits, such as plant weight, fresh weight, turgid weight, dry weight, and relative water content. In the case of groundnut, a bi-parental mapping study identified sixteen major main-effect QTLs for drought tolerance traits (10.0–3.9% phenotypic variation explained, PVE)¹⁸⁷. Genome-wide association analysis revealed two important SNP clusters on chromosomes Ah10 and Ah18, where 11 significant associations, explaining 0.07% to 0.26% of the phenotypic variance, were found (M.K. Pandey, unpublished). More recently, another

QTL mapping study reported three promising clusters on chromosomes Ah03, Ah12, and Ah20, harbouring more than half of the major QTLs for various agronomic, phenological and physiological traits, explaining phenotypic variance under heat stress¹⁸⁸.

Optimal contributions selection (OCS)¹⁸⁹ has been applied to crop breeding to optimise future genetic gain based on pedigree and/or genomic relationship information^{190–192}. A model of crop breeding with OCS resulted in improvements in heat stress tolerance, together with other commercial traits, while minimising the rate of population inbreeding¹⁸⁹. Its usefulness was verified recently in the field, where high rates of genetic gain for multiple traits were achieved in a canola breeding program in Australia and Canada¹⁹³. Future pathways towards adaptation of crops to climate change include a look-ahead algorithm for genomic selection, which provides another pathway towards rapid and sustainable genetic gain in multiple traits¹³, or prediction-based crop redesign through the integration and interpretation of big data (-omics and genotype-by-environment data) with artificial intelligence (machine and deep learning)¹⁹⁴.

In summary, leveraging genetic diversity and genomic technologies can greatly improve the ability to develop climate resilient crops (Table 1). Whatever method is used to optimise future crop breeding, it is essential to incorporate multiple stresses and developmental traits into the selection index to protect future potential genetic gains in yield, quality and disease resistance during climate change (Box 1).

Conclusions

In this review, we have highlighted the challenges of enhancing crop resilience to climate change (Box 1 and Table 1). A holistic approach encompasses whole plant physiology, signalling, metabolic and molecular mechanisms, optimizing cropping systems and potential genetic solutions to breed tolerant crops¹⁹⁵. It is implicit in our approach that genetic or other interventions to enhance crop tolerance must encompass considerations of sustainable intensification and the needs of society. Social licence and harmonised governance are essential to reap the benefits of these technologies at a global scale^{10,196}.

Evidence summarised in this review shows how the soil microbiome and crop management practices can help to improve crop productivity in challenging environmental conditions¹⁴⁸. It is possible to select varieties with deep root systems, efficient water use, optimised stomatal density, early maturity, and greater stress tolerance to reduce the risk of crop failure in challenging growing conditions^{13,49}. Similarly, genotypes with good stand establishment can improve performance in areas prone to drought and heat through reduced evaporation and soil heating^{197–200}.

Plant breeding programs can deliver improved crop varieties and minimise the risks posed by unpredictable extreme weather events (Table 1). The integration of genomics and phenomics combined with efficient database management and modelling could be used to unlock the genetic potential of gene bank germplasms^{157,180} and accelerate breeding of novel climate-resilient crops (Figure 3). Adoption of new technologies is essential to generate high-quality data for faster decision-making and policy development (Table 1). Although gene editing

approaches are increasingly used²⁰¹ (Figure 1I,J), the current low efficiency in homology-directed repair in plants using CRISPR approaches and the challenges in regulation, customer perception and acceptance restrict applications in plant improvement programs²⁰².

The participation of collaborative interdisciplinary teams (as part of initiatives such as PlantACT!, www.plant-act.org/) is essential to achieve the translation of basic knowledge into plant breeding and biotechnological approaches²⁰³. In cooperation with society and political decision-makers, research knowledge can be used to leverage commitment at the level of individuals, institutions, and research funding agencies. Open access to scientific information for representatives of the political world, society and stakeholders is of utmost importance and public engagement approaches including the arts can facilitate communication between these parties (Figure 1).

The present review was developed between individuals from different disciplines, institutions and countries united under the umbrella of the World University Network (WUN) Research Development Fund (RDF) program ‘Addressing the impact of heatwaves and drought on food security’. The team of researchers encompassed expertise in crop physiology, pathology, breeding, molecular biology, agronomy, atmospheric chemistry and pollution, crop-climate modelling, and food safety, who are not all included in this review. This review represents a call for the research community to work collaboratively in developing stress-resilient crops and sustainable systems for their production, delivery, and safe consumption. Although many questions remain unaddressed (Box 1), significant progress is being made in key areas (Table 1), revealing potential solutions that can only be implemented with the concerted effort of the research community in liaison with policy and regulatory entities in the upcoming years.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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