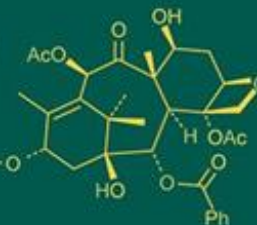
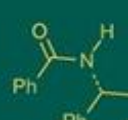
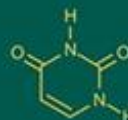
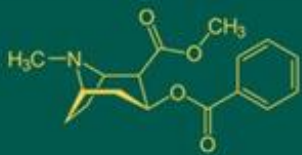


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Lavi Dabas

Research Scholar, Department of Genetics and Plant Breeding, College of Agriculture, Sardar Vallabhbhai Patel University of Agriculture and Technology, Meerut, Uttar Pradesh, India

Shivendra Singh

Research Scholar, Department of Genetics and Plant Breeding, College of Agriculture, Acharya Narendra Deva University of Agriculture and Technology, Ayodhya, Uttar Pradesh, India

Ehsas Pachauri

Research Scholar, Department of Genetics and Plant Breeding, College of Agriculture, Punjab Agricultural University, Ludhiana, Punjab, India

Gaurav Kumar

Research Scholar, Department of Genetics and Plant Breeding, College of Agriculture, Sardar Vallabhbhai Patel University of Agriculture and Technology, Meerut, Uttar Pradesh, India

Soyal Kumar

Research Scholar, Department of Genetics and Plant Breeding, College of Agriculture, Sardar Vallabhbhai Patel University of Agriculture and Technology, Meerut, Uttar Pradesh, India

Harshit Tomar

Research Scholar, Department of Vegetable Science, College of Horticulture, Sardar Vallabhbhai Patel University of Agriculture and Technology, Meerut, Uttar Pradesh, India

Corresponding Author:

Lavi Dabas

Research Scholar, Department of Genetics and Plant Breeding, College of Agriculture, Sardar Vallabhbhai Patel University of Agriculture and Technology, Meerut, Uttar Pradesh, India

Breeding for Heat Stress Tolerance using Multi-Omics Approaches

Lavi Dabas, Shivendra Singh, Ehsas Pachauri, Gaurav Kumar, Soyal Kumar and Harshit Tomar

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Abstract

The increase in heat wave frequency, severity and duration in response to global warming is recreating potential food security and agricultural production challenges around the world. Relationships between heat stress and stunted growth, development, reproductive success, and yield are extremely close, and especially detrimental during occurrence, as it affects physiological, biochemical, and molecular processes of plants, particularly when in blooming and grain filling stages. Conventional breeding efforts have produced heat-tolerant cultivars, but results have been limited due to the polygenic nature of heat tolerance and an important genotype x environment interaction. The ability to characterise heat stress adaptation-related genes, transcripts, proteins, metabolites, epigenetic alterations, and phenotypic characteristics has revolutionised plant breeding thanks to recent breakthroughs in omics technology. Transcriptomics defines dynamic networks of gene expression which are involved in stress responses, and genomics simplifies identification of candidate genes and molecular markers and the identification of quantitative trait loci. Proteomics, metabolomics and the analysis of metabolic changes, protein regulation and enzymatic activities which help to maintain cells that are "not too hot to live" could be beneficial. Epigenomics is used to explore inherited regulatory pathways leading to stress memory and adaptation, as opposed to high throughput phenomics, which enables heat tolerance to be measured across a wide range of genotypes in a rapid, accurate and non-destructive manner. By combining these multi-omics datasets with systems biology, AI, and machine learning, researchers have gained insights into several critical regulatory pathways and made much progress in the field of genomic prediction as well as precision breeding methods. Moreover, genome editing, speed breeding, and multi-omics offer unprecedented opportunities to develop new, improved crop varieties that are better equipped for a changing climate and better able to yield more crops under the same weather conditions. This review aims to present a brief summary of the recent advances in the field of multi-omics techniques for investigating the mechanisms of responses to heat stress. It then explores how these approaches have been applied to cultivar improvement; the challenges associated with bringing data into a cultivar improvement program and into practice; and then presents some suggested future plans for a sustainable breeding program to help support worldwide food security in the face of climate change. Refers to related terms, such as heat stress, metabolomics, proteinomics, transcriptomics, phenomics, artificial intelligence, plant breeding, climate resilience, and systems biology.

Keywords: Heat stress, Global warming, Climate change, Food security, Plant breeding

Introduction

Heat Stress in Plants

Due to the increased rate of global warming, one of the most harmful abiotic stresses for agricultural output worldwide – heat stress – is becoming more prevalent. A number of studies [Hall (2001)^[1]; Wahid *et al* (2007)^[2]; Bitra and Gerats (2013)^[3]] indicate food security is at odds with rising frequency, intensity and duration of heat waves. High temperatures upset many physiological, biochemical and molecular processes, such as photosynthesis, respiration, membrane integrity, enzyme activity, reproductive development, among others. Plants are organisms with adaptive processes that are developed as a result of stress in order to help them survive in high-temperature environments.

These include: osmotic adjustment, antioxidant defence, sensing, signal transmission, transcriptional control and heat shock protein production (Vierling, 1991; Kotak *et al.*, 2007) [4, 5].

Definition

Heat Stress in plant refers that during prolonged exposure to high temperature, the plant condition deviates from their optimum growth temperature and causes deterioration in physiological, biochemical and molecular processes which becomes irreparable (Wahid *et al.*, 2007) [2].

Heat stress is a longer time exposure than heat shock either to a high level or, more often, a fluctuating or constant level, and has a negative effect on plant development and yield; while heat shock is a short term exposure to extremely high temperature(s). The threshold temperature depends upon the environmental factor, developmental stage and the species. Thermotolerance is induced at temps. 10–15 above the optimal temperature for development, which causes damage to the cells (Vierling, 1991; Hasanuzzaman *et al.*, 2013) [4, 6]. Heat stress can cause reduced crop yield and results in protein denaturation, destabilisation of membranes, metabolic imbalance, retardation of reproductive development and excessive production of reactive oxygen species (ROS) (Kotak *et al.*, 2007; Bitá & Gerats, 2013) [5, 3].

Types of Heat Stress

Acute Heat Stress

Chronic heat stress occurs when plants are exposed to a high heat for an extended duration (minutes to hours). They often result in such conditions during heat waves or periods of skyheralding intense radiation from the sun. Rapid increase in temperature will result in unfolding of proteins, breakage of membranes, oxidative stress, inhibition of photosynthesis and increased cell death. Plants respond to high temperature by rapidly inducing heat shock factors (HSF) and synthesizing heat shock proteins (HSP) that help regulate the stability and equilibrium of proteins within the cell (Vierling, 1991; Kotak *et al.*, 2007) [4, 5].

Chronic Heat Stress

Chronic heat stress can be caused by exposure to slightly higher temperatures for long periods of time (days or weeks). Over time, metabolic processes, morphology, and reproductive maturation are all impacted by chronic heat stress, in contrast to acute stress. A prolonged exposure to high temperature reduces growth of leaves, chlorophyll content, nitrogen uptake, biomass production and efficiency of photosynthesis, as well as senescence and grain filling length, (Wahid *et al.* 2007; Hasanuzzaman *et al.* 2013) [2, 6]. Acclimation is a process in which plants adapt to the stress they have experienced by changing the way they function and use their metabolism but over time their ability to adapt is not as efficient.

Terminal Heat Stress

Terminal heat stress is caused by high temperatures at the end of the crop's cycle when it is in the reproductive and grain filling stages. It commonly occurs during periods of high temperature during late growth stages of winter crops like mustard, chickpea, wheat. Terminal heat stress has negative effects on grain filling time, assimilate translocation, starch synthesis, grain size, seed weight, and grain yield at harvest. Terminal heat stress is considered to be one of the most economically problematic types of agriculture heat stress as reproductive organs are particularly sensitive to heat stress (Hall, 2001; Wahid *et al.*, 2007) [1, 2].

Critical Growth Stages Affected by Heat Stress

The sensitivity to heat stress also differs greatly as the plant grows, typically being highest at the reproductive phase.

Germination

High temperatures during germination period reduce germination percentage, delay time of radicle emergence, decrease the activity of hydrolytic enzymes and prevents

mobilization of stored reserves for early seedling development (Hasanuzzaman *et al.* 2013) [6]. Heat stress will also reduce plant stand, inhibit seedling establishment, damage membranes, and increase oxidative damage.

Vegetative Stage

In vegetative growth heat has an inhibitory effect on leaf expansion and stem elongation, on the formation of chlorophyll and on root development. Under heat stress, the carbon consumed for respiration takes a larger share of the fixed carbon, hence biomass staying will be lower. As a response to stress, plants often undergo adaptive processes like rolling the leaves, adjusting the leaf angle, improving water evaporation and other processes to keep cell homeostasis in check (Wahid *et al.*, 2007; Bitá & Gerats, 2013) [2, 3].

Flowering

Flowering is one of the most susceptible stages of growth to heat. Hot weather causes distortion of the developing flowers during the process of flower initiation, anther development, meiosis and pollen maturation, which all affect the fertility of flowers. Hot weather affects the fertility of flowers by interfering with the process of flower initiation, anther development, meiosis and pollen maturation, resulting in increased floral abortion. Heat stress during anthesis, even for a short period of time, can drastically lower grain yield and number of grains produced (Hall, 2001; Bitá & Gerats, 2013) [1, 3].

Pollination

Pollen viability, pollen germination, pollen tube growth and fertility are reduced by heat stress. Male reproductive tissues are more sensitive than female tissues, because the development of pollen demands severely coordinated cellular/metabolic processes. Overexposure to high temperatures can often result in pollen sterility, lower seed-set and higher spikelet sterility in cereals like wheat and rice (Barnabás *et al.*, 2008, Saini & Aspinall, 1982).

Grain Filling

High air temperatures in the grain filling period cause more leaf senescence, reduce grain filling time, inhibit the synthesis of starch as well as the moving of food from source to sink organs. This results in significant reductions in grain weight, grain quality and nutritional values. Heat stress in the terminal phase during grain filling is a significant factor contributing to the yield losses of cereals all over the world (Stone & Nicolas, 1995; Wahid *et al.*, 2007) [7, 2].

Physiological Effects of Heat Stress

Photosynthesis Inhibition

High temperatures are one of the first physiological processes to impact; photosynthesis. Heat stress harms and destabilizes photosystem II (PSII), harms thylakoid membrane organization, decreases Rubisco activity, decreases chlorophyll content, and decreases carbon assimilation. With high temperatures, stomatal closure further reduces the availability of CO₂ for photosynthesis, which consequently reduces photosynthetic efficiency and biomass production (Berry & Björkman, 1980; Allakhverdiev *et al.*, 2008) [8, 9].

Increased Respiration

When the temperature is raised, metabolic reactions speed up and hence the respiration rate increases at an exponential rate. Respiration has been activated during stress, likening the supply

of ATP needed for stress adaptation and repair processes, but high respiration during a prolonged period will result in excessive consumption of carbohydrates, depletion of energy resources in the body, accelerated senescence of plant tissues and reduced biomass growth (Wahid *et al.*, 2007; Hasanuzzaman *et al.*, 2013) [2, 6].

Altered Water Relations

Transpiration demand and VPD rise with temperature, thereby leading to accelerated transpiration, loss of water and decreased water potential of the leaf. A reduction in the relative water content will result in a drop in turgor, oppress the cell to growth and cause stomatal closure, which in turn will decrease photosynthesis and growth. Heat stress often coincides with drought stress, further aggravating the negative physiological effects (Blum, 2011, Bita & Gerats, 2013) [10].

Membrane Stability

Hyperthermia causes increased permeability and fluidity of cell membranes, which function as its primary targets in a heat injury. Electrolytes are leaked, ions transported is disturbed and the integrity of the cell membrane is lost in the event of heat-induced lipid peroxidation. Therefore membrane thermostability is an important physiological parameter for screening heat-tolerant crop genotypes (Blum & Ebercon, 1981; Larkindale & Knight, 2002) [11, 12].

Pollen Sterility

The formation of pollen is one of the most sensitive reproductive stages in plants to temperature increase. Pollen wall formation, carbohydrate metabolism, function of the tapetum, and meiosis, all suffer disturbance at high temperatures, which in turn cause a decrease in viability and pollen fertility. Pollen thermotolerance is particularly important for breeding as raising it increases pollen sterility, which is associated with reduced seed-set and significant losses in cereal, legume and horticultural crops (Saini & Aspinall, 1982; Zinn *et al.*, 2010) [13, 14].

Molecular Basis of Heat Stress Response

Plants have an extraordinarily tightly organised molecular network that is able to sense, translate and react to an increased temperature. The heat stress leads to a disruption of cellular homeostasis through protein denaturation, membrane fluidization, oxidative damage and metabolic imbalance. Plants trigger many signaling pathways that involve calcium ions (Ca^{2+}), reactive oxygen species (ROS), mitogen-activated protein kinases (MAPK) network, phytohormone responses, transcription factors, and other heat shock proteins (HSPs). These intertwined pathways affect the expression of genes that respond to stress, the stability of proteins, the protection of cell structure, and thermotolerance (Vierling, 1991; Kotak *et al.*, 2007; Bita & Gerats, 2013) [4, 5, 3].

Heat Sensing and Signal Perception

Change in the fluidity of the plasma membrane, change in protein conformation, and change in cytoskeletal organisation are early events in the perception of heat stress. When the fluidity of the membrane is increased, these membrane associated protein receptors and ion channels are activated and intracellular signaling occurs very quickly. The unfolding of proteins into the cytoplasm and endoplasmic reticulum serve as another important signal to initiate the heat shock response. The

primary sensing events trigger downstream signaling pathways which control gene expression and protection of the cell (Saidi *et al.*, 2011; Mittler *et al.*, 2012) [15, 16].

Calcium (Ca^{2+}) Signaling

Calcium ions function as universal second-messengers in case of heat stress. During elevated temperatures, cytosolic Ca^{2+} levels temporarily rise as a result of the opening of Ca^{2+} -permeable channels. Ca is taken up by sensor proteins like calmodulin (CaM), calcium-dependent protein kinases (CDPKs) and calcineurin B-like proteins (CBLs) that later activate proteins involved in stress responses and signal transduction cascades. The regulation of antioxidant defense, heat shock protein expression and acclimation to stress are well known to be regulated by calcium signaling (Liu *et al.*, 2008; Reddy *et al.*, 2011) [17].

Reactive Oxygen Species (ROS) Signaling

During heat stress, excessive production of ROS can occur in the form of superoxide radicals ($\text{O}_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radicals ($\bullet\text{OH}$) and singlet oxygen ($^1\text{O}_2$). While excessive ROS cause lipid, protein and nucleic acid damage, a regulated increase in ROS is important as a signal to activate antioxidant enzymes, HSPs and defense related genes. As a result ROS play a dual role in thermotolerance: they can be detrimental or as mediators of signaling (Mittler *et al.*, 2004; Miller *et al.*, 2010) [18].

MAPK Signaling Pathway

The signal from membrane receptors that occurs upon cooling is carried to the nucleus via a series of phosphorylation of mitogen-activated protein kinase (MAPK), MAPKK and MAPKKK. MAPKs can control transcription factors that regulate genes that regulate antioxidant defence, hormone signalling, and the production of heat shock proteins. Also, MAPK signaling coordinates the activities of calcium and ROS pathways to create a integrated stress signaling network (Rodriguez *et al.*, 2010; Xu & Zhang, 2015) [19].

Hormonal Regulation

Plant hormones play important functions in regulating heat stress-induced physiological and molecular stress responses.

- Under heat stress, abscisic acid (ABA) rapidly beings to accumulate and increases stomatal closure, the activity of antioxidant enzymes and expression of stress responsive genes, and osmotic adjustment, all of which promote water conservation and thermotolerance (Vishwakarma *et al.*, 2017; Zhang *et al.*, 2006) [20].
- **Ethylene:** Involved in regulating heat stress-induced senescence, antioxidant metabolism and heat stress gene expression. Ethylene Producers promote thermotolerance however excess ethylene promotes aging during long stress conditions (Larkindale & Knight, 2002; Iqbal *et al.*, 2020) [12, 21].
- Increased temperatures can promote cell division, vascular development and reproduction growth, enhanced by Auxin. Heat stress induced alterations in the production and transportation of auxin affect root architecture and flowering (Quint *et al.*, 2016) [22].
- Fourthly, cytokinins maintain a constant level of chlorophyll and delay leaf senescence and ensure that photosynthesis continues to occur despite the increase in

temperature. Several different crop species have been successfully engineered to become more tolerant to heat and also to gain in cytokinin signaling (Hare *et al.*, 1997) [23].

- **Jasmonic acid (JA):** JA is involved in enhancing the antioxidant defense mechanisms, helps stabilization of cellular membranes and activates stress-responsive genes and consequently increases the potential for plant survival at high temperatures (Wasternack & Hause, 2013).
- An antioxidant named salicylic acid (SA) can increase photosynthetic efficiency in heat stressed plant and decrease the oxidative damage (Khan *et al.*, 2015) [24].
- **Brassinosteroids (BRs):** Brassinosteroids have been seen to mediate thermotolerance through regulation of photosynthesis, stability of membranes, antioxidant metabolism and heat-sensitive genes transcription (Vardhini and Anjum, 2015) [25].

Heat Shock Factors (HSFs)

The transcriptional responses to heat stress are controlled by Heat Shock Factors (HSFs). As a result of their connection with molecular chaperones, HSFs stay inactive under typical circumstances. Heat stress-induced up-regulation of heat shock factors (HSFs) can induce the transcription (transactivation) of heat stress genes by binding to heat shock elements (HSEs) present in the promoter regions. Of these, HSFA2 appears to be involved in development of thermotolerance and in storage of stress responses, whereas HSFA1 seems to primarily initiate the heat stress response (Nover *et al.* 2001; Scharf *et al.* 2012) [26, 27].

Heat Shock Proteins (HSPs)

Proteins are help kept from denaturing by molecular chaperones called heat shock proteins (HSPs) and will help them fold, refold proteins if they have been broken and facilitate protein degradation if they are completely damaged. Huge HSP families are made up of HSP100, HSP90, HSP70 and HSP60, and smaller HSP families only include proteins of this type. known as sHSPs). The speedy accumulation of thermotolerance at elevated temperatures represents one of the major common pathways to thermotolerance found in several plant species (Vierling, 1991; Wang *et al.*, 2004) [4, 28].

Antioxidant Defense System

Plants have a powerful antioxidant defence mechanism that includes both enzymatic and nonenzymatic antioxidants. In fact this defence system is only activated if ROS stores up. Antioxidants can be enzymatic and/or non-enzymatic, such as peroxidases (POD), glutathione reductase (GR), ascorbate peroxidase (APX), catalase (CAT) and superoxide dismutase (SOD). Mittler, 2002 and Gill and Tuteja, 2010 [29] showed that antioxidants are involved in maintaining the safety of cellular components from oxidative damage and maintaining redox homeostasis.

Osmolytes

When exposed to high heat, osmolytes (compatible solutes) like proline, glycine betaine, trehalose, soluble sugars, polyols and even some amino acids are stimulated to build up. Such compounds are able to neutralize reactive oxygen species (ROS), help stabilize membranes and proteins, and regulate the osmotic equilibrium of cells. In many crop species, improvement of their heat tolerance was achieved with

enhanced osmolyte accumulation (Ashraf & Foolad, 2007; Szabados & Saviouré, 2010) [30, 31].

Transcription Factors Regulating Heat Stress Response

Many heat-responsive genes are regulated by transcription factors which are able to bind to DNA and regulate gene transcription by integrating many signalling pathways.

- **DREB (Dehydration-Responsive Element Binding):** The DREB proteins lead to increased salt, heat, and drought tolerance by controlling the expression of abiotic stress-responsive genes, which contain the DRE/CRT promoter elements (Sakuma *et al.*, 2006) [32].
- WRKY transcription factors promote thermotolerance through the modulation of ROS homeostasis, hormone signalling and gene expression of defense-related genes (Rushton *et al.*, 2010) [33].
- Thirdly, NAC proteins regulate the expression of Anti-aging, antioxidant metabolism, osmotic regulation and Stress-response genes at high heat (Olsen *et al.*, 2005) [34].
- The fourth function of MYB transcription factors is in regulating secondary metabolism, antioxidant biosynthesis and accumulation of osmoprotectants in plants, which enhances their tolerance of heat stress (Dubos *et al.*, 2010) [35].
- The bZIP proteins regulate stress-adaptation related genes, antioxidant-defence genes, protein-protection genes, and are also involved in ABA-dependent signalling pathways, as suggested by Jakoby *et al.* (2002) [36].
- The basic helix-loop-helix (bHLH) transcription factors play roles in thermotolerance by regulating the balance of reactive oxygen species (ROS), the activation of hormone signalling and adaptation of the embryo to high temperatures (Pires & Dolan, 2010) [37].

A complex web of signalling molecules, phytohormones, transcription factors, molecular chaperones, antioxidants, and osmoprotectants works together in plants' molecular response to heat stress to keep cells from overheating and increase their chances of survival. In order to create heat-tolerant cultivars using cutting-edge multi-omics-assisted breeding techniques, it is necessary to have a firm grasp of these processes.

Conventional Breeding for Heat Tolerance

Heat-tolerant crop types have been vitally developed using traditional breeding methods to harness the genetic variation of domesticated and wild relatives. Processing crops before molecular breeding involved the primary plant improvement techniques of phenotypic selection, hybridisation and repeated selection under hot conditions. Despite the fact that heat tolerance is a complicated quantitative trait, influenced by numerous gene and a lot of environmental factors, several crops have been equipped with thermotolerance through conventional breeding, such as wheat, rice, maize, sorghum, soybean, chickpea and tomato (Hall, 2001; Reynolds *et al.*, 2010; Bitá & Gerats, 2013) [1, 38, 3]. Success of conventional breeding is reliant on genetic diversity, phenotyping tools, and good selection.

Germplasm Screening

A basic approach to breeding heat tolerance is to look for seeds with a diverse gene pool that have shown an extreme level of heat tolerance. Large germplasm collections, landraces,

conventional cultivars, breeding lines and exotic accessions are tested for heat stress, both natural and artificiated. Phenological and yield parameters are included, as are features like yield stability, chlorophyll content, stay-green characteristics, pollen viability, grain filling time and canopy temperature depression. By applying high throughput phenotyping and controlled environment screening, Blom (1988) ^[39], Reynolds *et al.* (2010) ^[38] and Pinto *et al.* (2010) ^[40] each suggest it will be more efficient to identify heat tolerant genotypes.

Utilization of Wild Relatives

The majority of elite cultivars do not contain any special heat tolerance genes, but these can be provided by wild relatives and crop progenitors. The increased antioxidant capacity, stronger roots, more stable membranes and reproductive tolerance to high temperatures are an example of how these species have evolved to thrive in a variety of different environments. With introgression of useful genes from the wild relatives of wheat, rice, tomatoes, barley, and chickpeas, heat tolerant versions of all have emerged. Where linkage drag occurs for desirable gene transfers (Tanksley & McCouch, 1997; Hajar & Hodgkin, 2007) [41, 42], backcrossing may be needed to restore the desirable gene combinations to the crop pedigree.

Hybridization

Hybridisation consists of crossing different genetic lines of parents and traits to improve the ways that complement each other may be used for parent selection, including early maturity, pollen fertility, canopy cooling, and heat stress grain yield. The segregated populations are subjected to strict selection over many generations to isolate the best recombinants. Hybrid breeding has proved very effective in a number of crops, such as vegetable crops like sunflower, sorghum, rice and maize plants, where hybrid breeding has been very well applied to improve stress tolerance and yield (Hallauer *et al.*, 2010; Acquaah, 2012) ^[43].

Selection

Selection is the basis for traditional breeding. Many different kinds of selection methods including bulk population breeding, pedigree selection and mass selection, recurrent selection and single-seed descent are used depending upon variety of crop and/or breeding objectives. Direct selection of the genotype under heat-stressed conditions has been found more effective than indirect selection; it allows the identification of useful genotypes which can carry out a larger production in higher temperatures. The physiological traits chlorophyll fluorescence, pollen viability, photosynthetic efficiency, canopy temperature and membrane thermostability are important traits for selection because of their close relation with heat tolerance (Blum, 1988; Reynolds *et al.*, 2010) ^[44].

Backcross Breeding

A frequent use of backcross breeding is to introduce some desirable heat tolerance genes into a top cultivar, and preserve the excellent agronomic background of the top cultivars. Repeat crosses of the elite with the young that get the desired characteristic will speed up the recovery of the elite genome further. This is a superb method in cases the place several genes or examined QTLs are known to help heat tolerance. Some of the traditional backcross breeding techniques have been effective, but are time-consuming due to the number of

generations needed for breeding and the rigorous phenotypic selection applied (Allard, 1999) ^[45].

Mutation Breeding

The process of mutation breeding is to expose seeds or plant tissues to physical or chemical stressors like gamma rays, X-rays or ethyl methanesulfonate (EMS) so as to produce new variations of the genetic material. The development of heat-tolerant varieties through induced mutations in various cereals including rice, wheat, barley and legumes has been successful in providing both agronomic as well as physiological advances. In instances where there is limited genetic difference, mutation breeding can be useful, but the screening of the induced mutants with desirable traits has to be very high because most of the mutations induced are not desirable (Ahloowalia *et al.*, 2004; Shu *et al.*, 2012) [46, 47].

Advantages of Conventional Breeding

The advantages of conventional breeding are that cultivars can be developed to withstand heat. As they harness natural variation, the outcome is generally accepted and non-regulatory problems don't exist because it's not transmitted through transgenic genes. The technique requires no complex molecular structures, is inexpensive, and has Developed a wide range of heat tolerant cultivars which are now grown commercially worldwide. Continuous recombination and selection of their desired agronomical traits and heat tolerance can be achieved. Both Acquaah (2012) ^[43] and Reynolds *et al.* (2010) ^[38] have concluded that traditional breeding is the genetic foundation of molecular breeding and multiomics approaches.

Limitations of Conventional Breeding

Even though traditional breeding has proven to be successful, the method has its limitations with regard to raising heat tolerance. The complicated polygenic characteristic of heat tolerance is controlled by many genes, each of which has a limited individual effect, and is heavily impacted by interactions between genes and the environment. Trait assessment is difficult to make in field situations due to heat stress that may occur at the same time as drought and other environmental difficulties, which make it unpredictable. It takes some time to produce and document a new variety, which can be as long as 8-12 years. In addition, the following problems arise which will decrease breeding efficiency: limited amount of genetic diversity within elite germplasm, linkage drag during introgression from wild relatives, and inability to accurately identify causative genes. To address these limitations, other approaches have been quickly introduced in addition to traditional breeding to improve the accuracy of selection: molecular markers, genome editing, genomic selection and multi-omics technologies (Collins *et al.*, 2008; Bita & Gerats, 2013; Varshney *et al.*, 2021) [48, 3, 49].

Transition to Multi-Omics Breeding

It is noted that traditional breeding has resulted in significant progress on enabling crops to adapt to high temperatures, but still more accurate and effective breeding techniques are needed to overcome the complexity. Due to recent advances in genomes, transcriptomics, proteomics, metabolomics, epigenomics and phenomics, numerous genes, regulatory networks, proteins, metabolites and phenotypic features associated with thermotolerance have been conclusively identified in a systematical way, which has radically changed

the way crop is developed. Thanks to these additional omics technologies, more opportunities than ever are available to accelerate the development of climate-smart crop varieties that can be more productive under global warming.

Multi-Omics Technologies for Heat Stress Tolerance Breeding

Multi-omics technologies has revolutionised plant breeding through the ability to use this for extensive characterisation of biological systems that control heat stress responses. Multi-omics on the contrary to the conventional breeding relies on phenotypic selection to identify thermotolerance-related genes, regulatory network, proteins, metabolites and physicochemical traits, incorporates all omics data into a single platform, and is not limited by practical difficulties. Multi-omics is not restricted by practical constraints, is not limited to the mere phenotypic selection and entails the integration of all omics data in a single platform. These additional datasets can accelerate application of precision breeding to accelerate the development of climate-resilient crop varieties and provide a comprehensive view on how plants are affected by high temperatures (Hasin *et al.*, 2017; Yang *et al.*, 2021; Varshney *et al.*, 2021) [50, 51, 49].

Genomics

Genomics' ability to detect genetic variation associated with heat tolerance needs to inform multi-omics assisted breeding. These technologies have enabled identification of the genes and/or chromosomal regions underpinning thermotolerance, such as whole genome sequencing (WGS), next generation sequencing (NGS), pan-genomics, and genome-wide association studies (GWAS), Quantitative trait locus (QTL) mapping, linkage analysis and genomic selection. For marker assisted selection (MAS) and genomic prediction, one use for molecular markers is for the identification of possible candidates for a candidate gene/allele. The candidate genes for heat shock response, antioxidant metabolism, membrane function, reproductive development and rice and maize have been very improved in wheat, rice, soybean, tomato and chickpea through breeding. Another benefit of genomic selection is that value for prediction of breeding values with genome-wide markers (GWAPV) is achieved, and the breeding value could be reduced as well due to reduced breeding cycles, respectively (Collard & Mackill, 2008; Varshney *et al.*, 2014; Crossa *et al.*, 2017) [52-54].

Transcriptomics

Transcriptomics is the postgenomics study on the expression patterns of all the genes in the genome in response to heat stress. Various types of sequencing including RNA-Seq, microarray, short RNA-Seq, single cell RNA-Seq and alternative splicing events have aided discoveries of gene regulatory networks, miRNA, lncRNA, and differentially expressed genes. Studies have demonstrated that heat shock proteins (HSPs), antioxidant enzymes, transcription factors (DREB, WRKY, NAC, MYB, bZIP and bHLH), and hormone-related genes are all significantly induced under high temperatures. Wang *et al.* (2009) and Liu *et al.* (2015) [55] have suggested that using transcriptome and genomic information could facilitate heat tolerance breeding, while Jha *et al.* (2019) [56] has reported that genomic and transcriptome data could be integrated to develop heat tolerance tomato seeds. This enables identification of potential genes and their specific functional confirmation

Proteomics

Proteomics affects the abundance of proteins, post-translational modification of proteins, enzyme activities, and protein-protein interactions that all impact plant response to heat stress. In this era, multiple platforms including 2-D gel electrophoresis (2-DE), liquid chromatography-tandem mass spectrometry (LC-MS/MS), isobaric tags for relative and absolute quantification (iTRAQ) and tandem mass tag (TMT) labelling have allowed for the identification of all heat responsive proteins. Under heat stress, molecular chaperones accumulate such as heat shock protein 70, 90, 100, miniature heat shock proteins (HSPs), antioxidant/enzymes involved in metabolism, photosynthetic proteins, and signalling molecules. Proteomic studies have improved understanding of cellular protection mechanisms and identified heat stress induced protein markers that can be applied to identify heat stress tolerance traits in crop breeding programmes (Kosová *et al.*, 2011; Wang *et al.*, 2017).

Metabolomics

Metabolomics experiments analyses metabolites that are low-molecule size and reflect the physiological status of the plants under heat stress. Analytical systems like gas chromatography-mass spectrometry (GC-MS), liquid chromatography-mass spectrometry (LC-MS), capillary electrochromatography (CEC) are used to analyze the acquired data. Nuclear magnetic resonance (NMR) spectroscopy and electrophoresis-mass spectrometry (CE-MS) provide for thorough characterisation of metabolic alterations caused by stress. Heat stress frequently induces accumulation of compatibility solutes like proline, glycine betaine, trehalose, raffinose, soluble sugars, amino acids, organic acids, polyamines, flavonoids and phenolic chemicals. Membrane stabilisation, osmotic adjustment, antioxidant defence, and cellular protection are all roles played by these metabolites. Many studies (Obata & Fernie, 2012; Arbona *et al.*, 2013; Kumar *et al.*, 2022) [57-59] have shown that metabolic indicators can be very useful for identifying heat-tolerant genotypes and the way the body reacts during stressful periods.

Epigenomics

Epigenomics is the science of studying changes in the expression of genes that are heritable but not due to changes in the nucleotide sequences. Chromatin remodelling, epigenetic alterations (such as DNA methylation, histone acetylation, and methylation), and non-coding RNA regulation are all brought about by heat stress. These changes not only change the chromatin accessibility but also the transcriptional activation of susceptible genes to stress. Significantly, epigenetic alterations aid in stress memory, allowing plants to better react to future heat stress. Recent research by Chinnusamy & Zhu (2009) [60], Lämke & Bäurle (2017), and Ashapkin *et al.* (2020) [61] reveals new possibilities in how epigenetic regulation can be leveraged for breeding crop plants with greater tolerance to climate change conditions via an epigenetic regulation pathway and targeted genome editing.

Phenomics

To be able to properly evaluate plant reactions under both controlled conditions and in the field, phenomics also involves high throughput phenotyping technology. Modern phenomics platforms acquire morphological, physiological and

biochemical parameters associated with heat tolerance using thermal, hyperspectral and RGB cameras as well as unmanned aerial vehicles (UAVs) and automated greenhouse systems and LiDAR. Canopy temperature, NDVI, Fv/Fm, stomatal conductance, plant architecture, biomass accumulation, growth dynamics and stay-green phenotype may be quickly evaluated in large breeding populations. Furbank and Tester (2011)^[62], Araus and Cairns (2014)^[63] and Yang *et al.* (2020)^[64] reported that high-throughput phenotyping has greatly improved phenotyping accuracy and is adopted with genomic and transcriptome analysis in precision breeding.

Ionomics

The focus in ionomics is studying the distribution of elemental homeostasis and the mineral nutrient content in plants. Of the essentials that are impacted by heat stress with respect to absorption, transportation, and distribution, some of the most notable elements are Ca, K, Mg, Zn, Fe, Mn, P, and Si. Ionic balance maintenance is necessary under temperature stress for enzyme activity, cellular signalling, antioxidant defence, osmotic management and membrane integrity. Several crop species have had ionomic features linked to thermotolerance and nutrient-use efficiency discovered using high-throughput elemental profiling with inductively coupled plasma-mass spectrometry (ICP-MS) and X-ray fluorescence spectroscopy (Salt *et al.*, 2008; Baxter, 2015) [65, 66].

Microbiomics

Whether the function of the plant microbiome (endophytic, phyllosphere and rhizospheric microbes) for better heat stress tolerance is non-ignorable more and more pieces of evidence are emerging. All of this serves to regulate gene expression in the presence of stress, nutrient uptake, phytohormones and antioxidant metabolism by the cooperation of the endophytic microorganisms, arbuscular mycorrhizal fungi (AMF) and beneficial plant growth-promoting rhizobacteria (PGPR). In recent years, progress has been made in understanding the complex plant-soil-microbiome interactions that contribute to thermotolerance through microbiome profiling, amplicon sequencing, and metagenomics. The new generation of studies on the symbiosis of plants and microbes through microbiome profiling, amplicon sequencing and metagenomics has shed light on the complex microbiota-plants-soil interactions which contribute to thermotolerance. One ecologically friendly solution to improve Crops climate change resistant is beneficial microbial populations use according Berendsen *et al.* (2012)^[67], Compant *et al.* (2019)^[68] and Niu *et al.* (2020)^[69].

Integration of Multi-Omics

The prominent benefit of multi-omics is the possibility of a systems-level knowledge of a heat stress response acquired by integration of multiple biological information. Combining the various disciplines (microbiomics, epigenomics, phenomics, transcriptomics, proteomics and genomics) will enable us to identify molecular pathways, protein networks, metabolites and phenotypes, which regulate the thermotolerance. The integration and understanding of these complex datasets have become easier thanks to the modern computational tools, coupled with AI, ML, and systems biology, which allow for the identification of candidate genes' faster, creation of biomarkers, and the possibility of breeding for a more precise purpose. The authors Hasin *et al.* (2017)^[50], Yang *et al.* (2021)^[51] and Varshney *et al.* (2021)^[49] predict that such approaches will

prove essential in producing novel crop varieties that will be resistant to climate change and sustain yields of agricultural products even as the global climate warms.

Integration of Multi-Omics for Heat Stress Tolerance Breeding

The innovations brought by the use of different omics technologies have turned the plant breeding approach from the so called gene-based approach to a framework based on systems biology that would allow to understand the complex molecular pathways of heat stress tolerance. Individual omics technologies only tell a part of the story as many different genes, proteins, metabolites, epigenetic modifications, etc. interact and modulate heat tolerance. To scientifically link plants with the heat stress challenges requires several existing knowledge areas like Microbiomics, Genomics, Epigenomics, Phenomics, Transcriptomics, Proteomics, and Metabolomics. All of the papers discussed by Hasin *et al.*, 2017^[50]; Misra *et al.*, 2019^[70] and Yang *et al.*, 2021^[51] conclude that integrated analyses increase the speed by which novel and climate-resilient crop varieties can be developed through the better accuracy with which candidate genes can be discovered, biomarkers can be identified and breeding decisions can be made.

Systems Biology Approach

Systems biologists use a variety of different biological data for a comprehensive understanding of the reaction of the cells during the heat stress. As an alternative to looking at certain genes or This approach is based on understanding the interaction between genes, transcripts, proteins, metabolites and the phenotype, rather than between the proteins and the genotype. The regulatory mechanisms and biological processes that govern thermotolerance may be more easily reconstructed with the use of computational modelling. Kitano (2002)^[71] and Rajasundaram & Selbig (2016)^[72] point out that the premise of systems biology could be employed to identify key molecular regulators and understand their roles in complex stress adaptation processes.

Multi-Omics Data Integration

Multi-omics data integration combines variations in the genome with the abundance of transcripts, abundance of proteins, metabolite accumulation, epigenetic changes and phenotypical measurements. It is a method that builds a connection between changes in the DNA sequence and then the reaction that occurs; therefore the causal link that the genotype will lead to the phenotype can be uncovered. Discovering new regulatory pathways involved in heat stress adaptation is made easier using integrated studies, which also increase the reliability of candidate gene identification when compared to separate omics techniques (Hasin *et al.*, 2017; Misra *et al.*, 2019) [50, 70].

Gene Regulatory Networks

A systems analysis of gene regulatory networks (GRNs) provides insights into the interactions between transcription factors that regulate the heat stress response and signalling molecules and downstream target genes. Heat Shock Factors (HSFs), DREB, WRKY, NAC, MYB, bZIP and bHLH transcription factors are coordinators of expression of numerous stress-responsive genes involved in antioxidant defence, osmotic adjustment and protein protection. Reconstructing regulatory circuits controlling thermotolerance and stress memory is made possible by integrating transcriptomic and epigenomic datasets (Scharf *et al.*, 2012; Zandalinas *et al.*, 2021) [27, 73].

Protein–Protein Interaction Networks

The interactions between proteins can lend insights into the functional relationship between the heat stress signalling proteins. At elevated temperatures, increased stability to protein homeostasis and integrity of the cell is maintained by interactions of heat shock proteins, molecular chaperones, antioxidants, kinases, phosphatases, AND transcription factors. The findings of both transcriptome and proteome can be combined for the identification of proteins which are involved in thermotolerance, that could be candidates for genome editing and/or molecular breeding (Wang *et al.*, 2017; Kosová *et al.*, 2011).

Metabolic Network Analysis

Extensive metabolic rewiring via carbohydrates, amino acids, lipids, phytochemicals (flavonoids), and phytohormones happens in response to heat stress. The integration of transcriptome, proteome, and metabolome information makes it possible to reconstruct metabolic pathways related to energy metabolism, osmotic adjustment and antioxidant defence. Metabolic indicators that differentiate between tolerant and susceptible genotypes are uncovered by these investigations, which in turn provide useful targets for crop development (Obata & Fernie, 2012; Arbona *et al.*, 2013) [57, 58].

Candidate Gene and Biomarker Discovery

The discovery of heat tolerance-related molecular biomarkers and high-confidence candidate genes is a key benefit of integrated multi-omics. Genes that appear in multiple data sets, like genomic, transcriptomic, proteomic, or metabolomic, have a higher probability of representing a significant biological function than genes which are discovered in a single data set. Heat-tolerant cultivars can also be rapidly created using these proven candidates for marker-assisted selection, genomic selection, functional genomics and genome editing (Varshney *et al.*, 2021; Yang *et al.*, 2021) [49, 51].

Artificial Intelligence and Machine Learning for Multi-Omics Integration

AI and ML have emerged as powerful tools for exploring large-scale, multi-omics datasets in recent years. The integration of various biological data, such as gene expression, genealogical relationships, or protein information, through algorithms like random forests, support vector machines, deep neural networks, and Bayesian models can be used to predict gene function, identify biomarkers, estimate breeding values, and classify genotypes for their resistance or susceptibility to stress. Challenges to selection accuracy, a short breeding cycle, and precision breeding in challenging environmental conditions can all be solved with the support of AI assisted genomic prediction (Libbrecht & Noble, 2015; Washburn *et al.*, 2021) [74, 75].

Applications in Heat Stress Breeding

This breakthrough of integrated multi-omics has significantly helped with the speed at which heat stress breeding can be done with crops like chickpeas, wheat, rice, soybeans, maize and tomatoes. Combined analysis has enabled us to identify candidate genes, heat responsive QTL, regulatory proteins, metabolites and physiological characteristics that play a role in thermotolerance. These discoveries have been combined with marker assisted selection, genomic selection, speed breeding, and genome editing to breed efficiently and better cultivars that

can sustain yield with increased temperatures (Crossa *et al.*, 2017; Varshney *et al.*, 2021) [54, 49].

Challenges and Future Opportunities

Although there have been a number of advances, integrating multiple omics datasets remain challenging. To manage large and diverse datasets, strong statistical models need to be in place, bioinformatics pipelines need to be streamlined, computing infrastructure needs to be state-of-the-art and experimental techniques need to be standardised. Data are often encoded in different formats, sampled at different times, affected by different environmental and other factors, provided by different analytical platforms, etc., making it hard to integrate and understand the biological data. Future studies are needed to combine single-cell omics, spatial transcriptomics, long-read sequencing, digital phenotyping, artificial intelligence-based analytics and cloud based databases to enhance the precision breeding and accelerate the production of heat resistant crops (Hasin *et al.*, 2017; Yang *et al.*, 2021) [50, 51].

Artificial Intelligence and Machine Learning in Multi-Omics-Assisted Heat Stress Breeding

Tailored on a massive scale, AI and ML have revolutionized the plant breeding sector, as they enable the study of large, complex and. Multi-omics systems that deliver datasets which are multidimensional. It is difficult to integrate environmental, phenomic, transcriptomic, proteomic and metabolomic data with genetic data—traditional statistical approaches often fall short. AI-driven algorithms can quickly and accurately streamline breeding decisions, reveal patterns, and predict complex properties. By harnessing the power of AI to integrate data from various sources, Libbrecht and Noble (2015) [74] and Washburn *et al.* (2022) also suggest that AI could be used to identify candidate genes, forecast heat tolerance in specific crops, and streamline agricultural practices for these.

AI-Based Multi-Omics Data Integration

This is because sophisticated computational methods and tools are needed to deal with the vast amount of data generated by modern breeding operations, which comes in many different forms. Some machine learning algorithms that use phenotypic/genomic/transcriptomic, proteomic and metabolomic data to identify heat tolerance biomarkers are Deep Learning (DL), Extreme Gradient Boosting (XGBoost), Random Forest (RF), Support Vector Machine (SVM), Artificial Neural Networks (ANN), and Random Forest (RF). These techniques are better suited to candidate gene prioritisation than traditional analytical techniques and are more able to reveal regulatory networks (Libbrecht & Noble, 2015; Eraslan *et al.*, 2019) [74, 76].

Genomic Prediction and AI-Assisted Breeding

To determine an individual's breeding value without doing lengthy field evaluations, genomic prediction integrates genome-wide genetic markers with AI algorithms. In cases of complex traits such as heat tolerance, the ability of machine learning algorithms to generate more accurate predictions is enhanced by their capacity to detect and recognize non-linear interactions between the genes and environmental factors. Genomic selection, with the assistance of AI, can help identify superior breeding lines earlier in the breeding cycle, reducing cycle time, phenotyping costs, and also enhancing genetic gains, as stated by Crossa *et al.* (2017) [54] and Montesinos-López *et al.* (2021).

High-Throughput Phenotyping and Computer Vision

AI has revolutionized computer vision and image processing, ushering in the era of high throughput phenotyping. With the help of deep learning models, based on image captured by an RGB camera, a thermal camera, a hyperspectral sensor, a drone, or a satellite platform, features such as canopy temperature, chlorophyll content, plant senescence, biomass, plant architecture, or stress symptoms can be quantified. These techniques enable rapid (Aurus & Cairns, 2014) and non destructive (Singh *et al.*, 2018) ^[77] screening of breeding population in large scale under heat stress.

Digital Twins and Predictive Breeding

By combining crop simulation models with artificial intelligence, digital twins can be created that simulate the development of a crop in a number of different settings. These models are used to predict the likely performance of crops under various climates, to determine ideal parent plants to utilize and to evaluate the effectiveness of breeding operations prior to implementation. Because it would be desirable to reduce the risk of heat stress (HS) in breeds in hot environments, using predictive breeding to select more heat-stress resistant genotypes could be time-saving for breeders and conserve livestock resources (Hammer *et al.* 2020) ^[78].

Challenges and Future Perspectives

While AI breeding has made remarkable advances, it still faces challenges in areas such as data quality, computing infrastructure, interpretability of the models, and the standardisation of multi-omics datasets. Emerging advancements in explainable AI, cloud computing, federated learning, and digital agriculture are expected to drive further progress towards model transparency and the use of AI in crop improvement. Use of AI with genome editing, speed breeding, robot bionics and precision agriculture will speed the development of heat resistant crop varieties (Varshney *et al.*, 2021; Washburn *et al.*, 2021) [49, 75].

Genome Editing and Functional Validation

Genome editing can precisely modify the genes involved in important agronomic traits which are influenced by the heat stress, and this has tremendous implications in plant breeding. Unlike conventional breeding, genome editing can focus on specific regions of the genome to improve cultivars' development, while maintaining the rapid speed. By using multi-omics techniques for identifying potential genes for enhancing thermotolerance, the approach to genome editing has been much extended (Jaganathan *et al.*, 2018) ^[79].

CRISPR/Cas Systems

CRISPR/Cas9 - Gen bewusst, so extrem convenient, extrem präzise, extrem effizient - has unwittingly emerged as the genome Editing tool of choice. It makes it possible to activate or delete particular genes or to modify their sequence in those genes whose function is connected with the heat shock proteins, antioxidants, hormones, heat stress signalling, or heat shock signalling. Along with the CRISPR/Cas9 system (Jinek *et al.*, 2012; Anzalone *et al.*, 2020) [80, 81], sophisticated systems like CRISPR/Cas12, base editing and prime editing also achieve superior accuracy of editing without off-target effects.

Functional Validation of Candidate Genes

In the context of breeding, candidate genes identified through genomics, transcriptomics and proteomics need to be functional

validated prior to their use in programs. A set of functional genomics approaches are routinely employed, such as T-DNA insertion mutants, RNA interference, overexpression, genome CRISPR mediated gene silencing, and viral induced gene silencing (VIGS) to gain insight into the response created by genes to heat stress. Validation studies have indicated that the genes for heat shock proteins (HSPs), heat shock factors (HSFs), DREB transcription factors, NAC proteins and antioxidant enzymes play an important role in making rice plants thermotolerant (Kotak *et al.*, 2007; Scharf *et al.*, 2012) [5, 27].

Applications in Crop Improvement

Genome editing has been successfully demonstrated in a range of crops to improve their tolerance to heat and other abiotic stresses, such as drought, flooding, heat, and high temperatures. Gene editing that regulates flowering time, pollen production, scavenging of reactive oxygen species, signalling of hormones, and maintaining protein homeostasis improved the survival and yield of the plants under hot conditions. New possibilities for the quick creation of cultivars that are resistant to climate change have emerged with the combination of genome editing, genomic selection, and speed breeding (Chen *et al.*, 2019; Gao, 2021) [82, 83].

Crop-Wise Progress in Multi-Omics-Assisted Breeding for Heat Stress Tolerance

Multi-omics technologies have enabled accelerated progression towards understanding the discovery of genes, proteins, metabolites, and pathways associated with traits across key crops, facilitated by genetic editing, marker-assisted breeding, and genomic selection, and led to the generation of heat-resilient cultivars. The extent of application is different across different crops, but there has been success (Varshney *et al.*, 2021; Yang *et al.*, 2021) [49, 51] in cereals, legumes, oilseeds, vegetables and fibre crops.

Wheat (*Triticum aestivum* L.)

Wheat production and quality are compromised if the plant suffers from severe heat stress at anthesis and grain filling. It has been revealed through genetic analysis that there are numerous QTLs involved in the Grain Weight, Chlorophyll Content, Stay Green traits and Canopy temperature depression. Transcriptomic analyses indicated that the expression of heat shock proteins (HSPs), heat shock factors (HSFs), DREB, nuclear factor kappa B (NF- κ) and WRKY transcription factors was all found to change with heat stress. Proteomic and metabolomic analyses identified a number of additional proteins involved in thermotolerance, including photosynthetic proteins, osmolytes and antioxidant enzymes. The results have paved the way for genomic selection and marker-assisted selection (MAS) to breed wheat cultivars with heat tolerance (Pinto *et al.*, 2010; Reynolds *et al.*, 2010; Varshney *et al.*, 2021) [40, 38, 49].

Rice (*Oryza sativa* L.)

Rice is most vulnerable to heat stress, but pollen sterility and spikelet abortion are signs of heat stress in this crop. Through multi-omics studies, the genes regulating the processes of flowering, pollen viability, glucose metabolism and detoxification of reactive oxygen species have been identified. The genome-wide association (GWAS) and RNA-Seq analysis have resulted in the discovery of several potential genes, including OsHsfA2d, OsHSPs and SNAC family genes related to thermotolerance. Jagadish *et al.* (2015) ^[84], Li *et al.* (2015)

[85] and Gao (2021) [83] have reported metabolomic studies that found that proline, sugars, and antioxidant metabolites are increased during heat stress, and that CRISPR/Cas-mediated editing has confirmed several genes that are responsive to heat.

Maize (*Zea mays* L.)

Pollen viability, kernel set, and grain production are all drastically reduced when maize plants are subjected to heat stress during tasseling and silking. Genetic mapping has identified a number of quantitative trait loci (QTLs) that control reproductive resistance to heat in the hot climate, plant canopy temperature, and bloom initiation time. Proteins linked to photosynthesis, energy metabolism, and antioxidant defence have been discovered via proteomic investigations, whereas heat-induced expression of heat-shock proteins (HSPs), calcium signalling components, and ABA-responsive genes has been uncovered through transcriptomic studies. Cairns *et al.* (2013) [86], Cooper *et al.* (2014) [87], determined that genomic selection and high throughput phenotype were used to increase the efficiency of breeding heat-tolerant maize hybrids.

Soybean (*Glycine max* L.)

During the blooming and pod development stages of soybeans, high temperatures have a significant impact on production. Genes associated in heat shock response, hormone control, antioxidant metabolism, and seed development have been discovered via multi-omics investigations. In the heat stress treatment conditions it was revealed that NAC transcription factors, DREB, HSFs and HSP70 were all higher expressed in the transcriptomic analysis. Metabolic studies indicate build-up of a series of osmoprotectants (proline, raffinose, flavonoids and others) which help provide thermotolerance. These are results that lend support to the notion that Genome Editing and Genomic-assisted breeding could assist soybeans in adapting more readily to warmer climates as proposed by Prince *et al.*, (2015) and Wang *et al.*, (2020).

Chickpea (*Cicer arietinum* L.)

Terminal heat stress is a frequent occurrence during reproductive development of the chickpea plant, leading to loss of flowers, reduced pod set and seed yield. In the genomic studies, Quantitative trait genes (QTLs) and candidate genes associated with pollen viability, quantity of seeds filled under hot conditions, and flowering time were identified. Transcriptomic studies have shed light on the function of proteins that suppress heat, nuclear anti-oxidant gen transcription factor (NAC) proteins, anti-oxidant enzymes and hormonal signalling pathways. The combination of genomes and phenomics has aided by making the process of identifying breeding lines more suitable for heat more efficient (Varshney *et al.*, 2013; Devasirvatham & Tan, 2018) [88, 89].

Tomato (*Solanum lycopersicum* L.)

During the blooming and fruit development stages, tomatoes are very susceptible to high temperatures. Heat stress has negative effects on fruit set, fruit quality and pollen viability. Using multi-omics research, we now understand the genes for the control of hormone production, reactions to heat stress, glucose metabolism and fertilisation. A proteomic analysis revealed increases in more HSPs, as well as antioxidant enzymes, while a metabolomic analysis identified increases in more carbohydrates, amino acids, secondary metabolites that protect cells. Bitá and Gerats (2013) [3] and Fragkostefanakis *et al.*

(2015) [90] identified the thermotolerance of tomato further with the aid of genome modifying of the heat-responsive genes.

Cotton (*Gossypium hirsutum* L.)

It is a common occurrence in cotton where heat stress causes a reduction in fibre quality and lint yields in boll development and blooming stage. Genomic- and transcriptome-based studies have identified genes important for pollen production, glucose metabolism, scavenging of reactive oxygen species and hot environment responses to hormones. Studies on proteonomics (modification changes to proteins) have revealed that heat modifies protein structure for protein molecules such as molecular chaperones, antioxidant enzymes and proteins involved in photosynthesis. These findings have made it easier to find molecular markers that can be used to develop cotton varieties that can withstand higher temperatures (Wang *et al.*, 2019; Snider *et al.*, 2010) [82, 91].

Brassica Crops

Seed production and quality of oil, in plants of *Brassica* species (mustard, rape), are drastically reduced in response to heat stress during flowering and seed filling. Multi-omics analysis has led to the identification of candidate genes that play a role in heat shock responses, antioxidant defence, lipid metabolism and flowering control. Incorporating genomics, metabolomics and transcriptomics

The Mayan plant responses to heat have been better understood and breeding for them to withstand heat is now easier thanks to research (Angadi *et al.*, 2000; Singh *et al.*, 2021) [92].

Millet

Millets (sorghum, pearl millet, foxtail millet, finger millet) are important climate-resilient crops due to their inherent heat and drought tolerant. Genes that enable plants to survive in hot climates, to conserve water, to resist attack by antioxidants, and to ensure the stability of their photosynthesis have been discovered. Generating the benefits of other cereal crops through improvements in their heat tolerance has been demonstrated in research with millets (Varshney *et al.*, 2021; Muthamilarasan & Prasad, 2021) [49, 93].

Comparative Perspective

Comparative multi-omics analyses of thermotolerant crops have identified various conserved mechanisms underlying toleration, such as Biosynthesis of heat shock factors (HSFs) and heat shock proteins (HSPs), calcium signalling, detoxification of reactive oxygen species (ROS), and accumulation of compatible osmolytes like proline and glycine betaine. It is important to employ accepted methods, however, for the species involved as mammals can respond differently to these depending on the developmental needs and regulation of various crops. Furthermore, the amalgamation of Multi-omics, Artificial Intelligence, Genomic Selection, and Genome Editing is expected to speed up the crop development for increased heat tolerance under future climatic scenarios (Yang *et al.*, 2021; Varshney *et al.*, 2021) [51, 49].

Success Stories of Multi-Omics-Assisted Heat Stress Breeding

The use of multi-omics technology has greatly sped up the process of finding heat tolerance genes and incorporating them into crop breeding initiatives. Stable QTLs and candidate genes regulating canopy temperature, stay-green characteristics, and grain filling have been discovered in wheat using genomic

mapping and transcriptome investigations. This has enabled marker-assisted selection of heat-tolerant cultivars to be achieved (Reynolds *et al.*, 2010) ^[38]. Genomes and transcriptomics have allowed researchers to discover rice genes, including OsHsfA2d and SNAC as well as several HSP genes. These genes are also linked to improvements in reproductive thermotolerance and maintaining grain production at high temperatures (Jagadish *et al.*, 2015) ^[84]. The use of genomic prediction and high throughput phenotyping (HTP) has improved the selection of hybrids for reproductive resilience under heat stress in maize (Cairns *et al.*, 2013) ^[86].

Genome editing has been used to validate a number of genes found in multi-omics studies that are related to temperature. CRISPR/Cas technology has been applied to thermotolerate several crops such as tomato, rice, and others (Gao, 2021) ^[83]. Likewise, by using the proteomic and metabolomic approaches, early selection has become more feasible in breeding programs to find chemical markers associated with heat tolerance. The genomic, phenomic approaches, along with AI and speed breeding approaches have speeded up breeding cycles and improved accuracy in the selection process (Crossa *et al.*, 2017; Varshney *et al.*, 2021) [54, 49].

The above accomplishments demonstrate that selective breeding has transitioned from natural selection to knowledge-based breeding with the help of multi-omics approaches. Continued

The development of genome edited crops that can remain resilient to the impacts of climate change and ensure food security on a global scale is dependent upon planting together genome editing, computational biology and modern omics technologies.

Conclusion

With climate change, it becomes increasingly common and is a potential risk to good agricultural output, affecting food production and supplies on a global scale. Heat stress has negative effects on plant development, physiology, reproduction and yield that occur through several cellular, molecular and biochemical pathways. Traditional breeding methods have helped create heat-tolerant varieties, but they are limited in their advancement due to factors such as the

quantitative aspect of thermotolerance, robust interactions between genotype and environment, and long breeding cycles. The era of multi-omics technologies has started, which has offered insights into the molecular and genetic basis of response to heat stress in crop development. A wide variety of genomic, transcriptomic, proteomic, metabolic, epigenetic, phenomenological, ionic, and microbiomic approaches have made it possible to pinpoint potential thermotolerance-related genes, regulatory networks, proteins, metabolites, and physiological features. The integration of these omics data by applying systems biology, artificial intelligence and machine learning methods has improved the accuracy of the identification of these genes, as well as the genomic prediction, identification of markers and decision on breeding. Additionally, new varieties of crops are emerging that also have traits suited to hot climate, such as tolerance to increased temperatures, due to the innovations on multi-omics, genome editing technology, genomic selection, high-throughput phenotyping, and speed breeding. Despite recent progress, integration of separate datasets from the different omics technologies, harmonisation of laboratory dispatches, large-volume biological data handling and the translation of laboratory results into field applications remain a problem. Future studies combining precision genome editing, single cell and spatial "omics", digital phenotyping and AI-based prediction modelling by pangenomics will improve understanding of the regulatory networks that control heat tolerance. The implementation of multi-omics research into real breeding outcomes means that the close collaboration of plant breeders, molecular biologists, bioinformaticians, physiologists and computer scientists is essential.

Precision breeding is a radical transformation of crop improvement approaches as it is based on knowledge-driven rather than the phenotypic selection system. The current efforts in sustaining agriculture and ensuring long-term global security in food and nutrition in the context of the rising challenge of climate change can be realised by sustaining the development of the omics technologies and their application in contemporary breeding practices. These will be directed towards breeding heat-tolerant high yielding and climate-smart crops.

Table 1: Representative case studies on breeding for heat stress tolerance using multi-omics approaches

Case No.	Crop	Omics Approach	Target Trait	Major Finding	Breeding Significance	Reference
1	Rice	Genomics (QTL mapping)	Spikelet fertility	qHTSF4.1 identified for reproductive-stage heat tolerance	Marker-assisted breeding	Ye <i>et al.</i> (2012)
2	Rice	GWAS	Grain yield under heat	Multiple SNPs associated with heat tolerance identified	Genomic selection	Lafarge <i>et al.</i> (2017)
3	Rice	Transcriptomics	Heat-responsive genes	Upregulation of HSP70 and HSF genes	Candidate gene discovery	Mittal <i>et al.</i> (2012)
4	Wheat	GWAS	Grain filling	Stable MTAs detected across environments	Marker-assisted selection	Juliana <i>et al.</i> (2019)
5	Wheat	Transcriptomics	Flag leaf heat response	Heat shock proteins strongly induced	Molecular breeding	Liu <i>et al.</i> (2015) ^[55]
6	Wheat	Proteomics	Protein stability	Increased accumulation of HSPs and antioxidant enzymes	Stress-resilient cultivar development	Kosová <i>et al.</i> (2011)
7	Maize	QTL mapping	Grain yield	Major QTLs identified on chromosomes 3 and 8	Marker-assisted breeding	Cairns <i>et al.</i> (2013) ^[86]
8	Maize	RNA-Seq	Leaf heat tolerance	Differential expression of transcription factors	Gene discovery	Frey <i>et al.</i> (2015)
9	Maize	Metabolomics	Photosynthetic efficiency	Proline and raffinose accumulated under heat	Biomarker-assisted selection	Obata <i>et al.</i> (2015)
10	Tomato	Transcriptomics	Pollen viability	HsfA2 highly induced during heat stress	Hybrid breeding	Fragkostefanakis <i>et al.</i> (2015) ^[90]
11	Tomato	CRISPR + Genomics	Thermotolerance	Gene editing improved heat tolerance	Precision breeding	Li <i>et al.</i> (2018)

12	Soybean	GWAS	Seed yield	Significant SNPs associated with canopy temperature	Genomic selection	Dhanapal <i>et al.</i> (2018)
13	Soybean	Transcriptomics	Heat-responsive genes	Enhanced expression of HSP20 family	Candidate genes identified	Wang <i>et al.</i> (2018)
14	Chickpea	RNA-Seq	Flower retention	Heat-responsive transcription factors identified	Climate-resilient breeding	Barmukh <i>et al.</i> (2022)
15	Chickpea	Metabolomics	Heat adaptation	Increased sugars and amino acids under stress	Metabolic biomarkers	Khan <i>et al.</i> (2019)
16	Brassic napus	Proteomics	Seed development	Differential abundance of stress proteins	Heat-resilient hybrid development	Wang <i>et al.</i> (2020)
17	Cotton	Transcriptomics	Boll retention	Heat-responsive genes identified	Candidate gene validation	Li <i>et al.</i> (2020)
18	Sorghum	GWAS	Grain yield	Stable genomic regions controlling thermotolerance	Genomic prediction	Mace <i>et al.</i> (2019)
19	Pearl millet	Genomics	Terminal heat tolerance	Heat-tolerant genomic regions mapped	Marker-assisted breeding	Yadav <i>et al.</i> (2012)
20	Groundnut	Transcriptomics	Reproductive-stage tolerance	Differential gene expression associated with heat tolerance	Gene discovery	Kumar <i>et al.</i> (2021)
21	Common bean	Metabolomics	Membrane stability	Compatible solutes accumulated during heat stress	Physiological marker identification	Porch <i>et al.</i> (2020)
22	Arabidopsis	Epigenomics	Thermomemory	DNA methylation regulated stress memory	Epigenetic breeding	Lämke & Bäurle (2017)
23	Rice	Integrated multi-omics	Grain quality	Combined genomics and metabolomics improved candidate gene identification	Multi-omics-assisted breeding	Yang <i>et al.</i> (2021) ^[51]
24	Wheat	Multi-omics	Heat adaptation	Integration of transcriptomics and proteomics identified stress pathways	Systems breeding	Kumar <i>et al.</i> (2023)
25	Multiple crops	Multi-omics + AI	Climate resilience	Artificial intelligence integrated omics datasets for genomic prediction	Next-generation breeding	Varshney <i>et al.</i> (2024)

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