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## Heat-tolerant maize for rainfed hot, dry environments in the lowland tropics: From breeding to improved seed delivery



Pervez H. Zaidi<sup>a,\*</sup>, Madhumal Thayil Vinayan<sup>a</sup>, Sudha K. Nair<sup>a</sup>, Prakash H. Kuchanur<sup>b</sup>, Ramesh Kumar<sup>c</sup>, Shyam Bir Singh<sup>c</sup>, Mahendra Prasad Tripathi<sup>d</sup>, Ayyanagouda Patil<sup>b</sup>, Salahuddin Ahmed<sup>e</sup>, Aamir Hussain<sup>f</sup>, Atul Prabhakar Kulkarni<sup>a</sup>, Passang Wangmo<sup>g</sup>, Mitchell R. Tuinstra<sup>h</sup>, Boddupalli M. Prasanna<sup>i</sup>

<sup>a</sup> International Maize and Wheat Improvement Center (CIMMYT), Hyderabad 502324, India

<sup>b</sup> University of Agricultural Sciences, Raichur 584104, Karnataka, India

<sup>c</sup> ICAR-Indian Institute of Maize Research, Ludhiana 141001, Bihar, India

<sup>d</sup> National Maize Research Program, Rampur, Chitwan 44200, Nepal

<sup>e</sup> Bangladesh Wheat and Maize Research Institute, Dinajpur-5201, Bangladesh

<sup>f</sup> Maize and Millet Research Institute, Yusafwala, Sahiwal 57000, Pakistan

<sup>g</sup> Agriculture Research and Development Centre, Wengkhari 43001, Bhutan

<sup>h</sup> Institute of Plant Sciences, Purdue University, West Lafayette, IN 47906, USA

<sup>i</sup> International Maize and Wheat Improvement Center (CIMMYT), Nairobi, Kenya

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## ABSTRACT

Climate change-induced heat stress combines two challenges: high day- and nighttime temperatures, and physiological water deficit due to demand-side drought caused by increase in vapor-pressure deficit. It is one of the major factors in low productivity of maize in rainfed stress-prone environments in South Asia, affecting a large population of smallholder farmers who depend on maize for their sustenance and livelihoods. The International Maize and Wheat Improvement Center (CIMMYT) maize program in Asia, in partnership with public-sector maize research institutes and private-sector seed companies in South Asian countries, is implementing an intensive initiative for developing and deploying heat-tolerant maize that combines high yield potential with resilience to heat and drought stresses. With the integration of novel breeding tools and methods, including genomics-assisted breeding, doubled haploidy, field-based precision phenotyping, and trait-based selection, new maize germplasm with increased tolerance to heat stress is being developed for the South Asian tropics. Over a decade of concerted effort has resulted in the successful development and release of 20 high-yielding heat-tolerant maize hybrids in CIMMYT genetic backgrounds. Via public-private partnerships, eight hybrids are presently being deployed on over 50,000 ha in South Asian countries, including Bangladesh, Bhutan, India, Nepal, and Pakistan.

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## 1. Introduction

In South Asia's agri-food system, maize provides livelihoods for millions of smallholders. The crop serves as a staple food for the inhabitants of marginal lands and as feed for the poultry industry, which produces chicken meat and eggs that in turn provide relatively affordable sources of protein. In South Asia, maize is predominantly (~80% of the total maize area) cultivated as a rainfed crop largely by resource-constrained smallholder farmers in mar-

ginal agro-ecologies. Climate change-induced variability in weather conditions is one of the major reasons for year-to-year variation in global crop yields, including maize in Asia [1,2,3,4]. It places at risk the food security and livelihood of farm families living in the stress-vulnerable lowland tropics. Increased frequency of extreme events, such as heat waves and intermittent droughts, is one of the major effects of global climate change [5]. South Asia is highly vulnerable to the detrimental effects of climate change, with its high population density, poverty, and low capacity to adapt [4,6,7]. The region has been identified [4,8,9] as one of the hotspots for climate change.

\* Corresponding author.

E-mail address: [phzaidi@cgiar.org](mailto:phzaidi@cgiar.org) (P.H. Zaidi).

Heat stress impairs the vegetative and reproductive growth of maize, starting from germination to grain filling [10]. Spells of heat along with moisture stress (or physiological drought) are common in tropical arid and semi-arid maize growing regions. Heat stress alone, or in combination with drought, is projected [11] to become a major production constraint for maize in the future. Lobell and Burke [12] reported that a 20% decrease in precipitation would reduce maize yield less than a 2 °C increase in temperature. Increasing temperatures would result in a greater reduction in maize yields than increased intra-seasonal variation in precipitation [13]. A study [9] of historical trends and future projections indicated that by 2050 about 45% of the global maize production area is likely to face maximum temperature ( $T_{max}$ ) greater than 35 °C for an average of five days annually during the reproductive stage. This is an alarming projection, given that a mere 1 °C rise in mean seasonal temperature is projected [14,15] to reduce maize yield by 3%–13%. A study of current and future heat stress hotspots in South Asia indicated that the extent of heat-stressed areas in South Asia could increase by up to 12% by 2030 and up to 21% by 2050 relative to the baseline year of 2000 [16].

Global warming increases global surface temperatures [17]. It increases the saturation vapor pressure of the atmosphere, whereas actual vapor pressure does not increase at the same rate. This difference between saturation and actual vapor pressure results in a rising vapor-pressure deficit (VPD) [18], a measure of the desiccation power of the air. Maize plants are sensitive to changes in VPD because it alters the plant's hydraulic capacity and soil–plant–atmosphere continuum by affecting the rate of transpiration, water and nutrient uptake from soil, and plant functions, including photosynthesis rate. The effects of VPD on plant functions seem independent of other drivers associated with climate change, such as drought or high temperature. Among studies of plant responses to high temperature, reduced precipitation, and rising atmospheric CO<sub>2</sub>, specific effects of high VPD due to climate change have been relatively little investigated. Climate change-mediated heat stress is not equivalent to high temperature, but depends on VPD at  $T_{max}$  [19], which is a function of both  $T_{max}$  and relative humidity (RH) at  $T_{max}$ . A maize crop exposed to similar high-temperature regimes in different locations may respond differently depending upon the corresponding VPD of the locations.

Accelerated plant growth and development due to faster accumulation of growing-degree days (GDD) because of increased day and night temperatures reduces the total duration of the crop cycle [20] and thus the period of light energy interception [21]. This in turn affects total biomass accumulation, eventually translating into low yields [22,23,24]. Because under heat stress, an increase in VPD results in greater water requirements for evapotranspiration, plants suffer from physiological drought along with high-temperature stress. These effects are more challenging for crops, such as maize, in the lowland tropics, grown largely in rainfed systems, and thus more exposed to vagaries of climate. A study conducted by Tesfaye et al. [25] suggested that while climate change will reduce maize yield in South Asia and sub-Saharan Africa, the impact may vary with location, level of heat stress, and rainfall pattern. Maize genotypes with tolerance to heat stress combined with high yield potential will be necessary in the face of climate change, in particular global warming.

## 2. Maize plant response to heat stress

As a warm-humid season crop, maize can survive brief exposures to high temperatures, but is sensitive to extreme heat-degree days (HDD). The  $T_{max}$  for optimal growth and development of the maize crop ranges between 25 and 33 °C, the minimum temperature ( $T_{min}$ ) ranges between 17 and 23 °C, and the mean optimal

temperature during the full growing season ranges between 20 and 22 °C [26,27]. Prolonged exposure to extreme HDD due to temperatures above threshold limits results in irreversible damage to the crop. High-temperature stress combined with increased VPD forces stomatal closure and causes physiological drought, as transpirational cooling is not sufficient to maintain optimal canopy temperature. This response is often visible as heat-stress injury signs such as leaf firing [28,29]. A transcriptome profiling study [30] also suggested that combined heat plus water stress tolerance in maize involved 770 unique transcripts that are not altered by drought or high-temperature stress.

An increased number of extreme HDD causes an array of morphological, physiological, biochemical, and anatomical changes in maize plants. Earlier studies [31,32] in temperate maize highlighted the damage done by increased temperatures during the cropping season. Temperature regimes beyond threshold limits, and especially prolonged extreme HDDs, affect most of the structural and functional traits of maize plants. They affect photosynthesis, transpiration [33,34,35], accumulation of phenolic compounds, causing cell necrosis [36], impaired phytohormone homeostasis [37], increased pollen sterility [9], and reduced kernel size [38]. The integrity of the plasma membrane functioning of mitochondria and chloroplast is also severely damaged by heat stress, which results in accumulation of active oxygen species [39] that cause photooxidative stress. It also induces transcription of heat-shock proteins (HSPs) and accumulation of unfolded or misfolded proteins that cause cell toxicity, leading to cell death, especially in leaf tissues.

Almost all crop stages suffer under extreme HDDs, though their eventual influence on grain yield may vary with intensity and duration of the stress. Effects of heat stress vary among plant tissues and organs, depending on the susceptibility of active metabolic process(es) at the time of the stress [40]. The temperature threshold for heat-stress damage is lower in the reproductive organs than in the vegetative parts [21,41]. Effects of heat stress on maize at various crop growth stages, starting from germination and seedling establishment to late grain filling stage, have been extensively reviewed [42]. Methods used to impose heat stress and its duration resulted in degrees of yield reduction that differed among studies [42]. There is stage sensitivity for heat stress in maize. The maximum yield penalty was observed when it occurred around reproductive stage, i.e., during flowering and the lag phase of grain filling, followed by the grain-filling phase and late vegetative stage [40,41,42].

The major effect of heat stress at reproductive stage is expressed as reduced pollen viability, which in turn affects pollination, fertilization, and kernel number [43], and reduced seed set resulting from increased kernel abortion rate [28]. In general, maize pollen is intolerant to desiccation because it rapidly loses moisture content at high VPD [44,45] caused by low RH at high temperature [46]. Usually, maize pollen grains are released from anthers at 55–60% moisture content, and their subsequent fate depends on air temperature and RH [47]. A moderate level of humidity is generally considered ideal for maize pollen dehiscence and viability, as extreme humidity levels, both too high or too low, can disrupt pollination by affecting pollen availability and eventually reduce crop yields [47]. While low humidity desiccates pollen grains, exposure to prolonged high humidity can reduce pollen viability [48] and especially the dispersal process from anthers, as pollen grains absorb moisture from the air that makes them heavier to disperse and/or reduces their dispersal range, affecting pollination efficiency [49]. The placement of the male inflorescence (tassel) at the apex of the stalk also provides maximum exposure to hot, dry conditions, increasing the probability of pollen damage from heat stress [8,28]. Heat stress reduces pollen viability not only after dehiscence but during its growth and development before dehiscence

cence [50,51]. Owing to increased sterility in inflorescences [52] the period between pollination and fertilization has been identified as one of the most sensitive stages causing low grain yield under heat stress [53]. Visible heat-stress signs include stunted growth, leaf scorching, reduced effective flowering period, increased anthesis–silking interval (ASI), and low pollen viability [28,54,55]. The cumulative effects of all these detrimental effects of heat stress are eventually translated to yield losses.

Besides high  $T_{\max}$  the increase in night temperature also impairs various plant functions. An increased rate of night respiration under high  $T_{\min}$  reduces net photosynthesis owing to altered carbon balance and growth [56,57]. It affects kernel set via increased kernel abortion due to reduced photo-assimilate production per unit of thermal time [58] and diversion of assimilates towards tissue maintenance at the cost of kernel filling. High night temperature also contributes to reduced pollen shedding duration and viability, leading in turn to reduced numbers of fertile kernels [56].

A combination of high temperature and drought stress reduced the growth and productivity of various field crops, including maize, more than did the individual stresses [59,60,61]. Based on data collected across locations and over years of heat stress phenotyping, Zaidi et al. [4] found that heat stress at high VPD combines two stresses: high-temperature stress and physiological drought, whereas at low VPD it is largely the first. Under high VPD, unless the maize crop is frequently irrigated to maintain high humidity in the crop canopy (likely not an economic choice for many farmers in the tropics), the crop faces the compound effects of high temperature and physiological drought due to high VPD, leading eventually to high yield losses [4,42].

### 3. Breeding for heat-stress tolerance in maize

A study [15] of more than 20,000 historical maize trial yields in southern Africa showed that maize production decreased linearly with every accumulated degree day above 30 °C. A subsequent simulation study [25] of maize in South Asia and sub-Saharan Africa showed that combined hot and dry scenarios resulted in greater average simulated maize yield reduction (respectively 21%, 33%, and 50% under 1, 2, and 4 °C warming) than under only high temperature stress (respectively 11%, 21%, and 41%). Thus, tolerance to combined heat and drought stress should be considered a new abiotic stress and not simply the sum of two individual stresses [11].

In the past, breeding for heat stress tolerance in maize was not accorded as high a priority in tropical maize breeding programs as other abiotic stresses, such as drought, waterlogging, and low nitrogen in soil. However, in the last 12–15 years, heat stress tolerance has emerged as one of the key traits for CIMMYT maize breeding program, especially in the South Asian tropics [4]. The two major factors behind this are a) increased frequency of weather extremes, including heat waves with prolonged dry period due to climate change during the main maize crop season in the lowland tropics; and b) increasing demand for maize grain, where the crop is being grown year-round, including in the hot, dry spring and summer season, when it is prone to facing heat stress. A simulation study [16] suggested that use of heat-tolerant varieties could reduce yield loss (relative to current maize varieties) by up to 36% and 93% by 2030 and by 33% and 86% by 2050 under rainfed and irrigated conditions, respectively.

At CIMMYT, systematic breeding for heat stress tolerant maize was initiated under the project Heat Tolerant Maize for Asia (HTMA) funded by the United States Agency for International Development (USAID) Feed the Future program. The project was launched in 2013 in a public–private alliance mode, in collaboration with public-sector maize research institutions and private

seed companies in Bangladesh, Bhutan, India, Nepal, and Pakistan. Under the HTMA project, an array of activities is undertaken, including genetic dissection of traits associated with heat stress tolerance, development of new heat-tolerant maize germplasm and experimental hybrids, evaluation of the improved hybrids across target populations of environments (TPEs) using a heat-stress phenotyping network in South Asia, selection of elite maize hybrids for deployment; and scaling via public–private partnerships. The key components in breeding for heat-stress tolerance in maize are described below.

## 4. Precision phenotyping and selection

### 4.1. Secondary traits associated with heat-stress tolerance

Grain yield is a trait of primary interest, but it is a sum of a series of plant structural and functional traits that includes a range of physiological and biochemical pathways, and phenological growth and development and reproductive success during the crop cycle. Selection of genotypes tolerant to abiotic stresses, such as drought or heat, based on grain yield alone might result in false positives, as heritability of grain yield is usually low under abiotic stresses [62]. A better understanding of the components (secondary traits) that eventually define grain yield under stress would help in robust selection of heat-tolerant maize genotypes [28]. Several secondary traits have been identified as being affected by heat stress in tropical maize [41,42,52,63,64,65]. However, not all the traits (constitutive or stress-responsive) that are affected by heat stress can be used as selection targets in genetic enhancement for heat-stress tolerance. Such a trait must meet a set of minimum requirements: i) it should be more heritable than that of grain yield under stress; ii) there is genotypic variation for the trait under stress; iii) the trait should be strongly correlated with grain yield under stress; iv) it should be associated with stress tolerance and not avoidance (as would be the case for early maturity), which might incur a yield penalty under optimal conditions; and v) it should be non-destructive, easy to measure in field trials even in small plots, and more economical to measure than grain yield itself [66,67].

At CIMMYT, data on a range of morpho-physiological traits was collected from several field trials across locations in South Asia under heat stress and secondary traits suitable for improving heat-stress tolerance in tropical maize were identified (Table 1). All of these traits are routinely used in field-based phenotyping and selection of heat-tolerant maize genotypes. Besides traits strongly correlated with grain yield under stress, additional traits such as leaf firing, tassel blast, and root lodging are used in selection indexes.

### 4.2. Selection environment for heat stress

High temperature and heat stress are often considered the same thing, and even the terms are used interchangeably. In fact, they are related to each other but distinct in practical terms. High temperature refers to a measure of the degree of hotness of an object or an environment, measured in °C or °F, whereas heat is a type of energy, the thermal energy (measured in joules, J), that is transferred from a hotter to a cooler object or environment. High temperature can lead to heat stress if the rate of thermal energy transfer exceeds the plant's ability to dissipate the excess heat (for example, under high-VPD conditions). Such an imbalance can impair multiple physiological and biochemical pathways, and eventually lead to reduced growth and development, tissue scorching, and even plant death in severe cases.

Precision and accuracy in evaluation of test genotypes to generate high-quality phenotyping data is key to selection decisions and

**Table 1**  
Correlations among secondary traits and grain yield of maize under heat stress.

Traits	GY	AD	ASI	PD	PH	PL	EPP	LF
AD	−0.36							
ASI	−0.58**	0.21						
PD	0.49**	−0.44**	−0.39*					
PH	0.38*	−0.08	−0.14	0.12				
PL	−0.33*	−0.15	0.14	0.08	0.32*			
EPP	0.66**	0.01	−0.39*	0.41**	0.18	−0.30*		
LF	−0.20	−0.01	0.20	−0.42**	−0.47**	0.14	−0.19	
TB	−0.16	−0.96**	0.84**	−0.98**	−0.55**	−0.02	−0.36*	0.78**

\* and \*\* indicate statistical significance at  $P < 0.05$  and  $P < 0.01$ , respectively. GY, grain yield; AD, anthesis date; ASI, anthesis–silking interval; PD, pollen duration; H, plant height; PL, plant lodging; EPP, ears per plant; LF, leaf firing; TB, tassel blast.

for increasing genetic gain in breeding pipeline for a targeted trait. An appropriate environment is a prerequisite for precision phenotyping for a targeted abiotic stress trait such as heat-stress tolerance [29]. A controlled heat-stress environment permits applying the desired level of stress for precisely a given period at a targeted crop stage and avoiding confounding effects of other unintended stress(s) [68,69,70]. However, response to heat stress in a controlled environment assay must be validated as equivalent to heat stress in representative field environments. Telfer et al. [71] showed that genotype-by-environment interaction for heat stress tolerance under field conditions could be partly explained by performance under controlled environment conditions. The study suggested that phenotyping for heat stress under field conditions where stress conditions may influence multiple physiological processes and growth stages is valuable. With careful selection of trialling locations based on envirotypes and climate similarity to those of the TPE, and appropriate experimental design, heat-stress evaluation in trials is possible even in the presence of other confounding stresses.

Field-based precision phenotyping helps in identification of progeny with traits of interest, building strong statistical models for genotype–phenotype associations, identifying genomic regions of potential influence, and using these in forward breeding or in genomic selection [72]. Depending upon the level of VPD at  $T_{max}$ , maize crops exposed to similar high temperatures at different locations may respond differently. To establish a heat-stress phenotyping network, CIMMYT-Asia team analyzed the past 10 years of daily weather data of summer–spring season, including  $T_{max}$ ,  $T_{min}$ , RH, and rainfall, and soil characteristics (key physical and chemical properties), cropping system, and major biotic stresses from over 50 potential sites in South Asia. They then selected sites where  $T_{max}$  and  $T_{min}$  were above threshold limits for tropical maize during most parts of the targeted crop growth stages and at least one month was rain-free during that period. Based on two years of multilocation trials, the sites were broadly grouped into three types of heat-stress sites, including low VPD ( $< 3.0$  kPa) or warm-humid, moderate VPD (3.0–5.0 kPa) or moderate heat stress and high VPD sites ( $> 5.0$  kPa) or severe heat stress (Fig. 1). Managed heat stress phenotyping experiments were undertaken at these selected sites by adjustment of planting time in such a way that most of the late vegetative and reproductive growth stage (from tassel emergence to effective grain-filling stage) coincided with the high-temperature regime. A field manual [29] was published by CIMMYT covering various aspects of field-based managed stress precision phenotyping of maize under heat stress.

## 5. Genetic and molecular dissection of heat-stress tolerance in tropical maize

Functional genomic studies [73–76] on the effect of heat stress have been performed in many crops, including maize, under controlled laboratory conditions. However, reports of genetic mapping

of traits associated with heat-stress tolerance in maize, especially under field conditions, are rare. A few studies have investigated the molecular and genetic basis of heat-stress tolerance at seedling stage in maize [73,76]. In six connected segregating populations from European dent and flint parents, there was low correlation between heat tolerance at seedling and adult stages [77,78].

As part of the HTMA project, a genome-wide association study (GWAS) for heat stress tolerance was performed. An association-mapping panel (the HTAM panel) of 534 maize inbred lines included 449 breeding lines from CIMMYT, 52 inbred lines from the Maize and Millet Research Institute (MMRI), Sahiwal, Pakistan, 23 temperate lines from Purdue University, USA, and 10 lines from Kaveri Seed Company Ltd., India. The CIMMYT lines in the panel were derived from various abiotic stress breeding pools and populations, including several biparental pedigree populations developed by the CIMMYT-Asia maize program, and selected lines from lowland tropical pools/populations from CIMMYT-Mexico, such as La Posta Sequia-C7 (tropical late white dent), DTPY-C9 (drought-tolerant population, yellow), DTPW-C9 (drought-tolerant population, white), G18 Sequia C5 (drought-tolerant early yellow tropical population) and Pool16 BN Sequia-C5 (drought- and low-nitrogen-tolerant early white tropical population), adapted to the Asian tropics. High-density genotyping-by-sequencing of the HTAM Ppanel generated an imputed dataset of 955,690 SNPs of which 281,268–289,061 SNPs were used in several GWAS runs [79]. All the lines in the panel were testcrossed with two CIMMYT tester lines from opposite heterotic groups (CML286 in HG-A and CML451 in HG-B) and the testcross hybrids were evaluated in nine locations across India and Nepal under natural heat stress in field conditions, ensuring that most of the late vegetative and reproductive stages were exposed to severe heat stress. In addition to the primary trait, grain yield in testcross hybrids under heat stress, data for several secondary traits associated with heat-stress response, including anthesis–silking interval, leaf firing, tassel blast, and tassel sterility were recorded.

In GWAS on the HTAM panel, a 269 significant SNPs and 26 haplotype blocks with significant effect on grain yield under heat stress were identified across nine locations [79]. This finding was consistent with those from genetic mapping of grain yield under diverse abiotic stresses, indicating the polygenic nature of this trait [78,80,81]. Of the candidate genes identified in the study, 51 SNPs or haplotypes were located within physical intervals identified in previous GWAS and QTL studies. Several of the SNPs for grain yield under heat stress had been previously reported for other abiotic stress tolerance traits: drought and waterlogging stress [80,82]. Similarly, in a QTL mapping study in temperate maize for heat-stress tolerance under field conditions involving European dent and flint corns forming six connected biparental populations, Frey et al. [78]) identified two QTL hotspots for grain yield on chromosome 2 and 3. The QTL hotspot on chromosome 2 overlapped with a meta-QTL for cold tolerance identified in multiple studies [83] and also with a QTL associated with multiple traits under water-

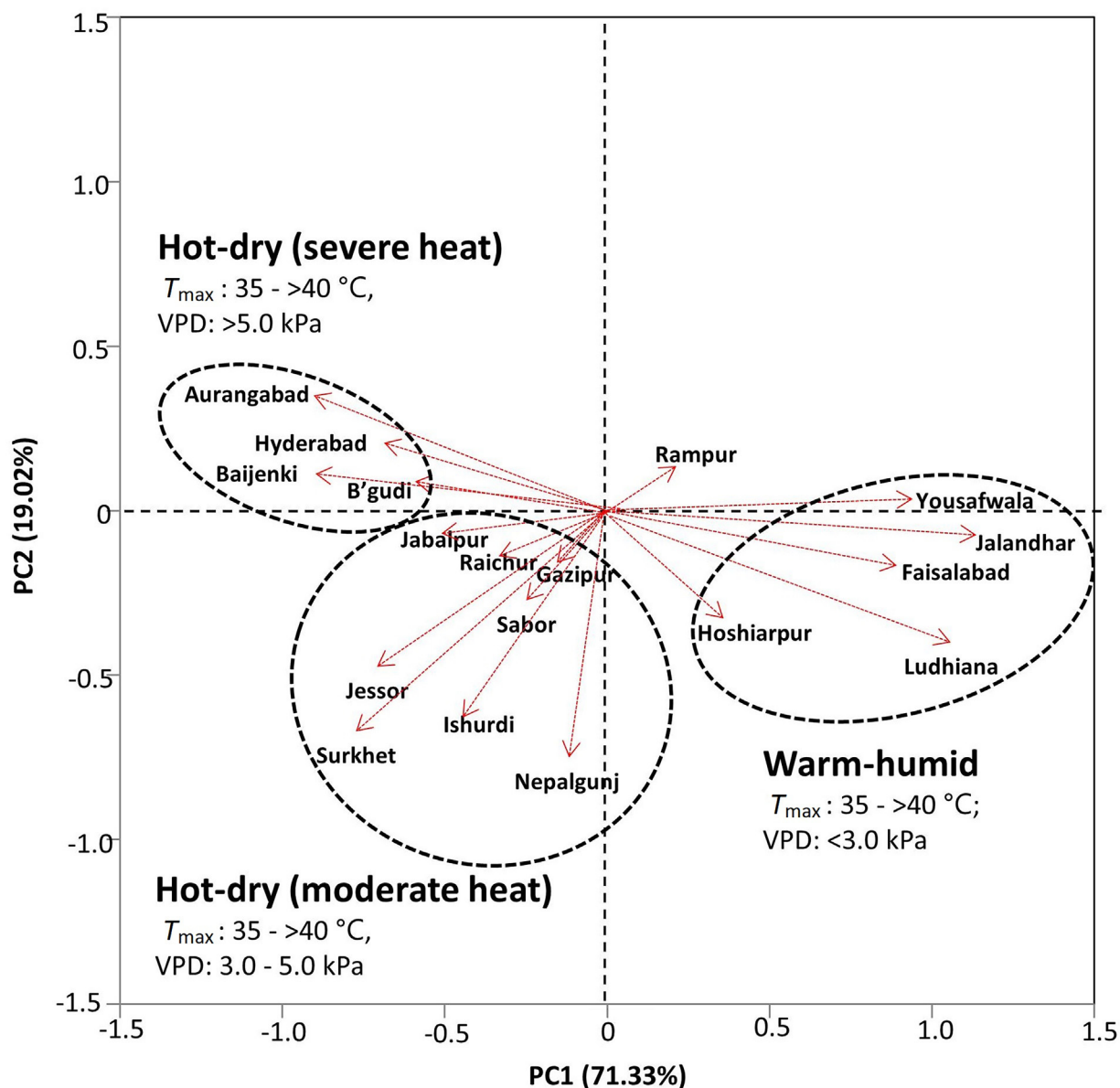


Fig. 1. Diverse types of heat-stress environments in South Asia due to differing vapor-pressure deficit (VPD) conditions at similar high temperatures ( $T_{max}$ ).

stress conditions [84]. They suggested that these genomic regions were associated with general abiotic stress tolerance in maize, rather than with any specific stress response. In another association mapping analysis, 662 doubled haploid (DH) lines derived from nine biparental populations of sub-tropical or tropical origin were used to map grain yield and other secondary traits under heat stress and under normal temperature in their testcrosses with a susceptible tester [85]. The study revealed genomic regions associated with the primary and secondary traits under heat stressed and non-stressed conditions.

Heat stress affects lipid composition and saturation, which are believed [86] to confer heat-stress tolerance. Field trials of the HTAM panel, inbred lines *per se*, were conducted in Hyderabad, India (17.5111°N, 78.2752°E) during the spring season (March to June) of 2015. Two replications were grown under heat-stress conditions where the mean daily high temperature during pollination was 40.4 °C. The highest temperature reached was 43.2 °C during pollination. The inbred lines were evaluated for numerous agronomic traits: grain yield, anthesis, silking, anthesis–silking interval,

plant height, ear height, number of ears per plant, leaf firing, and tassel blast. Leaves were sampled for assay of lipid concentration at tassel emergence (VT) stage following Welti et al. [87]. Lipid concentration was quantified at the Kansas Lipidomics Research Center, Manhattan, KS, USA using a triple quadrupole tandem mass spectrometer (4000 QTRAP, Applied Biosystems, Foster City, CA, USA). Best linear unbiased predictions (BLUPs) of the inbred lines for the heat stress trial were created using genotype as a random effect and block nested in replication as a fixed effect for both agronomic traits and lipids. Genomic prediction was performed following VanRaden [88] using a genomic BLUP (GBLUP) model using the genomic relationship matrix of the 506 inbred lines derived and 377,138 SNPs. Fivefold cross-validation was performed for lipidomic prediction and genomic prediction, repeated 10 times to assess model accuracy. Among the 224 lipids evaluated, the mean repeatability was 0.48 (range: 0 to 0.91) (Table S1). Forty-six lipids had a repeatability greater than 0.7, indicating that certain lipids were more heritable than other lipids. Genomic and lipidomic prediction gave a mean prediction accuracy across all nine agronomic

traits of 0.40 and 0.33, respectively, (Fig. 2). Genomic prediction outperformed lipidomic prediction for anthesis date, silking date, anthesis–silking interval, leaf firing, and tassel blast. Comparable prediction accuracy for the two datasets was found for grain yield and plant height. Ear height and ears per plant showed greater prediction accuracy using the lipidomic rather than genomic dataset. The results suggested that prediction of certain agronomic traits using lipidomic data is comparable to genomic prediction and should be explored further.

## 6. Genetic improvement for heat stress tolerance

Selections for grain yield under heat stress is indicated for enriching breeding pipelines with favorable alleles for the trait of interest. However, the complexity of the trait [89], along with high  $G \times E$  [90] limits the ability to select effectively based only on grain yield.

### 6.1. Base germplasm

During the mid-1980 s, as part of intensive efforts to develop maize germplasm with improved drought tolerance, a large array of maize germplasm, mainly early-generation testcrosses, were screened at CIMMYT’s Ciudad Obregon research station in Sonora, Mexico [91,92]. Although heat stress was not considered a priority trait at that time, germplasm screening at a research station located in a hot, dry environment led to some unintended selection for heat-stress tolerance.

A more systematic effort to develop elite heat-tolerant maize germplasm was initiated in 2013 under the HTMA project in South Asia. To identify potential sources for heat-stress tolerance, the HTAM panel testcrosses were evaluated in various locations in South Asia under natural heat-stress conditions during the spring season, in which plants are well exposed to severe heat stress in

April and May. Promising lines with moderate heat tolerance were identified and further used for developing base populations, both biparental and multiparental, for genetic improvement using genomic selection (GS) and to recycle elite heat-tolerant lines in the breeding program.

### 6.2. Genomics-assisted breeding for heat stress tolerance

#### 6.2.1. Improved heat-tolerant populations with introgression of validated genomic regions

Haplotypes associated with heat tolerance in maize, identified by GWAS [79], were validated using QTL analysis of two biparental populations formed by crossing heat-tolerant and -susceptible parents. Doubled-haploid (DH) lines derived from the two populations were evaluated under heat stress at two locations in India for 11 traits, including grain yield and secondary traits associated with heat-stress response [29]. Using composite interval mapping, 49 QTL were detected on nine chromosomes in one of the populations and 16 QTLs were detected on all 10 chromosomes in the second population for eight traits. Nine QTL were detected for grain yield under heat stress, six for ASI and two and one QTL for leaf firing and tassel blast, respectively. QTL hot spots, where overlapping QTL were detected for multiple secondary traits, were detected on chromosomes 2, 5, and 9 (Fig. 3). Overlapping QTL were detected for leaf firing and tassel blast on chromosome 9. Four of the QTL for grain yield corresponded to marker–trait associations (MTAs) detected by GWAS for grain yield in the HTAM panel. Similarly, one QTL each covered MTAs for leaf firing and tassel blast. In North American maize germplasm, a QTL mapping study [93] conducted for leaf and tassel traits associated with heat tolerance in two recombinant inbred lines (RIL) populations identified 22 and 15 QTL. Only one QTL was identified for tassel blast, on chromosome 5. One QTL on chromosome 9 for leaf firing mapped to the physical interval of a QTL identified in tropical maize [82] and

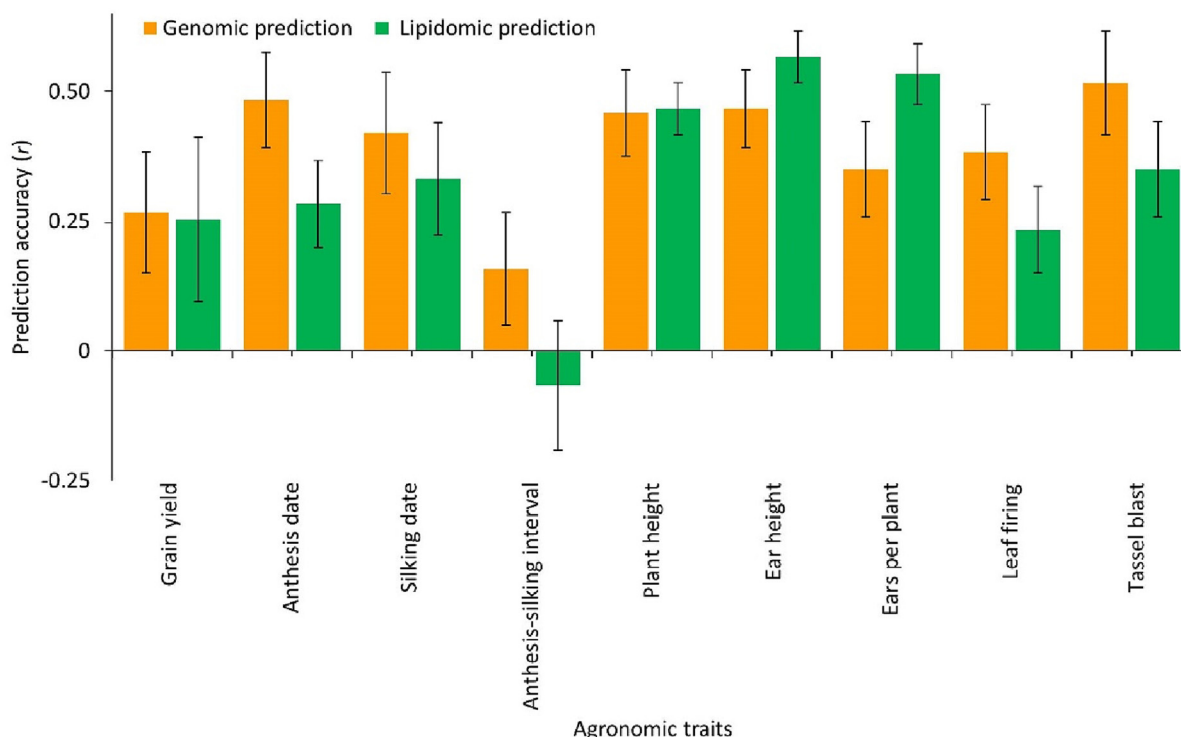
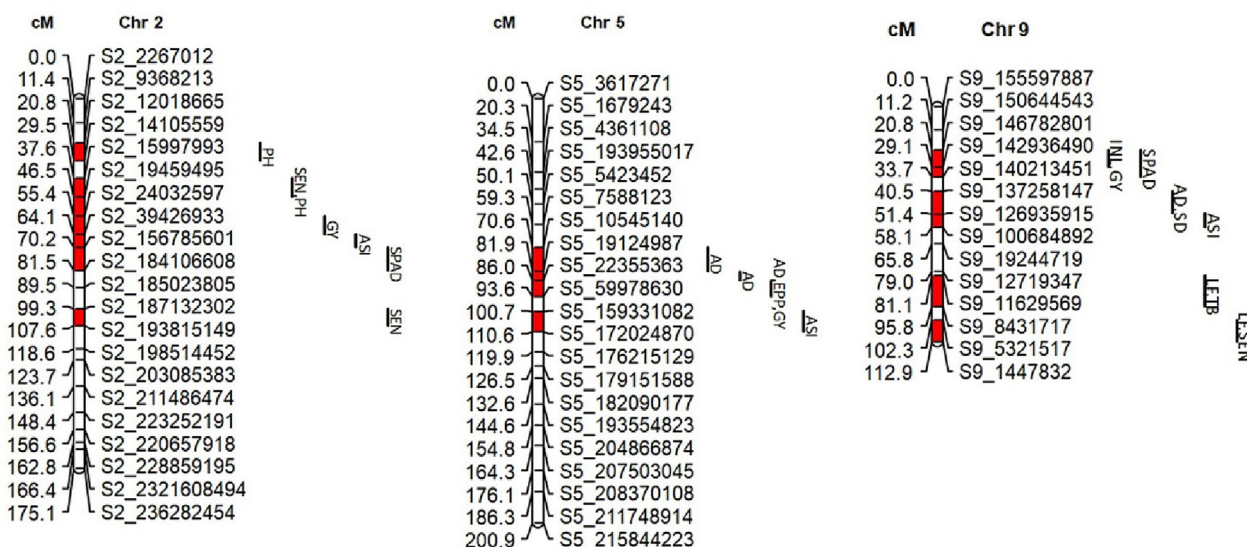


Fig. 2. Prediction accuracy of genomic and lipidomic prediction for grain yield and secondary traits in tropical maize under heat-stress conditions.



**Fig. 3.** QTL hotspots detected by composite interval mapping for grain yield and secondary traits of maize inbred lines involved in a biparental population developed from a heat stress-tolerant by -susceptible cross. GY, grain yield; AD, anthesis date; ASI, anthesis–silking interval; PD, pollen duration; H, plant height; PL, plant lodging; EPP, ears per plant; LF, leaf firing; TB, tassel blast.

European maize [78], suggesting a genomic region meriting further study. Although secondary traits are considered less complex than grain yield under stress, complex genetic mechanisms could underlie heat stress tolerance in maize even for leaf and tassel traits.

A CIMMYT group used QTL-indexed heat stress-tolerant donor lines in the breeding pipeline to introgress favorable haplotypes into elite lines by backcrossing. Twelve backcross (BC) populations were formed from crosses of four heat-tolerant (HT) lines with three lowland tropical Asia-adapted elite lines (CML472, CML451, and CML286), and BC-intercrosses were made by intermating BC lines to accumulate favorable alleles from multiple donor lines. Backcrosses and BC intercrosses were genotyped with markers associated with identified and validated QTL for grain yield under heat stress. Twenty BC bulks were selected based on favorable QTL, and 1023 DH lines were derived from these HT-introgressed BC populations. The DH lines were testcrossed with two opposite heterotic group testers and evaluated across VPD regimes in South Asia under field conditions. Elite HT lines from this stream are parents of 16 high-yielding HT pre-commercial hybrids that are currently being tested in heat stress-vulnerable ecologies across South Asia.

### 6.2.2. GS for heat-stress tolerance

Although a BC approach can help in improving specific elite lines for heat-stress tolerance, it may have limited use in breeding pipelines aiming at improving complex traits such as heat-stress tolerance. It is in this context that GS was suggested by Meuwissen et al. [94] as an extension of marker-assisted selection, where the breeding value of an untested genotype is predicted based on phenotypic and genome-wide genotypic data from related genotypes. In CIMMYT's global maize program, GS is mainstreamed in various maize breeding pipelines, and several studies [81,95–104] have shown the applicability and outputs of the strategy in maize breeding, especially in genetic improvement for abiotic stresses such as heat, drought, and waterlogging and for optimal conditions. With DH technology being the main route for inbred line development in maize, breeders could face a problem of handling large number

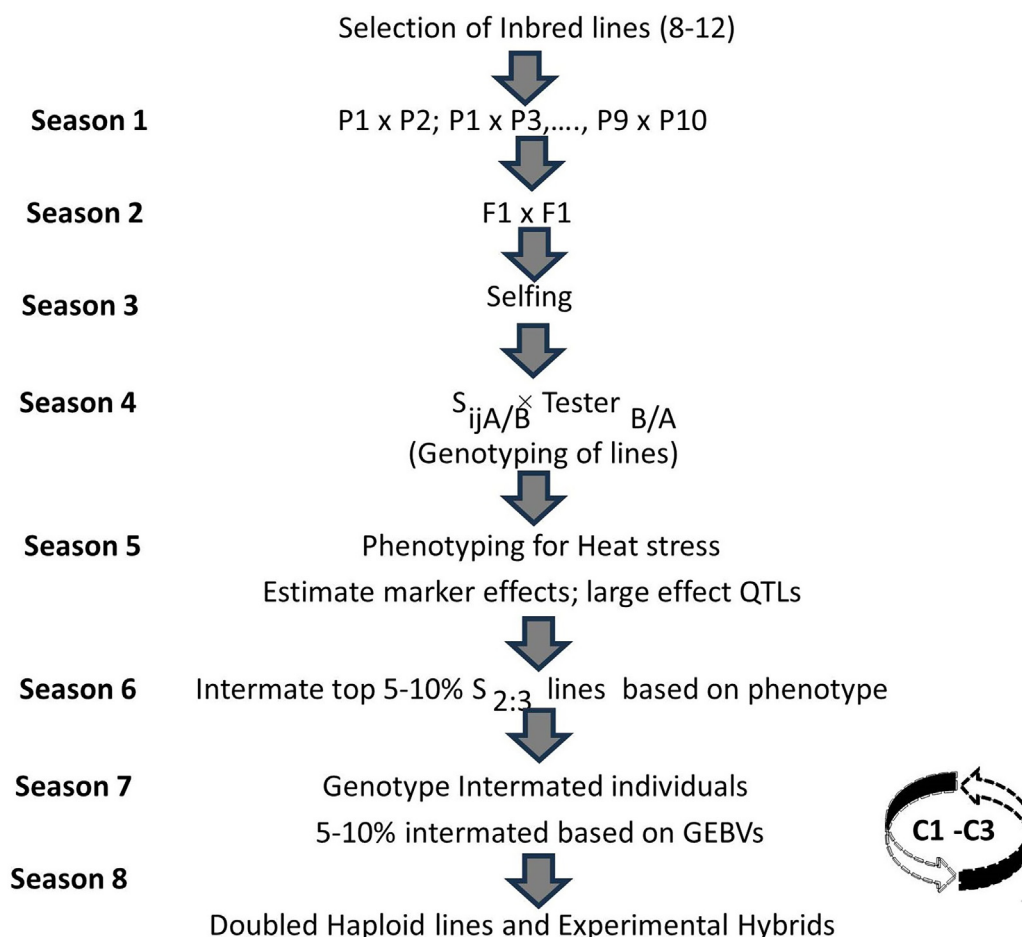
of lines if enabling technologies such as genomic selection are not strategically used in breeding schemes.

The principal advantages of GS in breeding pipelines are tied to the variables affecting the genetic gain equation [105], where GS increases selection intensity by increasing the capacity to test more lines per cycle, increasing accuracy by addition of an extra layer of information in the form of genomic relationships in selections, and reducing generation interval time and thereby reducing the cost per breeding cycle [106]. Use of GS in a recurrent-selection breeding scheme could increase the efficiency of selection by reducing the need for repeated phenotyping of plants in multiple cycles of recombination. In this scenario, GS saves resources by requiring only a single season of phenotyping at representative locations followed by two cycles of advancement through genomic estimated breeding values (GEBVs) of plants predicted employing a genomic relationship matrix. Prediction accuracies are generally greater, resulting in higher genetic gains, in crosses involving fewer (~2) parents, owing primarily to higher linkage disequilibrium (LD) [99,102], relatedness of recombinants to the testing set and limited or no population substructure [103,107]. However, use of biparental crosses often limits breeders' selection scope owing to limited allelic diversity and recombination. A multiparent population could increase the allelic diversity and number of recombinants for effective selection [108], and thus suitable as a source of populations for implementing recurrent-selection schemes [107,109,110].

In the heat stress-tolerance breeding pipeline of CIMMYT, GS is being employed in multi-parent synthetic (MPS) populations as rapid-cycle genomic selection (RCGS) to improve source populations and to extract high-value breeding lines. GS is also being routinely employed in the breeding pipeline as multiple biparental breeding populations are developed using elite heat stress-tolerant lines. Four multi-parent synthetic populations were constructed at CIMMYT-Asia, two each representing the two major heterotic groups (A and B) using 8–10 elite founding parental lines (Table 2) for implementing GS-based recurrent selection scheme in the heat-stress breeding pipeline (Fig. 4). The lines that were involved in constructing MPS populations were identified by extensive multilocation testing of the HTAM panel for GWAS,

**Table 2**  
Grain yield under heat stress of testcrosses of lines involved in development of multi-parent synthetic (MPS) populations.

Population (HG-A)	Elite lines	Grain yield (t ha <sup>-1</sup> )	Population (HG-B)	Elite lines	Grain yield (t ha <sup>-1</sup> )
MPS 1	ZL114704	3.69	MPS 2	ZL11884	3.80
	ZL114622	3.14		ZL114585	3.70
	ZL114620	2.85		ZL114586	3.78
	ZL114576	3.81		ZL114587	2.70
	ZL114577	3.76		CML425	3.37
	CML472	3.36		ZL11259	3.00
	ZL11253	4.18		ZL11345	3.05
	ZL11251	3.45		ZL114595	3.50
	ZL114581	2.98		ZL11428	3.00
	ZL114568	3.01		ZL11412	3.00
MPS 3	ZL136827	2.53	MPS 4	ZL11794	2.70
	ZL114888	3.00		ZL114637	2.48
	ZL114742	2.87		ZL1315	2.44
	ZL136817	2.00		ZL136818	3.20
	ZL167	1.90		ZL138	2.75
	ZL126628	5.09		ZL126623	2.54
	ZL14499	3.59		ZL1310	2.68
	ZL132230	3.36		ZL114636	2.29
	ZL114591	4.04		ZL11428	3.00
	ZL126626	2.22		ZL126624	2.55
ZL11817	3.14	ZL136835	2.63		
			ZL1312	3.00	



**Fig. 4.** Rapid-cycle genomic selection scheme implanted in four multi-parent populations in the heat stress breeding program.

where elite lines with reasonably high levels of heat tolerance and resistance to major diseases in targeted agro-ecologies were selected. The RCGS scheme was implemented for three cycles for

improvement of the MPS populations: a first cycle (C1) based on phenotyping selection across locations under natural heat stress and two further cycles based on GS.



After completion of three cycles, genetic gains were estimated to range from 40 to 234 kg ha<sup>-1</sup> year<sup>-1</sup> across the four populations. In a biparental RCGS study of drought tolerance in CIMMYT's eastern Africa maize breeding program, Beyene et al. [99] reported nearly three times higher average genetic gain from GS than from conventional pedigree-based phenotypic selection. RCGS was also implemented by CIMMYT in Asia to simultaneously improve two MPS populations for drought and waterlogging tolerance [98]; the study showed that the genetic gains (110 and 135 kg ha<sup>-1</sup> year<sup>-1</sup>, respectively) were significant for drought stress tolerance in both MPS populations, though it was less (38 and 113 kg ha<sup>-1</sup> year<sup>-1</sup>) for waterlogging tolerance. Zhang et al. [104] also implemented RCGS in a multiparent population, where they reported a genetic gain of 225 kg ha<sup>-1</sup> cycle<sup>-1</sup> under optimal growing conditions.

### 6.2.3. Mainstreaming GS in heat-stress breeding pipeline

To integrate GS in a breeding pipeline we followed a test-half-predict-half (THPH) strategy, where 50% of the lines entering the first stage of field testing (stage 1) from a full-sib family were used to predict the performance of remaining 50% based on their GEBVs. These 50% of untested lines entered into stage 2 of field testing after testcrossing with a wider set of testers [100]. The THPH strategy also helped in building training populations for the breeding pipeline for future work on genomic prediction using historical training populations. In the THPH strategy, high prediction accuracies were observed under drought stress and well-watered conditions [90], as the training populations were highly related and purposefully designed for reducing field phenotyping. The THPH strategy reduced the cost by 32% over conventional phenotypic selection under managed stress, with similar selection gains. In the heat-stress breeding pipeline, the performance of the 10% DH lines selected from stage 1 multilocation trials was estimated based on phenotypic data and GEBVs by evaluating the stage 2 hybrids in common stage 2 yield trials in three heat-stress environments. The grain yield did not differ significantly between the stage 2 testcross hybrids of the DH lines advanced from stage 1 based on phenotypes or GEBVs (Fig. 5). This study established that genomic prediction using the THPH strategy was effective in breeding for heat-stress tolerance.

Heat-stress tolerance-associated haplotypes that were identified through the GWAS in the HTAM panel and validated in linkage-mapping populations were further analyzed, as well as in combination with genome-wide random SNPs genotyped by the

rAmpSeq method [111]. The objective was to study the predictive ability of the haplotypes either alone or in combination with random SNPs employed in genomic prediction in seven breeding populations in stage 1 testing. Fivefold cross-validation was used to estimate prediction parameters, and to measure the accuracy of the predictive models, the Pearson correlation coefficient ( $r$ ) and the root mean squared error (RMSE), comparing observed and predicted values, were calculated. Two alternative GBLUP models were fitted: a G model that did not include the haplotype effects and used only a genomic relationship matrix derived following VanRaden [88], and the H model in which haplotype effects were included. Including the haplotypes (identified by GWAS) in prediction models gave high prediction ability; the best prediction parameters were obtained using the genomic relationship matrix obtained from random genome-wide SNPs ( $r = 0.57$ ; RMSE = 0.46).

Although the THPH approach is effective, a major limitation is that it requires large full-sib populations, limiting the ability to shorten variety testing and breeding cycle times [112]. In the heat-stress breeding pipeline, the THPH strategy has since been extended to include half-sib or genomically related populations in the stage 1 testing cohort to remove some of these limitations without affecting prediction accuracy, while still building on the historical training population data (phenotypic and genotypic data of DH lines in stage 1 testing). When the historical training population data from the same breeding pipeline becomes available, there is the potential to bypass stage 1 trial evaluation and move the breeding lines directly into stage 2 testing [100]. With accurate predictions from training sets composed of historical data, this approach would reduce both cycle time and cost. To identify the most efficient use of historical data collected from relatives for genomic prediction, Atanda et al. [112] studied training population design strategies in breeding pipelines and found that the use of multiple biparental populations from one breeding pipeline as a training population was the most effective when they were selected to maximize the relatedness between the training and prediction sets. In the heat-stress breeding pipeline in CIMMYT-Asia, every new cohort of stage 1 lines are tested for genomic relationship matrix within the cohorts and with the historical training population dataset to optimally use information for prediction of untested lines.

### 6.3. Genetic modification for heat-stress tolerance

Work on heat-stress tolerance of maize at CIMMYT is based on exploiting native genetic tolerance, but genetic modification by genetic engineering and gene editing are also powerful strategies. In rice, as many genes for heat tolerance have been cloned, some key heat-tolerance signaling pathways have been elucidated [113]. These pathways include post-transcriptional regulation, the ubiquitin proteasome pathway, metabolic pathways, and the calcium ion signaling pathway [114]. In maize, transcriptome and metabolome studies have identified hundreds of heat-responsive and heat-tolerance genes, as well as increased production of branched-chain amino acids, raffinose-family oligosaccharides, lipolysis products, and tocopherols under heat stress [115]. Heat shock transcription factors (HSFs) that regulate production of heat shock proteins (HSPs) are studied in detail for their utility in engineering heat tolerance in crops. There are at least 31 HSF members in maize, of which several have been cloned [116]. Li and Howell [115] summarized the heat stress tolerance pathways in maize in terms of crosstalk between *bZIP60*, *IRE1*, and HSFs located in the cytoplasm and endoplasmic reticulum triggering protective mechanisms. These genes could be considered future targets for gene editing in maize for heat-stress tolerance. Gene networks regulating the biosynthetic or response pathways for compounds like abscisic acid, salicylic acid, and ethylene precu-

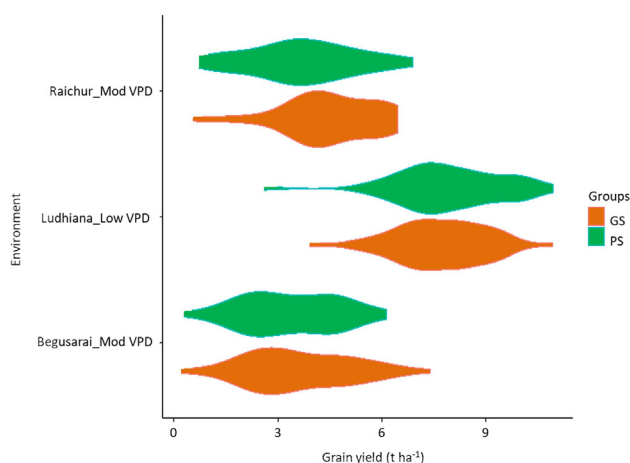


Fig. 5. Comparative performance of new maize hybrids advanced using the test-half predict-half (THPH) approach under three vapor-pressure deficit (VPD) regimes. GS, genomic selection; PS, phenotypic selection.

sors [117] are potential targets of future genetic modification efforts. Transgenic maize with constitutive ectopic expression of a heterologous glutaredoxin S17 from *Arabidopsis thaliana* (*AtGRXS17*) showed heat tolerance due to increased chaperone activity and modulation of heat stress-associated gene expression [118]. These heat-tolerant lines yielded a sixfold increase in grain production in comparison to the non-transgenic counterparts under heat stress field conditions. Overexpression of *OsMYB55*, a member of the plant MYB transcription factors, which regulate numerous processes including responses to environmental stresses, in maize reduced the negative effects of high temperature and drought, resulting in improved plant growth and grain yield under these conditions [119]. Similarly, the overexpression of chloroplast-localized 6-phosphogluconate dehydrogenase (6PGDH) PGD3 resulted in an overaccumulation of starch in maize endosperm under heat stress, leading to increased grain size and weight. Transgenic and gene editing strategies for complex traits like heat-stress tolerance are being actively researched to accelerate development of heat stress-tolerant maize varieties.

#### 6.4. Traits donors and improved populations

Besides elite hybrids, the HTMA project led to the identification of several elite heat stress-resilient lines, of which eight were globally released as CIMMYT Maize Lines (CMLs): CML562, CML564, CML565, CML578, CML579, CML580, CML613A, and CML614B [120]. As part of ongoing improvement, a few more trait donor lines with good general combining ability for heat-stress tolerance have been identified for use in the breeding pipeline. New and improved breeding populations, including biparental, multiparental, and backcross populations were developed and are being shared with partners in South Asia for use in their breeding pipelines and/or to test and release as heat-tolerant open-pollinated

varieties in areas where the hybrid seed sector has not yet evolved or is still at a nascent stage.

### 7. Genetic gains in heat stress-tolerance breeding pipeline

Genetic gain is a measure of the success of a crop breeding program, and represents the average change achieved by breeding and selection for the primary trait of interest, such as grain yield [121]. Genetic trends can be measured by regressing on years the trait values of the tested entries in the breeding pipeline [122]. Although the most accurate estimation of gains can be made by era studies [123], such studies are resource-intensive and do not suggest measures for improving a breeding pipeline [124]. Use of historical data to assess genetic gains may help breeders apply real-time corrective solutions.

Genetic trend analysis based on mean grain yields of field trials conducted in CIMMYT-Asia’s heat-stress breeding showed estimated genetic gains of 6 kg ha<sup>-1</sup> year<sup>-1</sup> under high VPD and 118 kg ha<sup>-1</sup> year<sup>-1</sup> under low VPD in the same pipeline [124]. The low gains in trial means for grain yields under high-VPD conditions reflects the challenge in breeding for a complex trait that involves both high temperature and drought stress. But genetic gain analysis based on historical data on mean yields of the top five hybrids among test entries in advanced breeding trials showed gains under all VPD regimes: high VPD (322 kg ha<sup>-1</sup> year<sup>-1</sup>), moderate VPD (287 kg ha<sup>-1</sup> year<sup>-1</sup>) and low VPD (177 kg ha<sup>-1</sup> year<sup>-1</sup>) (Fig. 6). The trend was reversed for commercial checks, where gain was highest under low VPD and lowest under high VPD. HT maize hybrids are the products of targeted selection for heat-stress tolerance, which resulted in relatively high gains under high and moderate VPD without any yield penalty under low VPD, associated with warm and humid conditions, a favorable environment for tropical maize. In contrast, most private-sector commercial

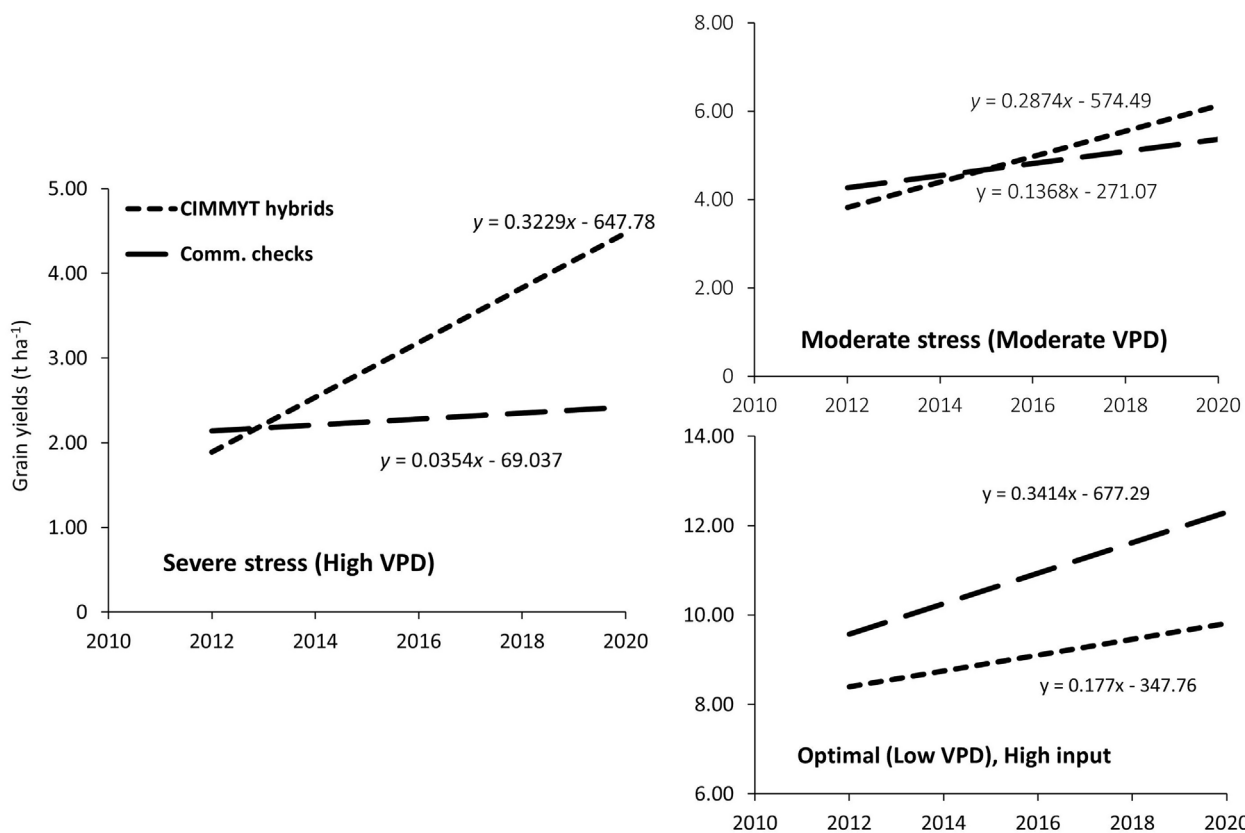


Fig. 6. Genetic trends estimated from grain yield of the top five advanced-stage CIMMYT’s heat tolerant maize hybrids and commercial checks under heat stress.

hybrids are products of breeding under optimal conditions and are not selected for heat-stress tolerance. These hybrids showed greater gains under low VPD but not under moderate and high VPD, as they are particularly vulnerable to severe heat stress (Fig. 7).

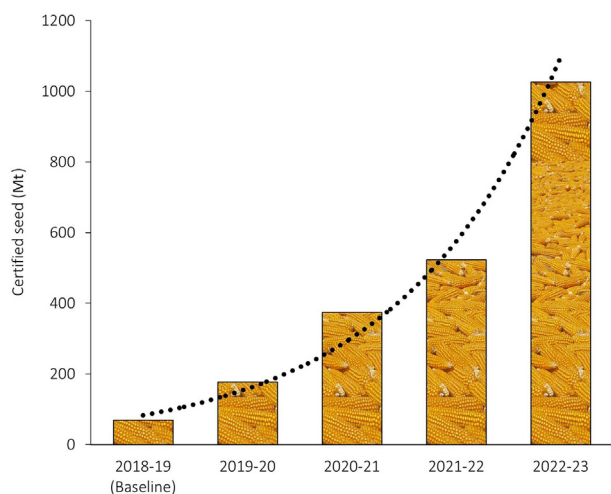
#### 8. Delivery of heat-tolerant maize hybrids to smallholder farmers in south Asia

Over a decade of dedicated breeding efforts has resulted in successful identification, variety release, and deployment of HT maize hybrids in South Asia, especially in Bangladesh, Bhutan, India,

Nepal, and Pakistan [125]. Via genomics-assisted breeding strategies, improved heat stress-tolerant populations were developed and subjected to DH induction, resulting in over 5000 DH lines. These lines were evaluated in cross combinations across locations in heat stress-vulnerable environments of South Asia. Cross-site data analysis within and across VPD regimes was performed and the best-performing hybrids were identified. Maize hybrids combining heat-stress tolerance, yield potential under optimal growing conditions, and other farmer-preferred traits (including disease resistance) were advanced using a stage-gate advance process that is routinely used by CIMMYT's global maize program for product advance [126].



**Fig 7.** Phenotypic responses of a heat-tolerant maize hybrid (right) and a heat-susceptible commercial check (left) exposed to severe heat stress during the late vegetative and reproductive stages.



**Fig. 8.** Heat-tolerant maize hybrid seed deployed in climate-vulnerable agroecologies of South Asia.

Based on data from across-site on-station evaluation followed by on-farm trials, a set of new-generation HT maize hybrids were identified and formally announced, and requested hybrids were licensed to seed partners (both public institutions and private seed company partners) using CIMMYT's product licensing policy. The first batch of 18 HT hybrids were licensed to partners in 2015 and by year 2022 a total of 53 elite HT hybrids were licensed. Partners multiplied the licensed hybrids for large-scale on-farm testing along with benchmark commercial maize varieties in their respective target environment(s) prone to heat stress. After extensive testing and simultaneous assessment of hybrid seed production and other traits for commercial viability, the finally selected hybrids were officially released or registered for commercialization. The first batch of five HT-maize hybrids were released in 2017 and by 2022 20 elite HT-maize hybrids were officially released or registered and over 1000 Mt of seed of HT hybrids was deployed (Fig. 8) on over 50,000 ha in heat stress-vulnerable environments in five south Asian countries (Bangladesh, Bhutan, India, Nepal, and Pakistan).

Impact assessment of heat-tolerant maize hybrid seed was conducted in targeted areas in India [127] and Nepal [128] where HT maize is being deployed. The studies showed significant gains by HT-maize adopter farmers over non-adopters in terms of additional yield under less-favorable weather conditions, while under favorable conditions the yield was on par with those of other hybrids. It was also demonstrated that HT-maize hybrids provide guaranteed minimum yield ( $\sim 1.0 \text{ t ha}^{-1}$ ) to farmers under hot, dry unfavorable weather conditions. Adoption of new HT hybrids was comparatively high (19.5%) in women-headed households, mainly because of the stay-green trait (conferring green biomass at harvest) that provides green fodder in addition to grain yield, as women in these areas are largely responsible for arranging fodder for their livestock. The value of HT-maize hybrids was also well appreciated by the smallholder farmers who grow maize in stress-vulnerable ecologies in the *Tarai* region of Nepal, as they expressed willingness to pay (WTP) a premium price for HT-maize hybrid seed compared to seed of other available hybrids in their areas. The farmers also expressed 71% more WTP if seed is available through a government channel with subsidy or at least 19% more without any subsidy [129].

## 9. Conclusions and future perspectives

Climate change effects often surpass projections, especially in lowland tropics where episodes of extreme weather in addition

to seasonal variation have emerged as a recurring problem. Stress resilience must be incorporated into new maize hybrids to increase yields in climate-vulnerable agro-ecologies. Our work in South Asia demonstrates that combining high yields and heat-stress tolerance is difficult, but not impossible, if one adopts a systematic and targeted breeding strategy [4,124]. Effective integration of enabling breeding tools and strategies, such as - field-based precise phenotyping, doubled haploidy, genomic selection and prediction, and public-private partnerships for multilocation on-station and on-farm testing of hybrids, is vital for accelerated development and deployment of heat stress resilient maize hybrids to address the climate change effects on maize in Asian tropics.

Variety release or registration systems in most of the national or provincial government systems follow the criterion of percent superiority over existing commercial hybrids in on-station trials conducted under favorable or optimal conditions. The present variety-release system in many countries does not adequately recognize the relevance of climate-resilience traits and the stability of performance of new candidate hybrids. With recent climate shocks and year-to-year variation in maize productivity due to weather extremes, yield stability is emerging as an important trait. It should become an integral target of the variety evaluation and release system.

Breeding institutions must overcome structural and developmental challenges in positioning and promoting new heat-tolerant maize hybrids in climate-vulnerable agro-ecologies. This activity requires stronger public-private partnerships for increasing awareness of, access to, and affordability of HT-maize seed to smallholder farmers.

Maize farmers in climate-vulnerable ecologies are often misled by high yield promises. Through an extensive awareness campaign for HT-hybrid seed, smallholder farmers should be educated to inquire about the guarantee of yields under less-favorable weather conditions, in addition to claims of higher yields under favorable conditions. There is a myth that stress-resilient crop varieties face yield drag under optimal growing conditions. Multilocation evaluation of stress-resilient maize hybrids by CIMMYT in sub-Saharan Africa [130] and in Asia [4] have shown that compared to normal hybrids the stress-resilient hybrids are superior under unfavorable conditions and on par with or even superior to the best commercial checks under favorable conditions. This truth should be widely demonstrated to maize farming communities in climate-vulnerable ecologies via extensive and inclusive on-farm demonstrations across both favorable and stress-vulnerable agro-ecologies.

In the stress-vulnerable agro-ecologies (considered "unfavorable markets" by large commercial seed companies) in many of the low- and middle-income countries, the formal seed sector is either weak or in a nascent stage. Intensive efforts are needed to develop and/or strengthen local seed production and value chains, involving especially small- and medium-sized enterprise, farmers' cooperatives, and public-sector seed enterprises. These efforts will lead to wider dissemination of climate-resilient crop varieties to resource-constrained smallholders.

## CRedit authorship contribution statement

**Pervez H. Zaidi:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – original draft. **Madhumal Thayil Vinayan:** Investigation, Data curation, Formal analysis, Writing – original draft. **Sudha K. Nair:** Conceptualization, Investigation, Data curation, Formal analysis, Writing – original draft. **Prakash H. Kuchanur:** Data curation, Implementing field phenotyping experiments, Writing – review & editing. **Ramesh Kumar:** Data curation, Implementing field phenotyping experiments, Writ-

ing – review & editing. **Shyam Bir Singh:** Data curation, Implementing field phenotyping experiments, Writing – review & editing. **Mahendra Prasad Tripathi:** Data curation, Implementing field phenotyping experiments, Writing – review & editing. **Ayyanagouda Patil:** Data curation, Implementing field phenotyping experiments, Writing – review & editing. **Salahuddin Ahmed:** Data curation, Implementing field phenotyping experiments, Writing – review & editing. **Aamir Hussain:** Data curation, Implementing field phenotyping experiments, Writing – review & editing. **Atul Prabhakar Kulkarni:** Data curation, Formal analysis, Writing – original draft. **Passang Wangmo:** Data curation, Implementing field phenotyping experiments, Writing – review & editing. **Mitchell R. Tuinstra:** Investigation, Data curation, Formal analysis. **Boddupalli M. Prasanna:** Conceptualization, Funding acquisition, Project administration.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data for this article can be found online at <https://doi.org/10.1016/j.cj.2023.06.008>.

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