Breeding Cultivars for Heat Stress Tolerance in Staple Food Crops

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Abstract

Food and nutritional security will be worsened by climate change-induced high temperatures, droughts and reduced water availability in most agricultural food crops environments, particularly in developing countries. Recent evidences indicate that countries in the southern hemisphere are more vulnerable to food production due to greater frequency of extreme weather events. These challenges can be addressed by: (i) adoption of climate mitigation tools in agricultural and urban activities; (ii) development of heat and drought tolerant cultivars in major food crops; (iii) bringing back forgotten native minor food crops such as millets and root crops; and (iv) continued investment in agricultural research and development with the strong government policy support on native crops grown by small holder farmers. The native crops have inherent potential and traits to cope with adverse climate during the course of its evolution process. Therefore, diversifying the crops should be a prime framework of the climate-smart agriculture to meet the global food and nutritional security for which policy-driven production changes are highly required in developing countries. The adverse effects of climate change on agricultural production need to be addressed by multidisciplinary team and approaches through strong network of research consortium including private sectors and multinational governments for global impact.

Keywords: breeding, cultivars, heat stress, staple food crops, tolerance

1. Introduction

The major challenge of this century is to produce sufficient food to meet the ever-growing population (10 billion by 2050) despite reductions in quantity and quality of arable land, water and increasingly variable weather patterns that are associated with climate change [1]. Abiotic stresses such as drought, salt, cold, and high temperature continue to affect the crops individually or in combination. Climate change has increased the intensity of heat stress that adversely affects both agricultural and horticultural crops resulting in serious economic losses, particularly in agricultural dependent countries. Global climate change risks are expected to be as high as global mean temperature increase of ≥4°C would pose large risks to global and regional food security [2]. The combination of high temperature and humidity would be compromising the current production of the major food crops such as wheat, rice, and maize in tropical and temperate regions. The climate change without adaptation is projected to negatively impact production for local temperature increases of ≥2°C above the late twentieth-century levels [2].

Extreme climates including very high temperatures are predicted to have a general negative effect on crop growth and development leading to catastrophic loss of crop productivity and also widespread famine in future [3]. The increase of temperature by 3–4°C is expected to reduce crop yields by 15–35% in Africa and Asia, whereas by 25–35% in the Middle East [4]. Hence, adopting the mitigation strategies such as reforestation, water harvesting in field and households, optimal use of CO_2 emitting devices and reducing wetland crops to avoid methane emission, etc., are essential, but as they are dependent on government policies, it is difficult to achieve them in short term. For long term, the adoption of extinct native crops and its diversity in individual farm is highly required to meet not only the food and nutritional security but also the feed security for farm livestock. The development of heat stress tolerant cultivars would be an ideal solution for sustainable food production for which research is still in preliminary stage and needs donor investment to progress competitively to deliver climate-smart cultivars to farmers. A recent study has shown the climatic shift in >25% of its geographical area in India [5] and also significant increase of aridity in several parts of the country. Therefore, government needs to re-standardize the climate zones with respect to aridity and temperature while planning for any developmental and agricultural intervention.

2. Heat stress and associated effects on food productions

A threshold temperature (TT) refers to a value of daily mean temperature at which a measurable reduction in growth begins. This is the range wherein changes in the photosynthetic capacity are irreversible, but other characters such as growth, flowering, etc., are reversible. The upper and lower developmental threshold temperatures are the ones at which growth and development ceases and they differ based on the plant species and genotypes. Cool season and temperate crops often have lower threshold temperature values compared to tropical crops. Every crop plants have threshold temperatures for different developmental stages (**Table 1**); upon exceeding this, crop experiences the stress.

High-temperature sensitivity is particularly important in tropical and subtropical climates as heat stress may become a major limiting factor for field crop production [6]. Heat stress (HS) is often defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. A transient increase in

Crops	Threshold temp. (ºC)	Developmental stage
Rice	15–35	Germination
	33	Biomass
	25	Grain formation and yield
	34	Grain yield and quality
Wheat	10–35	Germination
	20–30	Vegetative
	15	Reproductive
	35	Postanthesis
	35	Protein accumulation
Maize	15–40	Germination
	33–38	Photosynthesis
	38	Vegetative
	36–40	Pollen viability and fertilization
Sorghum	20–40	Germination
	26–34	Vegetative
	25–28	Reproductive
Pearl millet	10–34	Germination
Chickpea	10–35	Germination
	15–30	Growth
	25	Reproductive growth
Common bean	23	Reproductive development
Pea	15–20	Vegetative growth
Soybean	26	Reproductive development
	23	Post-anthesis
	30.2	Pollen germination
	36.1	Pollen tube growth
Groundnut	10–41	Germination
	29–33	Vegetative development
	25–28	Vegetative growth
	22–24	Reproductive growth
Lentil	32/20	Reproductive stage
Cotton	31.8–43.3	Pollen germination
	28.6–42.9	Pollen tube growth

Table 1. Critical growth stages and threshold temperatures of important food crops.

temperature of 10–15°C above ambient is generally considered as heat shock or heat stress (HS). However, HS is a complex function of intensity (temperature in degrees), duration, and rate of increase in temperature [6]. Some researchers believe night temperatures are major limiting factor, while the others argue that day and night temperatures do not affect the plant independently. Hence, diurnal temperature is a better predictor of plants response to high temperature with day temperature having a secondary role [7]. At high temperatures, severe cellular injury and even cell death may occur within minutes, which could be attributed to catastrophic collapse of cellular organization [8]. At moderately high temperatures, injuries or death may occur only after long exposure. Direct injuries due to high temperatures include protein denaturation and aggregation, and increased fluidity of membrane lipids. Indirect or slower heat injuries include inactivation of enzymes in chloroplast and mitochondria, inhibition of protein synthesis, protein degradation and loss of membrane integrity [9]. These injuries eventually lead to starvation, inhibition of growth, reduced ion flux, production of toxic compounds and reactive oxygen species (ROS) [10, 11].

Plants can experience wide range of HS on daily or seasonal basis. Temperature plays an important role in all stages of crops such as seedling emergence, vegetative stage, flowering/reproductive, and grain filling stages. Optimal temperature for growth and development differs for different plant species and genotypes within species. Exposure to temperature outside optimal range though not necessary be lethal, but can be stressful. The observed effects depend on species and genotype, with abundant inter- and intra-specific variations [12, 13]. Under elevated temperatures, various physiological injuries have been observed such as scorching of leaves and stems, leaf abscission and senescence, shoot and root growth inhibition, or fruit damage that leads to decreased plant productivity [14]. Heat stress induces changes in respiration and photosynthesis and thus leads to a shortened life cycle and diminished plant productivity [12]. In many crop species, the effects of high-temperature stress are more prominent on reproductive development than on vegetative growth, and the sudden decline in yield with temperature is mainly associated with pollen infertility [15, 16]. The effect of high temperature among different crop plants during germination, vegetative growth, reproductive growth, and different physiological processes such as photosynthesis, membrane fluidity, respiration, water balance, oxidative stress, and antioxidant defense have been discussed in detail elsewhere [17].

A wide range of plant developmental and physiological processes are negatively affected by HS. Sexual reproduction and flowering in particular have been recognized as extremely sensitive to HS that often results in reduced crop productivity [18]. High temperature is found most deleterious at flower bud initiation stage, with sensitivity being maintained for 10–15 days [18, 19]. Many legumes and cereals show a high sensitivity to HS, during flowering, and cause severe reductions in seed set probably due to reduced water and nutrient transport during reproductive development [15]. Generally, the male gametophyte is found sensitive to high temperatures at all stages of development, while the pistil and female gametophyte are more tolerant [20]. But in pearl millet, female reproductive parts was found more heat sensitive than male [21] as the stigma protrudes out of the florets. The HS often accelerates rather than delays the onset of anthesis that means the reproductive phase will be initiated prior to the accumulation of sufficient resources [16]. Shorter developmental phases for field crops have relatively negative effects on final grain weight and yield [22, 23]. Male sterility due to HS is widely observed among many sensitive crop plants, wherein the impairment of pollen development has been the prime factor for reduced yield under HS [13, 24]. Continuing HS beyond a successful fertilization can also halt further development of the embryo [12]. HS during seed development may result in reduced germination and loss of vigor, leading to reduced emergence and seedling establishment as noted among several crop plants [25, 26]. Both grain weight and grain number appears to be affected by HS in many temperate cereal crops, wherein decline in grain number was found directly proportional to increasing temperatures during flowering and grain filling [27, 28]. HS during seed development in several crop species has been found to cause reductions in quality parameters such as starch, protein, and total oil yield [29]. High temperature affects different stage and part of the crop growth in terms of morphology. The anatomical and phenological changes also affect plant growth and development.

3. Heat tolerance mechanisms in food crops

Heat tolerance (HT) is generally defined as the ability of the plant to grow and produce economic yield under high temperatures [6]. For surviving under HS, crop plants could manifest short-term (avoidance) and long-term (evolutionary changes) strategies. Short-term avoidance or acclimation mechanisms include changing leaf orientation, transcriptional cooling, altering membrane lipid composition, reflecting solar radiation, leaf shading of tissues that are sensitive to sunburn, and extensive rooting [30, 31]. Early maturation is found closely related to smaller yield losses in many crop plants [32], which is mainly due to escape mechanism. For example, tolerant wheat genotypes are defined by maintenance of photosynthesis, chlorophyll content, and stomatal conductance under heat stress, while the yield of these genotypes is maintained through higher seed set, grain weight, and extended grain filling duration (GFD) even at elevated temperatures [33]. At supraoptimal temperatures, heat tolerance grass species and cultivars exhibit higher activity in the photosynthetic apparatus [34, 35] and higher carbon allocation and nitrogen uptake rates [36]. Plants also utilize various mechanisms against HS such as ion transport, osmoprotectants, free-radical scavengers, and late embryogenesis abundant (LEA) proteins, wherein factors ubiquitin and dehydrin involved in signaling cascades and transcriptional control are essentially significant to counteract stress effects [37].

Transpiration is a mechanism of heat avoidance and serves as the primary mediator of energy dissipation. Generally, the rate of transpiration increases with increasing of canopy temperatures due to its effects on both vaporization and vapor pressure deficit (VPD). Crop transpiration is the most active and common method of cooling crop tissues (transpiration cooling effect), with plant cooling requirements increasing with temperature [10]. The ability to maintain high stomatal conductance at high temperatures promotes transpirational heat dissipation, as observed in heat tolerance bread and durum wheat genotypes [11] and various heat tolerance and sensitive chickpea genotypes [38]. Heat stress has been known to cause malfunction of photosystem (PS) II, reduced efficiency in electron transport, and increase in ROS production. Heat tolerance has been linked to increased tolerance of the photosynthetic apparatus [39]. ROS detoxification mechanisms are known to play important roles in protecting plants against HS [40, 41]. HT is closely correlated with increased capacity of scavenging and detoxifying of ROS. Induction of thermotolerance may be ascribed to maintenance of a better membrane thermostability and low ROS accumulation [36, 42] due to an improved antioxidant capacity [43].

HS responses among plants are mainly due to their inherent ability to survive and also to acquire thermotolerance to lethal temperatures. Genetic variability among crops for HT is mainly due to expression of different stress-responsive genes [44], acquisition of thermotolerance, and synthesis and accumulation of HSPs that are well correlated with the antioxidant defense system [45]. The maintenance of high membrane thermostability (MTS) is related to thermotolerance [46] and an important selection criterion which is determined by measuring the electrical conductivity. MTS has been successfully employed to assess thermotolerance in many food crops worldwide. The role of thermoprotectants such as HSPs, proline, glycine betaine, trehalose, brassinosteroids, salicylic acid, abscisic acid, polyamines, and nitric oxide in offering heat tolerance through endogenous synthesis or by exogenous application in different crops has been discussed in detail by Kaushal et al. [17]. Future pioneering studies in model plants can pave the way to identify key regulators as target for gene manipulation of stress tolerance in crop plants. It has also been envisaged that metabolic fingerprinting can be used as breeding tool for development of plants with the best potential to tolerate abiotic stresses.

4. Screening methodologies for heat tolerance breeding

Efficient screening procedures and identification of key traits in diverse donor or tolerant lines are very much essential toward breeding for heat tolerance. Screening for heat tolerance in the field is very challenging due to interactions with other environmental factors, but a wide variety of relevant traits are available that allows successful selection in the field conditions [47]. Tolerant genotypes may also be selected in controlled environments provided validated screening tools are in place. However, very often the more expensive controlled environments do not allow natural selection for other factors that interact with the heat stress tolerance mechanisms under field conditions, thus limiting its potential of wider applications in any trait screening [48]. Heat tolerance can be evaluated by a variety of viability assays, measurements, visual assessment, and testing under hotspot locations as described below.

i. *Cell membrane thermo-stability test*: Cellular membrane dysfunction due to stress leads to increased permeability and leakage of ions, which can be readily measured by the efflux of electrolytes from affected leaf tissue into an aqueous medium. This method was initially developed by the C.Y. Sullivan (University of Nebraska) in the late 1960s for assessing sorghum and maize heat tolerance. This has been used to study cellular thermostability for heat in wheat [49, 50], soybean [51], maize [52], and chickpea [53]. A positive correlation between membrane injury and grain weight was observed in wheat suggesting that membrane thermostability (MTS) may be better indicator of heat tolerance [54]. The membrane thermostability (MTS) can be measured as follows: $\text{MTS} = (1 - T1/T2) \times 100$, where $T1$ is conductivity reading after heat treatment and $T2$ is conductivity reading after autoclaving [55]. This has been tested in pearl millet and found effective under field condition and thus can be used for screening large number of genotypes.

ii. *Chlorophyll fluorescence measurement*: Heat damage in photosynthetic tissue can be measured by chlorophyll fluorescence [56]. Chlorophyll fluorescence has been linked to a thermal kinetic window established by enzymatic assays [57]. In this approach, leaf discs are exposed to a brief illumination period and the time of dark recovery of the fluorescence parameter F_v/F_o (ratio of variable to minimum chlorophyll fluorescence) is determined as a function of temperature. It is simple, quick, and inexpensive and holds promise for the rapid screening in a large number of crops, e.g., wheat [58] and legumes (pigeon pea, chickpea, groundnut, and soybean) [59].

iii. *Estimation of membrane lipid saturation*: A higher share of saturated fatty acids in membrane lipids increases the lipid melting temperature and prevents a heat-induced increase in the membrane fluidity. To maintain the membrane fluidity, plants increase the content of saturated and monounsaturated fatty acids, modulating their metabolism in response to increasing temperatures [60]. Thus, increasing the saturation level of fatty acids appears to be critical for maintaining the membrane stability and enhancing heat tolerance in creeping bentgrass (*Agrostis stolonifera*) [61].

iv. *Canopy temperature depression (CTD)*: The surface temperature of the canopy is related to the amount of transpiration resulting in evaporative cooling. A hand-held infrared thermometer (IRT) allows canopy temperature (CT) to be measured directly and easily during afternoon (13:00 and 14:30 h) remotely and without interfering with the crop. The viewing angle should be around 40° to the horizontal line above the canopy so as to avoid the confounding effect of soil temperature. Studies have shown that CT is correlated with many physiological factors: stomatal conductance, transpiration rate, plant water status, water use, leaf area index, and crop yield. Genotypes with cooler canopy temperatures can be used to indicate a better hydration status. Under heat stress conditions, CTD is related to vascular capacity, cooling mechanism, and heat adaptation. CTD has been proved to be a rapid and stable test that can be used for selection, e.g., wheat [62].

v. *Visual assessment methods/morphological methods*: Male sterility in cowpea [63]; pollen viability, stigma receptivity in maize [64]; grain sterility in rice [65]; asynchrony of male and female floral organ development in chickpea [66], leaf firing, tassel blasting, tassel sterility, pollen viability, silk receptivity and some agronomic traits in maize [67].

vi. *Selection in hot production environments*: It has been effective in wheat [68] and maize [67]. Heat stress screening, one criteria for selection of site is high VPD area where low yield was found associated with high VPD during all the growing season, high maximum temperature during most of the growing season, and low photothermal quotient corrected by VPD in the critical period of grain set before flowering. The relationships found are agronomically robust and provide a guide for experimental research but cannot be taken as proof of cause-and-effect because weather variables are confounded [69].

vii. *Pollen-based screening of genotypes*: Using this method, various heat tolerance accessions have been identified in different crop species, e.g., DG 5630RR in soybean [70], AZ100 in maize [71], and ICC1205 and ICC15614 in chickpea [28, 72].

All these techniques need to be validated for a large number of crops for their applicability in future. Regardless of the screening method, a key objective for plant breeders is to develop an effective set of thermotolerance markers which can be used for further implementation of breeding for heat tolerance in various crop species.

Identification of the superior germplasm for heat tolerance is essential for effective genetic manipulation through breeding process. However, identification of reliable and effective heat screening methods is a major challenge in conventional breeding to facilitate detection of heat tolerance lines [6]. Although a number of screening methods and selection criteria that have been developed/proposed by different researchers are briefly discussed above, however, the primary field screening methods also include seedling thermo-tolerance index (STI) [73], seed to seedling thermo-tolerance index (SSTI) in pearl millet [74], and heat tolerance index (HTI) as growth recovery after heat exposure in sorghum [75]. Thermo-tolerance screening at germination and early vegetative stage is found effective for pearl millet and maize [76]. These field techniques would help in preliminary identification of heat tolerance lines and thus proceed with minimum number of lines for further screening and validation. At the same time, breeder should ensure the quality of individual line data by comparing with tolerant check at all the times. This will facilitate the more reliable way of advancing the heat tolerance genotypes in any afore-discussed screening tools.

5. Breeding for heat tolerance: a next-generation breeding approach

The emphasis of crop improvement has been primarily on improving the economic yield in majority of the crop plants. This targeted breeding for economically desirable traits in crops has resulted in reduced genetic variability in the commercial varieties/hybrids to reach homogeneity in appearance. Hence, other essential genes that enable growth and reproduction in adverse environments can be absent from modern cultivars owing to their exclusion or loss during domestication or subsequent germplasm improvement, and linkage to non-beneficial loci or drag on productivity in optimal environments [1]. Useful loci and allelic variants often correspond to the downregulation or disruption of genes in susceptible genotypes. Hence, continued and broader mining of germplasm could be advantageous. Toward breeding for heat tolerance in crops, the initial search for tolerant sources should begin among the modern cultivars/advanced breeding lines and landraces of the species. The further search should be shifted to primary and secondary gene pool in sequence. For efficient utilization of the identified sources, we need to understand the underlying component traits, their inheritance including genes/QTLs and also association among important traits. All this information generated would facilitate targeted breeding for heat tolerance in crops.

5.1. Germplasm as sources for heat tolerance breeding

Wide variation for heat tolerance has been noted in both cultivated and related wild species among different crop plants (**Table 2**). Landraces are the varieties preferably handled by local farmers which are adapted to their native environment and could be the potential sources of HT. Significant variability for HT has been noted among wheat landraces, wherein tolerant ones tend to have higher leaf chlorophyll contents [64] and higher stomatal conductance, which can be utilized in breeding programs. Early maturity under high-temperature conditions is closely correlated with lesser yield losses in many crop plants. In wheat, early heading varieties performed better than later-heading varieties because they (i) produced fewer leaves per tiller and retained more green leaves, (ii) had longer grain-filling periods, and (iii) completed grain filling earlier in the season when air temperatures were lower [107].

The early maturity-led escape mechanism enabled addressing heat stress in wheat in Eastern Gangetic Plains and various South Asian locations [108, 109]. Selection for early flowering and maturity has also enabled to escape heat stress in spring-sown chickpea in Mediterranean

Crop	Heat tolerance sources*	HT associated trait/index	References
Wheat	CWI # 59788, 60155, 60391	Leaf chlorophyll content (LCC) and canopy temperature depression (CTD)	[77]
	Raj 4014 × WH730 (HT) RIL population (113)	1000-grain weight (TGW)	[78]
	Aegilops tauschii Coss.	Cell membrane stability and TTC-based cell viability	[79]
	A. speltoides Tausch; *A. geniculata* Roth	Spikelet fertility	[80]
	ALTAR 84/AO'S'; ALTAR 84/*A. tauschii*	Leaf chlorophyll, grain weight, and grain yield	[81]
	Moomal-2000, Mehran-89	Germination-related traits	[82]
	Jimai-22	Photosynthesis, PS II, carboxylation, and grain yield	[83]
	CB # 367, 333, 335	Grain development and survival	[84]
	WH # 1021, 730	Grain yield	[85]
	SYN # 11, 36, 44	1000-grain weight	[86]
Rice	Dular, Todorokiwase, Milyang23, IR2006-P12-12-2-2, Giza178	Spikelet fertility and seed set	[87]
	N22, Bala, Co 39; CG14 (*O. glaberrima*)	Spikelet fertility and seed set	[88]
	N22, NH219	Spikelet fertility and pollen viability	[89]
	Bala (HT) × Azucena RIL population	Spikelet fertility	[90]
	—	Spikelet fertility	[91]
	Oryza meridionalis	Growth rate and photosynthesis	[92]
	N-22	Spikelet fertility	[93]
	Nipponbare, Akitakomachi	Spikelet fertility	[94]
Maize	ZPBL 1304 (HT); (ZPBL 1304 × ZPL 389) F2 population (160)	Heat shock protein (HSP)	[95]
	B76, Tx205, C273A, BR1, B105C, C32B, S1W, C2A554-4	Leaf firing and tassel blast	[96]
	—	Grain filling duration, kernel dry weight, starch, protein, and oil contents	[97]
	Hybrids: YH-1898, KJ.Surabhi, FH-793, ND-6339, NK-64017	Yield	[98]
Pearl millet	9444, Nandi 32, ICMB 05666, ICMB 92777; ICMB 02333	Seed set	[21]
	F1's: H77/29-2 × CVJ-2-5-3-1-3; H77/833-2 × 96 AC-93	Seedling thermotolerance index (STI), seed to seedling thermotolerance index (SSTI), and membrane thermostability (MTS)	[99]
	CVJ-2-5-3-1-3; 77/371 × BSECT CP 1	STI and SSTI	[100]

Crop	Heat tolerance sources*	HT associated trait/index	References
Sorghum	DeKalb 28E	Pollen viability, seed set, seed yield, and harvest index	[101]
Cowpea	California Blackeye 27 (CB27)	Flower production and pod set	[102]
	B89-200, TN88-63	Seed yield	[103]
Common bean	SRC-1-12-1-182; SRC-1-12-1-48; 98020-3-1-7-2; 98012-3-1-2-1	Heat tolerance index (HTI), and heat susceptibility index (HSI)	[104]
Chickpea	ICCV 92944; several genotypes	Seed set	[105, 106]

*Heat tolerance sources include germplasm, breeding lines, populations, varieties/hybrids, wild species, etc.

Table 2. Heat tolerance sources and associated traits/indices of important food crops.

region and south India [32, 110]. The genetic variability for HT in rice could be exploited to screen germplasm and select cultivars that open flowers earlier in the morning or that maintain a high number of spikelets per panicle in warm environments [111]. A positive correlation between canopy temperature depression (CTD) and membrane stability with grain yield have been noticed and recommended as useful traits in selecting high-temperature tolerant genotypes in wheat [80, 112].

Generally, there is a strong correlation between pollen production and viability, anther dehiscence, and seed set. The anthers of heat tolerance rice cultivars dehisce more easily than those of susceptible cultivars under high-temperature conditions [90, 93]. Higher pollen grain fertility under HS may serve as an important criterion for measuring HT [113]. Similarly, gametic selection has been proposed as a viable option for addressing HS in maize [71]. In wheat, maintaining grain weight under heat stress during grain filling is a measure of HT [114, 115]. Hence, it has been proposed that high grain-filling rate and high potential grain weight can be useful selection criteria for improving HT [116]. Stay-green character has also been suggested for mass screening of wheat genotypes for HT [117]. However, this trait may be disadvantageous as it is associated with the tendency to retain the stem reserves [118].

The sources identified for heat tolerance using suitable screening method have to be confirmed for their level of tolerance across different temperature regimes, and breeding approaches have to be outlined to incorporate the tolerance into desirable agronomic background. Transfer of tolerance from cultivated germplasm could be easy but the chances of finding the sources of tolerance are quite less. The crop wild relatives may have higher level of tolerance, but their incorporation into cultivated background needs a perfect prebreeding/backcross program. The availability of molecular markers in crop plants of economic importance could rather be put to use by forward and background selection for introgression of desirable genomic regions associated with heat tolerance.

5.2. Conventional breeding: a traditional approach

The conventional breeding efforts toward development of heat tolerance cultivars are comparatively less among different crops. However, the emphasis has been quite recent and some efforts are being made in few important food crops such as wheat, rice, maize, tomato, potato, etc. Heat escape is an alternative mechanism through which plant completes its life cycle before the onset of heat stress. In durum wheat, this property has been utilized in development of early maturing genotypes such as Waha-1, Omrabi-5, and Massara-1 [119]. In rice, introgression breeding has facilitated the transfer of HT from "N22" to "Xieqingzao B" line by developing BC_1F_8 lines [120]. Additionally, the advanced line derived from Gayabyeo/N22 cross has offered HT as well as high yield [121]. In wheat, *Aegilops tauschii* was successfully used as a donor for incorporating HT-relevant component traits such as cell membrane stability and chlorophyll retention into cv. PBW550 through backcrossing [122]. More recently, attempts were made in wheat aiming at introgression of wheat-*Leymus racemosus* chromosome to cv. Chinese spring to enhance HT and better adaptation under heat stress [123]. Impressive accomplishments were achieved in harnessing the natural genetic variation for HT, and additional efforts are underway to introduce the heat tolerance QTLs/genes into different genetic backgrounds [88, 120]. In cotton, through pollen selection under HS, heat tolerance genes were transferred from a donor line "7456" (*G. barbadense* L.) to a heat-sensitive genotype "Paymaster 404" through backcrossing [113]. In sunflower, by using temperature induction response (TIR) technique, adequate genetic variability was observed for thermotolerance among the parental lines of the hybrid KBSH-1, viz. CMS234A, CMS234B, and 6D-1 [124]. The availability of potential donors for HT would encourage plant breeders not only to deploy these novel sources directly in breeding schemes but also to excavate the resilient alleles that underlie tolerance.

5.3. Physiological traits-based breeding

The efficiency of direct selection for yield improvement under stressed conditions is hindered by low heritability and a complex network of major and minor QTLs governing them [125, 126]. Breeding for high-yielding and heat tolerance lines is limited by the influence of environmental factors, poor understanding of genetic inheritance of HT, and less availability of validated QTLs/cloned gene(s) for HT in plants [127]. Physiological trait-based breeding would be an ideal strategy for incorporating gene(s)/QTLs that determine heat tolerance. Such an approach has been adopted in wheat at CIMMYT to develop heat tolerance varieties [128]. Toward breeding for heat tolerance, physiological traits that need to be considered include those related to canopy structure, delayed senescence, photosynthesis efficiency, less respiration rates, reproductive traits, and harvest index [127, 129]. Genetic variability has been assessed in several crop plants under HS for several physiological traits and suitable tolerant sources and associated traits have been identified (**Table 2**).

Genetic variability existing for the plant phenologies conferring HT need to be exploited. Alternatively, selection for morphophysiological traits involved in heat stress adaptation, and also indirectly associated with yield, can be utilized for enhancing HT in crop plants that has been explored in wheat [127]. Substantial genetic variability for photosynthetic rate under HS has been noted in wheat and rice, which would serve as a potential indicator of HS tolerance [130, 131]. While screening over 1000 wheat genotypes, the chlorophyll fluorescence was established as an important physiological parameter [132]. Canopy temperature depression (CTD) has been found to act as heat escape mechanism in cotton [133], while for HT in wheat [81, 134]. The cooler canopy temperature (CT) under HS caused higher yield in wheat [109, 135]. Under HS, the CTD, flag leaf stomatal conductance and photosynthetic rate together are found to be positively correlated with yield in wheat [62].

Membrane thermostability MTS is considered as a useful component for measuring HT, while assessing genetic variability in different crops [49]. Selection for MTS during anthesis stage under HS led to significant yield improvements in wheat [50]. Various physiological traits and their relative contributions to HT in wheat have been discussed in detail earlier [129]. Screening against HS based on parameters such as electrolyte leakage from cell membrane and chlorophyll fluorescence revealed negative association of membrane injury with specific leaf weight in some legume species including groundnut and soybean [59]. The combination of the two selection parameters, viz. high chlorophyll content and MTS, was implicated to carry out selections in Brassica and wheat [34, 136]. The relative cell injury level (RCIL) under HS could also be taken as a reliable index in determining HS tolerance in cotton [137].

The adaptation of root respiratory carbon metabolism can offer tolerance to soil temperature by managing the ion uptake load as reported in *Agrostis* species [138]. The efficient carbon and protein metabolism is known to confer higher thermotolerance to roots at 45°C in *Agrostis scabra* (a C_3 perennial grass species) [139]. In wheat, stay-green trait associated with CTD has been indicated as a strong indicator of HT [140]. However, stay-green trait is less important in the context of yield on account of disability in translocation of stem reserves to grain under HS [118]. Whereas, the conditions encompassing heat stress alone, as well as heat stress and drought, stay-green trait is measured as normalized difference vegetation index (NDVI) at physiological maturity exhibiting a positive correlation with the yield [141]. Therefore, physiological trait-based breeding remains a promising improvement strategy to develop heat tolerance genotypes without causing yield penalty.

5.4. Molecular markers in breeding for HT

The efforts by conventional breeding schemes have led to identification of several HT-relevant gene(s) and their inheritance patterns [6, 142]. Recent advances in marker discovery and genotyping assays have led to the precise determination of chromosomal position of the QTLs responsible for HT in different crops [90, 143–145]. The identification of markers linked to QTLs enables breeding of stress-tolerant crops by combining or pyramiding of QTLs governing tolerance to various stresses. An elaborative list of QTLs associated with HT in various crops along with details of mapping populations used, number of QTLs identified, associated markers, chromosomal positions, and phenotypic variation explained (PVE) has been summarized by Jha et al. [146]. Several major or minor QTLs and linked markers for HT have been identified in major food crops such as rice [90, 147–149], wheat [143, 144, 150–152], and maize [153, 154]. QTLs for several HT-related traits have been identified such as cellular membrane stability, pollen germination, and pollen tube growth in maize [153, 154]; stay-green trait, photosynthetic genes, and HSPs in sorghum [155]; and pollen viability in adzuki bean [156].

In wheat, one candidate SNP marker that clearly distinguished heat tolerance and heat-sensitive cultivars was identified [157]. For grain-filling rate (GFR) that governs grain yield in wheat under HS, 12 closely linked SSR markers were identified [158]. Using a SNP marker for a RIL population, five important genomic regions that offered HT in cowpea were identified [159]. Genome-wide as well as candidate-gene-based association mapping using SNP and DArT markers in chickpea could establish marker-trait associations for HT [160]. Recently, a major dominant locus *OsHTAS* (*Oryza sativa* heat tolerance at seedling stage) was identified from the genotype HT54, which contributed high-temperature tolerance at 48°C especially during seedling and grain-filling stages [161]. The QTLs identified using molecular markers in different crops provide a way to transfer the causative heat tolerance gene(s)/QTLs to elite cultivars. In parallel, the fine mapping accompanied by cloning of candidate QTL will help the breeders to commence marker-assisted breeding for incorporating HT in various important crops in near future.

For transfer of quantitative traits such as HT, molecular markers would enable the recovery of desirable genotypes in a precise and time-saving fashion [162]. Molecular markers have been useful in identifying heat sensitive advanced generation introgression lines in rice [120, 149]. The near isogenic lines (NILs) created by introducing desirable allele into the heat sensitive cultivar showed considerable reduction in the incidence of heat-induced injuries such as white-back kernels [163]. Recently in rice, a 1.5-Mb chromosomal region harboring a robust QTL controlling better grain quality under HS has been transferred from "Kokoromachi" to "Tohoku 168" using marker-assisted backcrossing [162]. The resultant NILs had improved grain quality over the susceptible parent.

DNA markers related to various HT/component traits have been identified in different crops such as rice [148, 161, 163–165], wheat [143–145, 150, 152, 166, 167], and cowpea [159, 168]. Once the markers associated with QTLs have been identified, the candidate QTLs can further be introgressed into elite lines through marker-assisted selection (MAS) strategies. One of the difficulties of developing superior genotypes for heat stress is that these traits are generally controlled by small effect QTLs or several epistatic QTLs [3]. To overcome this problem, approaches that can be employed are pyramiding several QTLs in the same genetic background using large populations through marker-assisted recurrent selection (MARS) or genomic selection (GS) [169].

MAS programs for complex traits such as heat tolerance are not effective mainly due to the genotype × environment and gene-gene (i.e., epistasis) interactions, which frequently result in a low breeding efficiency [170]. In contrast to MAS strategies which use markers for which a significant association with a trait has been identified, the GS method predicts breeding values using data derived from a vast number of molecular markers with a high coverage of the genome. Its novelty is that it uses all marker data as predictors of performance and subsequently delivers more accurate predictions [3]. Simulation studies indicated that GS may increase the correlations between predicted and true breeding value over several generations, without the need to re-phenotype. Thus, GS may result in lower analysis costs and increased rates of genetic gain [171, 172].

QTLs often do not translate well across genetic backgrounds and often produce smaller than expected adaptation effects. Thus, improving crop abiotic stress tolerance by exploiting the segregation of natural alleles rather seems challenging for such an adaptive QTL strategy [170]. When quantitative hereditary characteristics such as heat stress tolerance are involved, recurrent selection seems to be one of the most efficient methods in plant breeding. In multiple crosses, the probability is very small of obtaining superior genotypes that reunite all the favorable alleles. However, in this circumstance, a large segregating population is required, aspect that becomes unfeasible in practice [3]. The alternative is to adopt recurrent selection to gradually accumulate, by recombination cycles, the desirable and available alleles in different parents [173]. The main aim of a recurrent selection program is to increase the frequency of favorable alleles for traits of interest, while conserving the genetic variability. The major advantages are: (i) greater genetic variability obtained by intercrossing of multiple parents; (ii) greater opportunity for recombination through successive crossings; (iii) greater efficiency in increasing the favorable gene frequency since it is a repetitive and accumulative process; and (iv) greater facility to incorporate exotic germplasm in the population [174]. In potato breeding program at the Federal University of Lavras, heat stress tolerance genotypes were successfully developed using recurrent selection, which led to gains in tuber production with improved quality [175].

A current approach to the challenge of high-temperature tolerance is "physiological" or "developmental" trait breeding through recurrent selection using crop germplasm from regions with hot growing seasons [127]. In both cases, the targets are loci with high heritability that sustain yield at normal and elevated temperatures. The selection can be on combined heat and drought tolerance, as required by many crops. Recurrent selection has been successfully used to improve heat tolerance in wheat [176, 177] and potato [175]. In wheat, the stable introduction of chromosomes from its wild relative *Leymus racemosus* provided heat tolerance in hot and arid fields [123]. The heat- and drought-tolerant rice variety N22 (*aus* ssp.) has provided QTLs associated with high levels of HSPs in anthers, spikelets, and flag leaves associated with maintenance of yield under high night temperatures [148, 178]. Additional targeted developmental breeding in rice takes advantage of QTLs from *Oryza officinalis* that avoid heat-induced spikelet sterility by promoting dehiscence and fertilization in the cooler early mornings [179]. In time, these approaches may yield loci and knowledge that can accelerate improvement in heat tolerance in combination with drought tolerance.

Field trials under real stress conditions allow for conclusive remarks on stress tolerance and yield performance of a genotype. Development of more precise phenotyping tools that can be applied to field conditions is a prerequisite for enabling the assessment of the complex genetic networks associated with QTLs. The small, yet significant phenotypic changes delivered by introducing single genes into breeding material require precision phenotyping protocols and the resource capacity to carry these out on very large populations. The integrated approach for HT has been illustrated in **Figure 1** with details of whole breeding process.

5.5. Transgenic approach

Tolerant sources if not found in a given species or not giving enough protection, transgenic approach is an alternative option. However, it requires identification of the gene responsible for the desired trait, but poses no barrier for transferring useful genes across different species within the plant kingdom or even from animal systems. Genes of nonplant species could potentially be introgressed as well and generally, several combinations of beneficial genes could be transferred into the same plant [3]. With increasingly refined transformation and regeneration protocols, transgenic techniques are becoming attractive tool for designing both biotic and abiotic stress-tolerant crops via manipulating native genes or introducing gene(s) that lie beyond the crop gene pools [180]. Toward development of transgenics for HT, primarily the focus has been on engineering genes that encode transcription factors (TFs), HSPs, chaperones, organic osmolytes, antioxidants and plant growth regulators. This has been earlier summarized by Grover et al. [181]. Most of the transgenics developed for HT are mostly

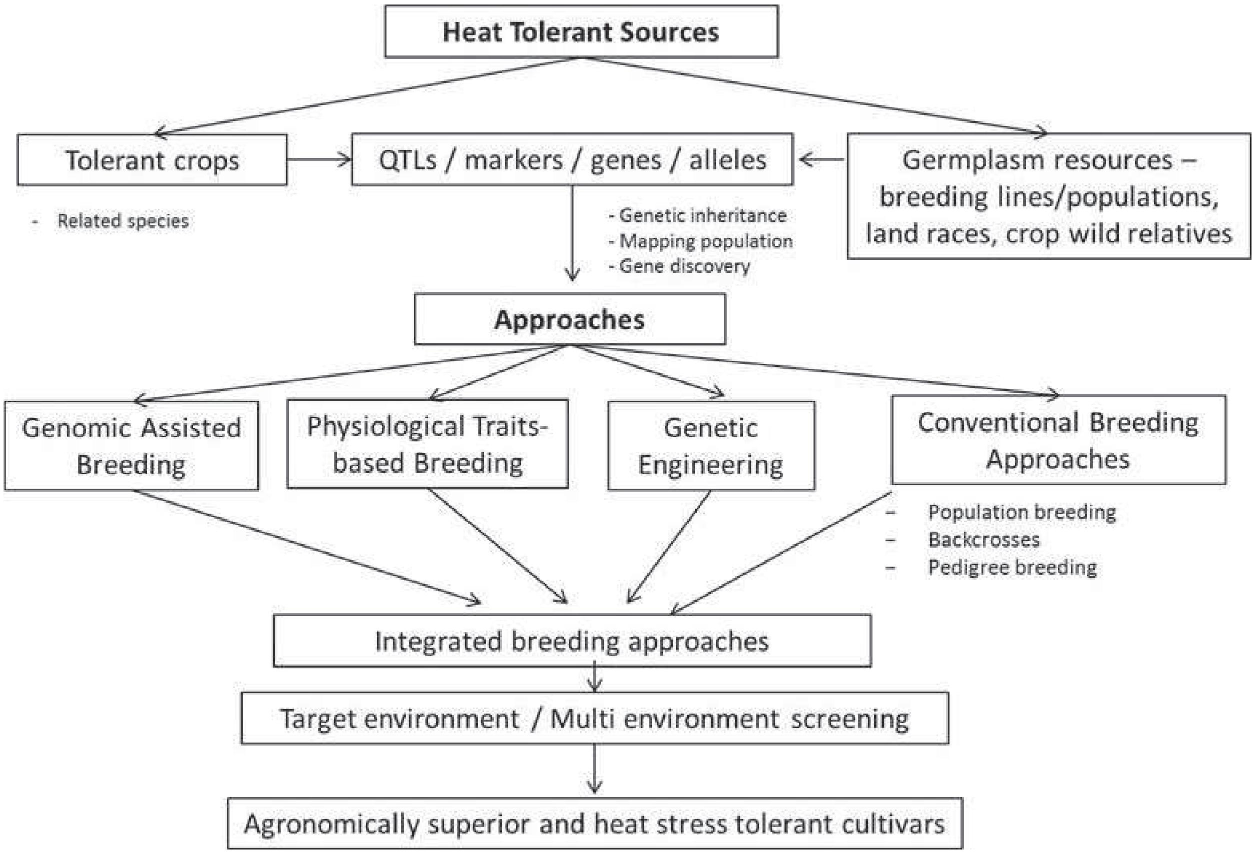

Figure 1. Schematic presentation of next-generation (integrated) breeding approach to develop heat tolerant cultivars.

in model plants such as *Arabidopsis*, tobacco, and rice. Further, it needs to be extended to other agriculturally important field crops.

To combine stress tolerance with high yield potential while avoiding the negative effects of a stress gene on plant growth under favorable conditions, strategies that spatially and temporally restrict transgene expression via tissue-specific and stress-inducible promoters are used [182]. Engineering promoters will facilitate gene pyramiding through genetic modification, addressing the issue of tolerance to multiple stresses at different stages of plant growth [183]. As an alternative, engineering with specific transcription factors and signaling components could be employed. Ultimately, this leads to the expression of their target transcriptome that consists of several genes involved in the response to stress. Transcriptome engineering emerges thus as a promising avenue for the development of abiotic stress-tolerant crops. Currently, however, plant genetic engineering is hampered by nonbiological constraints mainly related to the commercialization of transgenic crops, particularly in Europe [184]. Thus, the future commercial success of transgenic breeding will depend upon the development of clearly defined and scientifically based regulatory frameworks, and upon public acceptance of genetically modified plants and their produce [185].

5.6. Phenomics for precise and high-throughput phenotyping

Enormous sequence information is being generated through new-generation high-throughput DNA sequencing technologies [186]. But, precise, accurate, and high-throughput phenotyping of the traits on a large scale remains strenuous [187]. Field-based phenotyping (FBP) facilities are now being initiated to have a more realistic evaluation of the plant responses to environment [188]. Infrared thermography is being utilized for large-scale phenotyping of plants responses to abiotic stress including HT in wheat and chrysanthemum [189–191]. The chlorophyll fluorescence (Fv/Fm) and canopy temperature were assessed in wheat to identify HT types [132, 143, 192, 193]. Recently, high-resolution thermal imaging system was used to precisely measure the leaf temperature [194]. The phenotyping platforms established to screen for HT include "HTpheno" for image analysis [195] and "Rootscope" used to quantify heat-shock responses in plants [196]. In the near future, the new-generation phenomics platforms would allow cost-effective and user-friendly screening for HT in crop plants.

6. Conclusion and way forward

High temperatures reduce global crop productivity by limiting either through growth limit and grain set or grain filling, and can also affect the end-use quality of the grain by reducing its compositions. Thus, temperatures during flowering time are very common in the photosensitive genotypes or in crops growing in the arid and semi-arid regions of the world, where extreme heat is more frequent with the climate change. Breeders should consider and devise tools for flowering time heat tolerance screening which direct link to productivity of a crop. Tolerance to heat is difficult to assess in the field due to variation in the timing and severity of natural heat events; so, rapid and cost-effective screening tools should be in place for applied crop breeding. All the growing food crops are selected upon short duration and better yield in small piece of land through domestication; therefore, there is a long way to go in understanding the mechanisms and its dissections before we draw a truly comprehensive picture of heat tolerance breeding for food crops. At the same time, these type of research is essential to counteracting a future where climate change may lead to moderate-to-severe reduction in crop yield in tropical and subtropical regions by the end of this century. Finally, farmers and breeders are blamed for these development-oriented research activities which are not always true as connecting lab evidences to farmers' field still is undermanaged in agricultural systems, especially in public not in private sector (champions of seed systems). A day or two scientific and political conferences will never bring long-term comprehensive solution for climate-smart agriculture but building a strong global research network consortium is highly need of the century that would be a potential seed of the future climate-smart agricultural strategies to capture crop diversity including native food and fodder crops such as millets and grain legumes.

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