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Molecular Markers Mediated Heat Stress Tolerance in Crop Plants

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Abstract

Plants' developmental and growth rates can be influenced by temperature from seedling to maturity stage. Among the abiotic stress, heat stress has an impact on agronomic qualities at all phases of development; however, pre-flowering and anthesis stages are more vulnerable to high temperatures than post-flowering stages. As evident by massive yield losses in various food crops, the escalating adverse impacts of heat stress (HS) are putting the global food as well as nutritional security at great risk. In most of cereal crops, heat tolerance is a quantitative attribute that is influenced by a variety of genes and QTLs (quantitative trait loci). Attempts have been made over the last three decades to determine whether the condition under heat stress has been reviewed. Advances in molecular markers and quantitative genetics have made it possible to discover QTL that influence heat tolerance in cereal crop. Using various characteristics as indications of heat tolerance, many important QTL with significant effects on heat tolerance were discovered. There has been an increase in interest in using functional marker tools and technologies based on transcriptomics, proteomics, and metabolomics data to find and understand the molecular components of heat stress tolerance and the underlying mechanisms in recent years.

Keywords

Heat stress · Molecular markers · Quantitative trait loci

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2.1 Introduction

Heat stress severely limits the production of cereal crops in many areas of the world. The development of high yielding, heat stress tolerant cultivars will be aided by knowledge of the degree of genetic diversity within different grains, as well as their selection features (Sharma et al. 2016). Heat resistance is a multi-genetic trait, with different components of resistance controlled by different sets of genes in different tissues or at different stages of development. Plants react to extreme temperature stress by activating a series of events and turning on a slew of stress-responsive genes. However, the complex and poorly known mechanism of heat tolerance (HT), restricted access to precise phenotyping tools, and, most importantly, significant G X E effects all pose major roadblocks to breeding for improved HT (Jha et al. 2014).

DNA markers have a wide range of uses for strengthening a plant's genetic structure, including genetic identification of parents, genetic variation assessment, and the identification, genetic confirmation and establishment of high-resolution genetic linkage groups. For crop genetic study, a wide range of molecular markers is available. These markers are categorised according to how they are used, such as PCR (Polymerase chain reaction)-based vs. non-PCR-based. RFLP (Restriction fragment length polymorphism) markers are DNA markers that are based on hybridisation procedures. During the twentieth century, these markers were widely utilised in the field of molecular biology for gene mapping and other genetic analysis methods. Mullis and Faloona were the first to use PCR (1987).

PCR-based genetic markers dramatically lowered the time and cost required for genetic mapping utilising probe hybridisation. PCR is a technique for amplifying DNA sequences for a gene or locus in vitro. Primers are oligonucleotides that are tiny in size. Primers in a target sequence complement neighbouring gene sequences at both ends of the sequence. From a little quantity of a single pattern, the continual cycling of DNA replication and melting yields huge amounts of sequences of interest (Ullah 2009). PCR-based molecular markers such as single nucleotide polymorphisms (SNP), sequence-characterised amplified regions (SCAR) and simple sequence repeats (SSR) require gene sequence information from the sample to be used (Younis et al. 2020). Such markers are especially helpful in the mapping of stress-related genes' QTLs (quantitative trait loci) (Younis et al. 2020). When dealing with quantitative features like HT, molecular markers that allow for the exact and time-saving recovery of desired genotypes become essential (Shirasawa et al. 2013).

Because of the quantitative nature of heat, traditional breeding tactics have only made limited progress in generating heat-tolerant genotypes. Heat stress tolerance and unpredictability in the phenotyping and genotyping data of high quality are required for the discovery of quantitative trait loci (QTLs)/genes, as well as the development of markers for marker-assisted breeding, particularly for features that are difficult to breed. Heat tolerance, for example, is difficult to breed in the field with the help of traditional breeding approach.

2.2 Impacts of the Heat Stress on Major Cereal Plants

2.2.1 Effect of Heat Stress in Rice

The finding of genes/QTLs that increase tolerance to high temperatures has agricultural ramifications. Cao et al. (2003) were the first to map QTLs for heat tolerance in rice, based on percent spikelet fertility in a doubled haploid population produced from an IR64/Azucena hybrid. Following that, numerous research groups have used F2, backcross inbred lines (BIL) and recombinant inbred lines (RIL) populations to map QTLs for heat stress resistance, which were assessed at the time of heading in controlled environment circumstances (Shanmugavadivel et al. 2017). Rather than mapping QTLs based on phenotypic performance in a stress environment alone, the relative performance of genotypes under stress and control conditions can be utilised as an indicator to locate and map QTLs, which can then be employed in breeding crop varieties for stress tolerance (Raman et al. 2012). This has practical implications since genotypes with low production potential under control conditions generally demonstrate greater stress tolerance than genotypes with high yield potential.

For the heat stress breeding in rice, when cultivated rice var. of *O. sativa* ssp. Japonica and wild rice accession (*Oryza meridionalis*) grown under heat stress condition, wild rice grew faster and had less effect on photosynthesis at 45 °C (Scafaro et al. 2010). HS tolerance was higher in two rice genotypes, namely ‘Dular’ and ‘Todorokiw-ase’, at the booting stage at 39 °C, whereas ‘Milyang 23’ demonstrated tolerance at the flowering stage at 38 °C (Tonorio et al. 2013). Ginzberg et al., on the other hand, demonstrated tolerance at both the above-mentioned stages (2011). Under both controlled and HS circumstances, Jagadish et al. (2008) found that the genotype CG14 (*O. glaberrima*) achieved peak anthesis stage earlier than *O. sativa*.

Among the rice genotypes evaluated against heat stress, rice cultivar ‘N22’ demonstrated the highest level of HS tolerance (Jagadish et al. 2010a, b; Madan et al. 2012), with 64–86% spikelet fertility at 38 °C compared to the susceptible cultivars, namely ‘Azucena’ and ‘Moroberekan’, which had low fertility (up to 8%) (Jagadish et al. 2008). Higher pollen viability and spike fertility in rice genotypes ‘N22’ and ‘NH219’ were later confirmed under HS (Poli et al. 2013). Introgression breeding in rice has recently eased the transfer of HT from the ‘N22’ line to the ‘Xieqingzao B’ line by producing BC1F8 lines (Jiang-lin et al. 2011). Furthermore, an advanced line produced from the Gayabyeo/N22 cross has demonstrated HS tolerance as well as excellent yield (Manigbas et al. 2014). Given the relevance of anther dehiscence in conferring HS resistance, a rice study was conducted to assess anther characteristics, particularly the closure of locules under high temperatures (Matsui and Omasa 2002). As a result, the japonica rice cultivars ‘Nipponbare’ and ‘Akitakomachi’ have shown better fertility during flowering at 37.5 °C/26 °C (Matsui and Omasa 2002). Several QTLs for heat stress tolerance have been identified in rice (Table 2.1).

Molecular Marker and QTLs for Heat Stress Tolerance in Rice

With the development of molecular markers, several heat stress gene and responsive QTLs were discovered and transferred in the elite rice cultivars (Table 2.1). Three QTLs for HT were discovered on chromosomes 1, 4 and 7 using 245 restriction fragment length polymorphism (RFLP) markers in 98 backcross inbred lines (BILs) produced from the cross (Nipponbare 9 Kasalath) 9 Nipponbare (Zhu et al. 2005). During the grain-filling stage, these three QTLs explained 8.94%, 17.25% and 13.50% of the total PV, respectively (Zhu et al. 2005). In addition to QTL analysis, BSA utilising a set of SSR markers in 279 F2 (996 94 628) individuals resulted in the discovery of two loci linked to HT, namely RM3735 (chromosome 4) and RM3586 (chromosome 3), which controlled 17% and 3% of the total PV, respectively (Gui-lian et al. 2009).

Similarly, eight QTLs influencing spike fertility under high temperatures were found on chromosomes 1, 2, 3, 8, 10 and 11, among others (Jagadish et al. 2010a). From the genotype HT54, a large dominant locus OsHTAS (Oryza sativa heat tolerance at seedling stage) was recently found, which contributed strong temperature tolerance at 48 °C, particularly during the seedling and grain-filling stages (Wei et al. 2013). Similarly, in BC1F1 and F2 progeny generated from the cross IR64 9 N22, two significant QTLs for HT, qHTSF1.1 ($R2 = 12.6\%$) and qHTSF4.1 ($R2 = 17.6\%$), were found on chromosomes 1 and 4, respectively (Ye et al. 2012). QTL research comprising 90 introgression lines recently revealed five QTLs that explained PVs ranging from 6.83 to 14.63 percent (Lei et al. 2013). A QTL research comprising 90 introgression lines recently revealed five QTLs that explained PVs ranging from 6.83 to 14.63% (Lei et al. 2013). While transferring genes from wild rice (*O. rufipogon* Griff.) to the introgression line Y106, two QTLs for HS tolerance (qHTS1–1 and qHTS3) were discovered (Lei et al. 2013). In rice, sophisticated backcross was employed to create introgression lines in the background of 'Teqing', and later screening of these lines revealed one heat-sensitive line, 'YIL106' (Lei et al. 2013).

Heat-tolerant (XN0437T) and heat-sensitive (XN0437S) introgression lines were also recovered from another backcross inbred population derived from the cross (Xieqingzao B 9 N22) 9 (Jiang-lin et al. 2011). Heat-induced injuries such as white-back kernels were significantly reduced in nearisogenic lines (NILs) created by introducing the qWB6-allele from 'Hana-echizen' into the background of 'Niigata-wase' (Kobayashi et al. 2013). A 1.5-Mb chromosomal area bounded by markers ktIndel001 and RFT1 was transferred from 'Kokoromachi' to 'Tohoku 168' utilising marker-assisted backcrossing in a recent rice study. The grain quality of the NILs was much better than the susceptible parent 'Tohoku 168'. The chromosomal region in question had a strong QTL that influenced more than 20% of the PV and was responsible for higher grain quality under HS (Shirasawa et al. 2013). Table 2.1 contains a non-exhaustive list of DNA markers related to various HT/component features found in various crops. With such strong markers/candidate gene(s)/QTLs in place, early generation marker-based selection combined with a selective mating strategy would maximise genetic gains while breeding for HT.

Table 2.1 Important QTLs and linked marker in major cereal crops (Rice, barley, maize and wheat)

Crop	Markers linked to the QTLs	Name/No. of the QTL/loci	Chromosomal location/Linkage group (LG)	Mapping population	Range of PV (%)	References
Rice	–	*qhr1, qhr3-1, qhr4-3, qhr8-1, qhr11-1* and *qhr11-2*	1, 3, 4, 8 and 11	DH (IR64 9 Azucena)	1.3–22.8	Cao et al. (2003)
	RFLP	3 QTLs	1, 4 and 7	BIL Nipponbare/ Kasalath//Nipponbare	8.94–17.25	Zhu et al. (2005)
	–	9 QTLs thermotolerance for amylose content and gel	6 and 8	Nipponbare/Kasalath// Nipponbare	–	Zhu et al. (2006)
	SSR	WBK–*qWK1-1*, *qWK1-2*, *qWK2* and *qWK8*	1, 2 and 8	RIL (Chiyonishiki 9 Koshijiwase)	8.8–15	Tabata et al. (2007)
	SSR	2 putative QTLs associated with white-back kernels	4, 6	(Hana-echizen 9 Niigata-wase)	15.2–59.6	Kobayashi et al. (2007)
	SSR	*qHt3, qHt9a*	3 and 9	RIL (T219 9 T226)	7.6–11.4	Chen et al. (2008)
	SSR	3 QTLs (*qhts-2, qhts-3* and *qhts-5)*	LG 2, 3 and 5	RIL (Zhongyouzao No. 8 9 Fengjin)	6.59–10.72	Zhang et al. (2008)
	SSR	*RM3735* and *RM3586* loci	4 and 3	F_2 (996 94628)	3–17	Gui-lian et al. (2009)
	–	*qtl_2.3,qtl_4.1, qtl_1.1, qtl_2.2,qtl_8.2,qtl_1.1, qtl_8.1, qtl_10.1,qtl_1.1, qtl_3.4,qtl_8.3,qtl_10.1, qtl_1.1,qtl_11.1,qtl_10.1, qtl_1.1,qtl_10.1 and qtl_11.1*	1, 2, 3, 4, 8, 10, 11	(Bala 9 Azucena)	7–17.6	Jagadish et al. (2010a)

(continued)

Table 2.1 (continued)

Crop	Markers linked to the QTLs	Name/No. of the QTL/loci	Chromosomal location/Linkage group (LG)	Mapping population	Range of PV (%)	References
	SSR	2 QTLs	4 and 10	RIL (996 94628)	21.3–25.8 11.5–11.6	Xiao et al. (2011)
	SSR	*qPF4*, *qPF6*	4 and 6	RIL (996 9 4628)	15.1–9.31	Ying-hui et al. (2011)
	SNP	*qHTSF1.1*	1	BC_1F_1, BC_2F_2 and F_2 (IR64 9 N22)	12.6–17.6	Ye et al. (2012)
		qHTSF4.1	4			
	SNP	*OsHTAS* locus	9	F_1 and F_2 (HT54 9 HT13)	–	Wei et al. (2013)
	SSR	*qHTS1-1, qHTS1-2, qHTS2, qHTS3 and qHTS8*	1, 2, 3 and 8	Introgressed line YIL106 (Teqing 9 *O. rufipogon*)	6.83–14.63	Lei et al. (2013)
	SSR	(*qWB3*, *qWB4*, *qWB6* and *qWB9*) QTLs for WBK (*qKW3-1, qKW3-2, qKW6, qKW7* and *KW10*) QTLs for KW (*qDH1, qDH3 and qDH6*) QTLs for DTH	3, 4, 6 and 9 for WBK 3, 3, 6, 7 and 10 for KW 1, 3 and 6 for DTH	(Hana-echizen 9 Niigata-wase)	(31.5–36.8) WBK (8.4–12.1) DTH	Kobayashi et al. (2013)
	SSR SNP	QTL for white-back grains	6	RIL (Tohoku 168 9 Kokoromachi)	–	Shirasawa et al. (2013)
	SSR	9 QTLs	3, 4, 6, 8, 10 and 11	BC_2F_2 (OM5930x N22)	17.1–36.2	Buu et al. (2014)
	SSR	11QTLs	*1,2,3,4,5,7,8,10,11*	33 chromosome segment substitution lines [CSSLs (SL401–SL433)] and their parents Sasanishiki and Habataki,	–	Zhao et al. (2016)

	SNP	5QTLs	3,5,9,12	RIL derived from Nagina22, and IR64	–	Shanmugavadivel et al. (2017)
	SNP	6 QTLs	*1,4,6,7*	F8 recombinant inbred lines (RILs) obtained by crossing heat-tolerant ‘N22’ and heat-susceptible ‘IR64’	–	Kilasi et al. (2018)
	SSR	1 QTLs	*4*	F3 Uma × N22,	–	Waghmare et al. (2020)
	Bulked-segregant analysis (BSA)-seqmethod	1	*8*	F2: 3 population derived from a cross between Huanghuazhan (HHZ), a heat-tolerant cultivar, and 9311, a heat-sensitive variety	–	Chen et al. (2021)
Barley	SSR	34 putative QTLs	–	BC_2DH (Scarlett 9 ISR42–8)	–	Mohammed (2004)
	DArT markers	6 QTLs	4H, 5H and 6H	ND24260 x flagship doubled haploid population	2.6–5.9	Gous et al. (2016)
Maize	RFLP	6 QTLs (cellular membrane stability)	–	RIL (T232 9 CM37)	–	Ottaviano et al. (1991)
	RFLP	3–8 QTLs, heat-shock protein (HSP) expression	–	RIL (T232 9 CM37)	–	Frova and Sari-Gorla (1993)
	RFLP	5 QTLs for IPGG and six QTLs for IPTG	–	RIL (T232 9 CM37)	–	Frova and Sari-Gorla (1994)
	SNP	Fifteen QTL for leaf firing, leaf blotching, tassel blasting, reduction in spikelet size, plant death at early vegetative, middle vegetative and late vegetative stage	1,5,8, 9,10	B73 × NC350	–	McNellie et al. (2018)
			1,2,3	B73 × CML103	–	

(continued)

Table 2.1 (continued)

Crop	Markers linked to the QTLs	Name/No. of the QTL/loci	Chromosomal location/Linkage group (LG)	Mapping population	Range of PV (%)	References
	SNP	6 QTLs for heat susceptibility index (HSI) of five traits (leaf length: LL, plant height: PH, leaf scorching: SC, leaf greenness: SD, leaf growth rate: LR)	2,5,9,10	Segregating populations derived from pairwise crosses of four Dent (S067 = *D*1, P040 = *D*2, S058 = *D*3, S070 = *D*4) and four Flint (L012 = *F*1, L017 = *F*2, L043 = *F*3, L023 = *F*4) maize inbred lines	–	Inghelandt et al. (2019)
Wheat	SSR	1.4 genes, 2 QTLs	–	(Ventnor 9 Karl 92)	11–12.	Yang et al. (2002)
	AFLP and SSR	3 QTLs	LG1B, 5B and 7B	RIL (Kauz 9 MTRWA116)	27.3–44.3	Mohammadi et al. (2008)
	SSR	Common QTL for drought and heat stress traits	1B-a, 2B-a, 3B-b, 4A-a, 4B-b and 7A-a	RIL (Seri 9 Babax)	17 (yield QTL)	Pinto et al. (2010)
	AFLP, SSR	*(Q75%Gh.ksu-2A, Q75% Gh.ksu-2A,* Q75%Gh. ksu-3B) 75%G, *(Q25%Gh.ksu-2A, Q25% Gh.ksu-2A*) 25%G, (Q50%Gh.ksu-2A, Q50% Gh.ksu-6A) 50%G, (QMrsh.ksu-2A) (*QTmrsh.ksu-2A, QTmrsh.ksu-6A,QTmrsh. ksu-6B*) TMRS, *(QPgmsh.ksu-3A, QPgmsh.ksu-6B*) PGMS, (QFv/Fmh.ksu-7A) Fv/Fm	2A, 6B, 3A and 7A	RILs (Ventnor 9 Karl 92)	53 (75%Q), 28 (25%G), 63 (50%G), 40 (MRS), 55 (TMRS), 36.4 (PGMS), 11.2 (Fv/Fm)	Vijayalakshmi et al. (2010)

	SSR	5 QTLs	1A, 2A, 2B and 3B associated with HSI	RIL (Halberd 9 Cutter)	–	Mason et al. (2010)
	SSR	3 QTLs (*QSg. bhu-1A, QSg.bhu-3B* and *QSg. bhu-7D*)	1AS, 3BS and 7DS	RIL (Chirya3 x Sonalika)	38.7	Kumar et al. (2010)
	SSR	14 QTLs for heat susceptibility index (HSI), 7 QTLs co-localised for HSI and TD trait	1B, 3B, 4A, 5A, 5B and 6D	$F_{2:6}$ RIL (Halberd 9 Karl 92)	Individual QTL (4.5–19.3)	Mason et al. (2011)
	SSR	*Xgwm132-linked QTL*, *Xgwm577-linked QTL* and Xgwm617-linked QTL	6B, 7B and 6A	F_1, F_2 (Debra 9 Yecora Rojo)	3–25.	Barakat et al. (2011)
	SSR	12 QTLs	1A, 7A, (3B, 3A, 5B), 2D, 1D, (2A, 2B, 2D)	F_2 (Ksu106 9 Yecora Rojo)	22–64	Barakat et al. (2012)
	SSR	*QHthsitgw.bhu-2B, QHthsitgw.bhu-7B, QHthsitgw.bhu- 7D, (TGW), QHthsiYLD.bhu-7B, QlsYLD.bhu-7B, (YLD), QHthsigfd.bhu-2B (GFD),* QHtctd.bhu-7B (CTD), Qls-dm.bhu-7D (DM)	1B, 7D, (4A, 5D), (7A, 7B, 7D), 5A and 3B, BL, 7BL, 7DS (TGW), 7BL (YLD) 2B1 (GFD), 7BL (CTD) and 7DS (DM)	RIL (NW1014 9 HUW468)	9.78–20.34 (TGW), 13.21 (YLD), 20.15 (GFD), 19.81 (CTD) and 7.42 (DM)	Paliwal et al. (2012)
	DArT and SSR	2 QTLs, (*Q.Yld.aww-3B-2* and *Q.Yld.aww-3D)*	3B	DH, RIL (RAC875 9 Kukri)	22	Bennett et al. (2012)

(continued)

Table 2.1 (continued)

Crop	Markers linked to the QTLs	Name/No. of the QTL/loci	Chromosomal location/Linkage group (LG)	Mapping population	Range of PV (%)	References
	SSR	4 QTLs (*Qsdscon.tam-1B, Qsdsheat.tam-1D, Qsdscon.tam-4A* and *Qsdssta.tam-7A)*	LG 1B, 1D, 4A and 7A	RILs (Halberd 9 Cutter)	18–30	Beecher et al. (2012)
	SSR	Marker locus *gwm299*	3BL	DH, RIL (RAC875 9 Kukri)	–	Bonneau et al. (2013)
	AFLP, SSR, DArT	TKW QTLs linked or pleiotropic to DH and DM	4B and 7D-b	RIL (Barbax 9 Seri)	39 (TKW)	Lopes et al. (2013)
	AFLP, SSR, DArT	Few QTLs associated with ECG	7D-a and 7D-b	RIL (Barbax 9 Seri)	17.4 (ECG)	Lopes et al. (2013)
	AFLP, SSR, DArT	Consistent QTLs were detected for CTvg and CTgf	4A	RIL (Barbax 9 Seri)	16 (Ctgf)	Lopes et al. (2013)
	SSR	QChlc.tamu-1B (chlorophyll content), QFlt.tamu-2B	–	19 families consisting of 384 individuals developed from 3-way cross	–	Ali et al. (2013)
	SSR	7 QTLs associated with HSI traits, GFD, TGW, GY and CT 9 QTLs associated with GFD, TGW, GY and CT under HS	1D, 6B, 2D and 7A	DH (Berkut 9 Krichauff)	–	Tiwari et al. (2013)
	SSR	QTL for leaf and spike temperature depression and leaf wax	1B and 5A	RIL (Halberd 9 Karl 92)	8–12	Mondal et al. (2014)

	SNP	QTL for grain weight (SGW or GWS)	3B and 6B	DH (Drysdale and Waagan)	–	Shirdelmoghanloo et al. (2016)
	SSR	QTLs for various heat tolerance component traits	1B, 2B,3A,3B,5B, 7A AND 7B	Heat-tolerant accession of *Ae. Speltoides* pau3809 was crossed with Triticum durum cv. PDW274, and BC2F4-6 backcross introgression lines (BILs)	11.1–28.7	Awlachew et al. (2016)

2.2.2 Effect of Heat Stress in Wheat

Because of early senescence and acceleration of grain-filling activities in wheat (Paulsen 1994) and shortening grain filling duration (GFD) together with restriction of carbon absorption, terminal heat stress during crop growth is a major environmental factor that affects grain yield (GY). When the temperature was raised from 15 to 20 °C (day/night) to 40 to 15 °C (day/night) on the third day after anthesis, kernel weight loss was estimated to be up to 23% (Stone and Nicolas 1994). By 2050, approximately 51% of the Indo-Gangetic plain (IGP) may be classed as a heat-stressed, short-season producing mega-environment (Ortiz et al. 2008).

When comparing the wild progenitor *Aegilops tauschii* Coss. to the tolerant cultivar ‘C273’ for critical HT-related properties including cell membrane stability and ‘TTC’ (2, 3, 5-triphenyl tetrazolium chloride)-based cell viability, wide variation was found in the wild progenitor *Aegilops tauschii* Coss (Gupta et al. 2010). *A. tauschii* was recently employed as a donor for backcrossing cultivar ‘PBW550’ to incorporate HT-relevant constituent features like cell membrane integrity and chlorophyll retention (Sehgal et al. 2011). Similarly, the discovery of *A. speltoides* Tausch and *A. geniculata* Roth species with HS tolerance in the reproductive stage brings up new possibilities for HT gene inclusion in hexaploid wheat in the near future (Pradhan et al. 2012a).

By screening wheat genotypes for drought and HS stress, the ALTAR 84/AO′S′ and ALTAR 84/A. tauschii genotypes were shown to be the least impacted, particularly at two important stages: (1) emergence to anthesis and (2) emergence to post-anthesis (additional 21 days after anthesis) (Pradhan et al. 2012b). More recently, efforts have been done in wheat to introduce the wheat-Leymus racemosus chromosome into the ‘Chinese spring’ cultivar in order to improve HT and better adapt to HS (Mohammed et al. 2014). Hede et al. (1999) investigated the potential of wheat landraces in search of new sources of HT, and as a result, three Mexican landraces with superior canopy temperature depression characteristic were identified. Furthermore, two genotypes, ‘Moomal-2000’ and ‘Mehran-89’, performed better at 20–30 °C in terms of germination-related characteristics (Buriro et al. 2011). While researching photosynthetic activity in flag leaves during the grain-filling stage recently, Feng et al. (2014), reported that the cultivar ‘Jimai22’ has a 6% lower drop in grain yield under HS. Furthermore, this cultivar provided benefits such as PSII stability and carboxylation activity under HS. On the basis of maximum grain development and higher survival under challenged conditions, evaluation in the terminal growth stage focusing on the stay green trait resulted in the discovery of three potential genotypes (Rehman et al. 2009). In wheat, promising genotypes ‘WH1021’ and ‘WH730’ with increased yield under HS have just been developed (Dhanda and Munjal 2012). Similarly, using cluster analysis of morphological features and ISSR markers, three synthetic wheat lines, SYN 11, SYN36 and SYN44, were pronounced to be very heat resistant (Sharma et al. 2014).

Molecular Markers for Heat Stress in Wheat and Important QTLs
Many genes are implicated in stress tolerance because abiotic stimuli cause many physiological and biochemical changes. The identification of functional markers and, as a result, enhanced selection efficiency for improved heat stress tolerance will be aided by understanding the molecular and genetic underpinnings of stress tolerance (Table 2.1).

Senescence-related traits were evaluated in wheat and nine QTLs were discovered across distinct chromosomes (2A, 6A, 6B, 3A, 3B and 7A) (Vijayalakshmi et al. 2010). Using metrics such as spike yield and temperature depression (TD) of spike, a heat susceptibility index (HSI) was created, and a total of 14 QTLs related with HSI were found (Mason et al. 2011). Four QTLs for increased baking quality under HS circumstances were discovered on wheat chromosomes 1B, 1D, 4A and 7A after a sodium dodecyl sulphate sedimentation (SDSS) test (Beecher et al. 2012).

In 148 RILs (NW1014 9 HUW468), three significant QTLs related with HT were found on chromosomes 2B, 7B and 7D, accounting for up to 20% PV (Paliwal et al. 2012). BSA was used in an F2 population of Ksu106 9 Yecora Rojo employing SSR markers, with grain-filling rate (GFR) as a critical feature governing grain production in wheat (Barakat et al. 2012). As a result, 12 SSR markers in wheat were discovered to have a strong relationship with GFR. Kirigwi et al. (2007) also found QTLs for GFR on the 4A chromosome. In wheat, a large QTL with a 17 percent yield variation was discovered under HS on chromosome 4A (Pinto et al. 2010). Because single nucleotide polymorphism (SNP) markers are amenable to automated genotyping tests, one possible SNP marker was recently revealed in wheat that separated heat-tolerant (K7903) from heat-sensitive (RAJ4014) cultivars (Garg et al. 2012).

Fufa et al. (2005) used 51 SSR markers and ten morphological features in 30 bread wheat cultivars to investigate diversity analyses. Because morphological features continue to be an efficient technique of regularly evaluating multiple wheat elite lines developed in a breeding programme for breeders, the positive correlation from the outcome has crucial implications. Sharma et al. (2016) also looked at genetic diversity using 41 polymorphic simple sequence repeat (SSR) markers and 15 phenotypic variables averaged across stress and non-stress field conditions. It is critical to perform rapid and precise introgression of HT-related gene(s)/QTLs into heat-susceptible cultivars in order to restore genotypes with improved heat stress tolerance.

2.2.3 Effect of Heat Stress and Molecular Markers in Maize for Heat Stress

The current pace of maize yield growth, when combined with population expansion and projected climate change consequences, will not be enough to meet future food demand. The current tendency of growing maize in the winter, particularly in South Asia’s Indo-Gangetic Plains, has increased the chances of maize crops being exposed to suboptimal temperatures. In the winter, the average minimum temperature is below 5 °C, notably in the Indo-Gangetic Plains' North-West Plains. Under growing climate variability, improving crop yield and livelihoods for smallholders will necessitate a multi-disciplinary approach to crop genetic modification (Hansen et al. 2019; Prasanna et al. 2021). When it comes to resource allocation, temperate maize has gotten a lot more over time than tropical maize (Andorf et al. 2019).

In tropical regions, however, the potential to directly benefit smallholder farmers' lives through better maize yields is greater. According to a recent study, improvements in maize breeding have benefited an estimated 53 million individuals in Sub-Saharan Africa (Cairns and Prasanna 2018). In order to provide farmers with a consistent stream of improved varieties, increasing genetic gain, including a reduction in breeding cycle time, is critical (Atlin et al. 2017; Andorf et al. 2019; Bailey-Serres et al. 2019). Heat stress is becoming a serious limitation to maize output on its own and in combination with drought (Cairns et al. 2013). Depending on the emissions scenario, temperatures are expected to rise by at least 1 °C (Zhai et al. 2020). A 2 °C increase in temperature would result in a 20% drop in maize yields, while a 20% decrease in precipitation would result in a 20% reduction (Lobell and Burke 2010).

In most tropical semi-arid maize-growing locations, notably in South and Southeast Asia, frequent spells of high temperatures (typically above 35 °C) combined with moisture stress are a common occurrence, impacting maize reproductive growth in particular.

Aside from early development, the blooming stage of the maize crop is especially vulnerable to cold temperatures, as it causes male sterility (Heslop-Harrison 1961) or weak anthesis, and hence poor grain set (Thakur et al. 2010; Enders et al. 2019). Maize crops in northern India and Nepal's Tarai region were subjected to extreme cold stress during the winter seasons of 2002–2003, 2009–2010 and 2017–2018, resulting in significant production losses (Enders et al. 2019). Waterlogging affects more than 18% of the entire maize production area in South and Southeast Asia, resulting in yearly production losses of 25–30% (Zaidi et al. 2010; Cairns et al. 2012). Soil waterlogging is a common occurrence in areas with unpredictable and strong rainfall and low soil drainage ability. Because maize is a tropical non-wetland crop, it is particularly sensitive to waterlogging at practically all phases of development, especially before tassel emergence (Zaidi et al. 2004; Kuang et al. 2012). Salinity stress has been shown to impact maize seed germination, vegetative growth and reproductive capacity (Munns and James 2003; Abdullah et al. 2001; Kaya et al. 2013).

The molecular and physiological consequences of heat stress in maize seedlings were studied (Table 2.1) in controlled surroundings and then in field circumstances using managed heat stress phenotyping (Cairns et al. 2013; Rattalino-Edreira and Otegu 2013). Under HS, five QTLs influencing pollen germination and six QTLs controlling pollen tube growth were discovered using RFLP markers in a RIL population (Frova and Sari-Gorla 1994). Previously, six QTLs in maize that influenced cellular membrane stability under HS were found using the same mapping population (Ottaviano et al. 1991). Frey et al. (2016) created a heat susceptibility index to characterise segregating families of temperate maize populations developed for heat stress tolerance characterisation and discovered two QTL hotspots on chromosomes 2 and 3 for a variety of heat stress-related characteristics. The area previously discovered for pollen viability under heat stress was shown to be co-localised with QTLs identified on chromosome 3 (Frova and Sari-Gorla 1994). On chromosome 9, QTL hotspots for heat susceptibility index calculated for leaf blistering and plant height under heat stress were also discovered (Inghelandt et al. 2019).

2.2.4 Effect of Heat Stress and Molecular Markers in Barley for Heat Stress Adaptation

Wild barley, *Hordeum vulgare* ssp. spontaneum L. (hereinafter referred to as *H. spontaneum*), is thought to be a drought and heat-tolerant progenitor of barley (*Hordeum vulgare* ssp. vulgare L.) cultivars (Hubner et al. 2009; Bahrami et al. 2019; Arzani and Ashraf 2016). The main selective factors underpinning the evolution of wild barley (*H. spontaneum*) over the Fertile Crescent have been proposed to be high temperatures and aridity (Hubner et al. 2009). Due to a lack of genetic variety in modern barley cultivars, the wild spontaneum subspecies' genetic variability must be extensively exploited in order to generate barley cultivars with greater heat tolerance (Table 2.1). A breeding effort disucussed above could provide the different benefits for heat adaptation of wild subspecies (Bahrami et al. 2019).

It's also been suggested that *H. spontaneum*, which has evolved effective high-temperature tolerance techniques to adapt to the hot climate in south-west Iran, could be used as a rich genetic resource for enhancing the heat stress tolerance of farmed barley. The physiological basis of *H. spontaneum* resistance to both heat (Bahrami et al. 2019) and salinity (Ebrahim et al. 2020) conditions has recently been proven using this rich genetic resource of *H. spontaneum* germplasm from West-Iran. Drought tolerance in barley can be improved by identifying genomic areas associated with drought-related characteristics. On a collection of 107 barley accessions tested under well-watered and drought-stressed conditions, association mapping was used to study the correlations between 76 SSR markers and six drought-related characteristics.

All examined traits showed highly significant differences between well-watered and drought-stressed environments. With SSR markers, there was a significant level of polymorphism. For drought-related phenotypes, a total of 36 significant marker–trait correlations were discovered. Between markers on separate chromosomes, there was a high degree of significant LD ($> 61\%$), implying epistatic interaction. Several molecular markers are significantly related with multiple phenotypic traits, implying that pleiotropic or indirect effects may exist. Individual marker–trait relationships explained 6.33% to 35.78% of the phenotypic variation (Abou-Elwafa 2016).

Comadran et al. (2009) found significant marker–trait associations in a barley population that represents a historical survey of barley diversity in Mediterranean environments, with a large proportion of genetic variation underlying the different mechanisms for adaptation to drought-prone environments. The role of physiological characteristics such as reserved metabolites, as well as the genetic control of heat stress in barley, is little understood in comparison to other abiotic stresses like drought. There have been few research on the mapping of quantitative trait loci (QTL)/genes that govern heat tolerance in barley during flowering and seed set. The six heat stress QTLs on chromosomes 3H, 4H, 5H and 6H in barley are an exception. The QTL on chromosome 5H was found to be highly similar to a previously discovered QTL for root length and root–shoot ratio (Gous et al. 2016).

The transcriptome alterations of genes in barley during heat stress were the subject of two investigations. Mangelsen et al. (2011) discovered that heat stress enhanced the expression of 958 genes, whereas 1122 genes were downregulated in growing barley grains, using the Affymetrix 22 K Barley1 GeneChip microarray. The downregulation of genes tailors the manufacture of storage chemicals as well as cell growth, demonstrating that heat stress hampered grain formation quickly. Templer et al. (2017) discovered 25 metabolic QTL in barley under heat and/or drought stress, three of which matched with critical player genes in the production pathways of these metabolites. Weichert et al. (2017) looked at how the barley sucrose transport gene (HvSUT) affected seed quality and yield in wheat during heat stress.

They discovered that increasing the expression of this gene in a winter wheat cultivar (cv. Certo) boosted grain production, grain size and above-ground biomass by exposing plants to heatwaves. The heatwave reduced grain production, above-ground biomass, grain size, starch and water content in the wild-type, but increased grain sucrose content. Dawood et al. (2020) investigated a group of 60 Egyptian spring barley genotypes that had been subjected to heat stress testing in the field. Several features were scored to assess changes in yield-related traits and grain-reserve metrics as markers of heat tolerance. Using 16,966 single nucleotide polymorphisms, single-marker analysis was used to identify the causal genes that regulate the variation of all attributes of interest (SNP). The BC6 lines produced in this study can be used to unravel the involvement of the LTP2 gene in the response to various abiotic stressors, such as drought, salinity and heat. The BC6 lines established in this work can be used as a one-of-a-kind plant material to investigate the role of the LTP2 gene. The LTP2 may be important in lipidome change in response to abiotic stress because of its role in lipid transfer.

2.3 Summary

Heat stress is a major cause of yield loss, and heat events are predicted to become more often and longer in the future. Heat stress has become a major limiting factor in agricultural productivity since numerous crops are vulnerable to it, especially during the reproductive and early grain-filling stages. Because it is a polygenic regulating feature, heat tolerance is difficult to define. Until recently, there was no direct method for choosing heat-tolerant plants, but certain characteristics, such as canopy temperature depression and membrane thermo-stability, appear to be good indicators of plant heat tolerance and can be used in traditional breeding. It's vital to understand how heat stress affects wheat production and quality, as well as to provide useful indicators and genes for genetic improvement. Various mapping approaches and genetic research have greatly contributed in gaining a better understanding of the genetic roots of heat stress resistance in wheat. These studies discovered molecular markers connected to heat tolerance that could be utilised to diagnose MAS. However, there are few reports of molecular markers being utilised in cereal crop breeding. Increased knowledge of the molecular mechanisms of heat tolerance, on the other hand, is expected to pave the way for the development of heat-tolerant plants with acceptable commercial yields. Although several wheat genes have been successfully changed to improve heat stress tolerance, their function in different genetic backgrounds and under different heat stress settings remains unknown.

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