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REVIEW

Breeding approaches and genomics technologies to increase crop yield under low-temperature stress

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Abstract

Key message **Improved knowledge about plant cold stress tolerance offered by modern omics technologies will greatly inform future crop improvement strategies that aim to breed cultivars yielding substantially high under low-temperature conditions.**

Abstract Alarmingly rising temperature extremities present a substantial impediment to the projected target of 70% more food production by 2050. Low-temperature (LT) stress severely constrains crop production worldwide, thereby demanding an urgent yet sustainable solution. Considerable research progress has been achieved on this front. Here, we review the crucial cellular and metabolic alterations in plants that follow LT stress along with the signal transduction and the regulatory network describing the plant cold tolerance. The significance of plant genetic resources to expand the genetic base of breeding programmes with regard to cold tolerance is highlighted. Also, the genetic architecture of cold tolerance trait as elucidated by conventional QTL mapping and genome-wide association mapping is described. Further, global expression profiling techniques including RNA-Seq along with diverse omics platforms are briefly discussed to better understand the underlying mechanism and prioritize the candidate gene (s) for downstream applications. These latest additions to breeders' toolbox hold immense potential to support plant breeding schemes that seek development of LT-tolerant cultivars. High-yielding cultivars endowed with greater cold tolerance are urgently required to sustain the crop yield under conditions severely challenged by low-temperature.

Keywords Cold tolerance · Genomics · QTL · Genetic resource

Introduction

In view of the rising temperature extremities, LT stress remains one of the major abiotic factors that severely impact the normal growth and development of the plant. LT stress poses serious threat to crop production worldwide, especially in temperate and high-elevated regions (Sthapit and Witcombe 1998). For instance, the enormity of the risk becomes apparent from the area (15 mha) that is constrained annually by LT stress across the globe (IRRI 1979). Similarly, almost 7 mha of rice-growing area in South and Southeast Asia was constrained (Sthapit and Witcombe 1998). Given the tropical and subtropical origin, rice is rendered vulnerable to LT stress below 15–20 °C causing considerable yield loss (Yoshida et al. 1996; Nakagahra et al. 1997). In recent years, significant yield loss in rice due to LT stress was noted in Japan (Shimono et al. 2007), Korea (Lee 2001), and Australia (Farrell et al. 2001; Singh et al. 2005). In China, Li and Guo (1993) reported annual loss of 3–5 million tonnes of rice due to LT. Likewise, Crimp et al. (2016) concluded that 30% of the wheat-growing area in Australia is subject to frost-related events. Events of 'Post-head-emergence frosts (PHEF)' witnessed in wheat in subtropical, Mediterranean and temperate regions are considered to be devastating (Boer et al. 1993; Fuller et al. 2007),

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leading to severe yield penalty such as the instance of 85% crop loss in Australia (Boer et al. 1993). Further, Zheng et al. (2015a, b) assessed the yield loss in wheat in Australia due to frost via simulation and crop modeling study. LT stress covers injuries in plants caused by chilling (<20 °C) and freezing (<0 °C) (Thomashow 1999), hampering key metabolic processes (Pomeroy et al. 1985). For example, nonfunctioning of chloroplast (Allen and Ort 2001) impairs photosynthesis and, ultimately, causes cell death (Gomez et al. 2004). The negative impacts of LT stress on different growth stages include poor germination, seedling stunting, and reduced tillering (Kaneda and Beachell 1974). Importantly, reproductive phase, especially male reproduction processes (De Storme and Geelen 2014), remains most sensitive to LT, adversely affecting stages from gamete formation to fertilization stage (Thakur et al. 2010). In rice, spikelet sterility has been reported owing to inhibition or disruption in pollen development or reduced pollen grains in anther (Satake 1969, 1976; Mackill and Lei 1997; Shimono et al. 2007; Sakata et al. 2014). Similarly, inhibition in sporogenesis, pollen germination (Clarke and Siddique 2004), abortion of flower and pod were reported in chickpea due to LT (Nayyar et al. 2005; Kumar et al. 2011). Instances of seedling growth inhibition and low yield were also seen under LT stress in maize (Rymen et al. 2007). The negative impacts of LT at different growth stages in plants are discussed elsewhere (Croser et al. 2003; Thakur et al. 2010; Yadav 2010). Critical low temperatures causing damage in different crops are listed in Table 1.

Given the above description, cold acclimation remains a key mechanism adapted by plants to cope with LT stress (Thomashow 1999). To cope with the LT stress, plant increasingly activates “defense-related antioxidative” mechanism and induces genes producing molecular chaperones and cryoprotectants (Gill and Tuteja 2010; Guy and Li 1998).

Improved breeding techniques delivering genotypes that are able to sustain yield under LT are urgently required. Recent progress in genomics has provided a plethora of new-generation molecular tools to strengthen crop improvement schemes. Crop improvement schemes informed by the modern genomics hold great potential to sustain crop production under frequently witnessed temperature extremities, especially the LT stress. Here, we offer an overview on the molecular mechanism describing LT tolerance in plants, and discuss the role of candidate genes/QTLs vis-a-vis LT stress. The significance of plant

Table 1 Critical low temperatures causing damage in major crops

Crop	Critical temperature	Stages affected	References
Rice	<10 °C	Germination and vegetative	Yoshida (1981)
Rice (subtropical region in northern Laos)	< 15 °C	Germination affected	Sihathep et al. (2001)
Rice	15 to 20 °C	Growth rate and metabolism	Kabaki et al. (1982), Takanashi et al. (1987)
Rice	13 to 15 °C (night)	–	Farrell et al. (2006)
Rice	15 ± 5 °C	Reproductive stages viz., spikelet sterility	Nishiyama et al. (1969)
Rice	20 °C (sensitive genotypes) 15 °C (tolerant genotype)	Reproductive stage	Satake (1976)
Wheat (Australian winter cultivar)	−5 to −2 °C	–	Single (1985)
Winter wheat (non-acclimated)	−4 to −2 °C	Leaf injury	Drozdov et al. (1984)
Wheat (acclimated)	−13 °C	–	Drozdov et al. (1984), Porter and Gawith (1999)
Wheat seedling (acclimated winter)	Between −6 and −8 °C	–	Fuller et al. (2007)
Wheat seedling (non-acclimated winter)	−5 °C for non-acclimated	–	Fuller et al. (2007)
Winter wheat	<−5 °C	Ear emergence to anthesis	Spink et al. (2000)
Barley	−5 C to −4 °C	–	Frederiks et al. (2011)
Chickpea	15 °C in Indian subcontinent	Flower and pod abortion	Srinivasan et al. (1998)
Maize	10 °C	Seedling growth ceases	Miedema and Sinnaeve (1980)
Maize for temperate, subtropical, and lowland tropical	<9 to 10 °C	Tassel initiation affected	Ellis et al. (1992)
Sorghum	<10 to 15 °C	Chilling injury	Peacock (1982)

genetic resources to develop LT-tolerant cultivars in various crops is highlighted. We also examine the literature dealing with modern QTL mapping methods such as GWAS to genetically dissect plant LT stress tolerance. The relevance of emerging omics platforms including transcriptomics and proteomics is also discussed.

Cold tolerance in plants: underlying mechanism and key players

Plants respond to LT stress through perceiving stress stimuli subsequently subjected to precisely regulated signaling pathways (reviewed by Hughes and Dunn 1996; Thomashow 1999; Xin and Browse 2000; Chinnusamy et al. 2007, 2010; Zhou et al. 2011; Knight and Knight 2012; Miura and Furumoto 2013; Shi et al. 2015; Zhao et al. 2015a). As reviewed by various researchers (Chinnusamy et al. 2010; Shi et al. 2015), transmission of signals pertaining to cold stress in plants occurs via pathways regulated in C-repeat binding factor (CBF)-dependent or CBF-independent manner. The perception of LT shock in plants is followed by changes in physico-chemical properties in cell membrane involving membrane fluidity (described as "rigidification effect") and proteins (Orvar et al. 2000; Chinnusamy et al. 2007, 2010). Subsequently to it occurs a transient influx of cytosolic Ca^{2+} causing regulation of cold-responsive (*COR*) genes (Knight 2000). This Ca^{2+} signal is transduced to nucleus via activation of Ca^{2+} sensors viz., CaM (calmodulin) (Miura and Furumoto 2013; Yang et al. 2010), Ca^{2+}-dependent protein kinase (CDPKs), and CaM-binding transcription activators (CAMTA) embedded in nuclear membrane (Knight et al. 1996). In turn, kinase cascades are switched on to activate inducer of CBF expression1 (ICE1), which activates transcription of *CBF* genes (Stockinger et al. 1997; Liu et al. 1998; Novillo et al. 2004, 2007). Ultimately, these CBFs induce CRT/DRE-regulated downstream target *COR* genes (Gilmour et al. 1992; Kurkela and Franck 1990; Lin and Thomashow 1992; Jaglo-Ottosen et al. 1998; Kizis et al. 2001), thereby conditioning cold tolerance in plant (for details see Xiong et al. 2002; Chinnusamy et al. 2007, 2010; Zhou et al. 2011; Miura and Furumoto 2013; Shi et al. 2015; Zhao et al. 2015a, b). However, the complete mechanism of LT stress signaling pathways and tolerance still remains elusive and needs intensive future study.

To date, the "ICE1-CBF-COR transcriptional cascade" pathway is the best characterized with regard to LT acclimation (Shi et al. 2015). Upon sensing LT stress in plant, various kinds of CBF/DREB1 transcription factors (TFs) belonging to ethylene-responsive element binding factor/APETALA2 (ERF/AP2)-type TF (Mizoi et al. 2012) bind to CRT/DRE *cis* elements and CBF regulons genes. This in turn induces *COR* genes such as *COR15a* in Arabidopsis (Artus et al. 1996) and *WCS120* in wheat (Houde et al. 1992), which encode proteins akin to "cryoprotective proteins" to rescue plant from cold shock (Thomashow 1999). Mostly, three types of CBFs (CBF1, CBF2 and CBF3) (Liu et al. 1998; Thomashow 1998; Stockinger et al. 1997; Medina et al. 1999, 2011) are reported to control expression of *COR* genes in *Arabidopsis* (Gilmour et al. 2000, 2004). Importantly, this CBF cold response network has been found to be highly conserved across the flowering plant species (Jaglo-Ottosen et al. 2001; Chinnusamy et al. 2010). Recently, Park et al. (2015) have reported induction of nearly 1200 *COR* genes under LT stress, 170 of which are associated with CBF regulons. The authors also investigated 17 out of 174 *COR* genes regulating TF genes, that are early cold-induced TF genes bearing homology with the CBF-regulon TFs. Importantly, regulation of CBF3 is controlled by ICE1 master regulator (Chinnusamy et al. 2003), an MYC-type TF controlling 40% of *COR* genes and 46% of TF genes participating in LT stress regulation (Lee et al. 2005; Miura and Furumoto 2013). *TaICE141* and *TaICE187* homologs of ICE1-induced CBF group IV provided cold tolerance in wheat (Badawi et al. 2008). Similarly, calmodulin-binding transcription activator (CAMTA), a TF, controls the expression of *CBF2* in *Arabidopsis* under LT stress tolerance (Doherty et al. 2009). Involvement of CAMTA1, CAMTA2 and CAMTA3 in inducing transcription of CBF1, CBF2 and CBF3 to impart LT tolerance was demonstrated in *Arabidopsis* (Kim et al. 2013). By contrast, ICE1 negatively regulates expression of MYB15 TFs involved in negative regulation of *CBF* genes (Agarwal et al. 2006). Likewise, *ZAT12*, a TF serves as negative regulator of CBF1, CBF2 and CBF3 under LT stress (Novillo et al. 2007). To explore the contribution of non-coding regulatory RNA towards LT tolerance, Chan et al. (2016) reported that overexpression of '*RNA-DIRECTED DNA METHYLATION 4*) *RDM4*)' plays important regulatory role in LT stress tolerance via enhancing the expression of CBF regulons. More recently, genome editing technology CRISPR/Cas9 system was applied in *Arabidopsis* to precisely discern the role of CBF genes in cold acclimation (Jia et al. 2016; Zhao et al. 2016) and CBF2 was reported to be more important in conferring LT tolerance than CBF1 and CBF3 (Zhao et al. 2016). Several researcher groups have conducted overexpression studies of *CBF* gene with regard to LT tolerance across various plant species (Jaglo-Ottosen et al. 2001; Hsieh et al. 2002a, b; Ito et al. 2006; Pino et al. 2007). Towards this end, the role of OST1 kinase in enhancing cold tolerance in *Arabidopsis* through increasing transcriptional activity and stability of ICE1 is worth mentioning (Ding et al. 2015; Lang and Zhu 2015; Zhan et al. 2015). Given that the expression of *CBF* genes is also regulated by circadian clocks (Fowler et al. 2005; Dong et al. 2011; Lee and Thomashow 2012), "*CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*)" and "*LATE ELONGATED HYPOCOTYL* (*LHY*)" were found to positively regulate CBF genes under LT (Dong et al. 2011). By contrast, "*PSEUDO RESPONSE REGULATORs* (*PRRs*)" circadian clock negatively regulates CBF genes (Nakamichi et al. 2009). Significance of light in regulation of CBF gene expression has also been described (Fowler et al. 2005; Franklin and Whitelam 2007; Lee and Thomashow 2012; Novák et al. 2016). CBF regulons responsible for COR expression were involved in LT stress tolerance (Fowler and Thomashow 2002); however, freezing tolerance of *Arabidopsis eskimo1* (*esk1*) mutant was found to be independent of CBF regulon (Xin and Browse 1998). Role of *HOS 9* and *HOS10* TFs in cold tolerance in *Arabidopsis* was reported (Zhu et al. 2004, 2005). Tolerance to LT was investigated in soybean and *Arabidopsis* via overexpression of *GmWRKY21* (Zhou et al. 2008) and *TaERF1* TF (Yi et al. 2004), respectively. Binding of AtHAP5A TF to CCAAT motif of AtXTH21 promoter causing freezing tolerance is also a noteworthy example of CBF-independent cold tolerance (Shi et al. 2014; Shi and Chan 2014). Further, activation of heterochromatic tandem-repeat sequence regions plays important role in cold acclimation under LT stress in Arabidopsis (To et al. 2011), maize (Hu et al. 2012) and rice (Roy et al. 2014). Importantly, wheat low-temperature-induced protein 19 (WLIP19) assists activating *COR* genes under LT stress (Kobayashi et al. 2008). In this context, Ji et al. (2015) reported TCF1 protein regulating LT tolerance in *Arabidopsis* via modification of histones in *BCB* gene, thus leading to reduced lignin synthesis.

Equally important gene regulation occurs in response to LT stress at post-transcriptional level viz., at pre-mRNA splicing, and at the level of export of mRNA from nucleus (Chinnusamy et al. 2007, 2010; Miura and Furumoto 2013). Mastrangelo et al. (2005) reported regulation of two early *COR* genes containing introns in their mature mRNA under LT stress in durum wheat. Likewise, existence of *STABILIZED 1* (*STA1*), a nuclear pre-mRNA splicing factor which serves as regulator of pre-mRNA splicing, has been reported under LT stress in *Arabidopsis* (Lee et al. 2006). Recently, significant role of *RCF1* gene encoding DEAD-box RNA helicase, assisting in proper pre-mRNA splicing of *COR* genes in *Arabidopsis* has been examined (Guan et al. 2013a). Equally important, contributory role of DEAD-box RNA helicase, AtRH7/PRH75 in cold tolerance has also been registered (Huang et al. 2015). Additionally, considering the role of nucleoporins (NUPs) found in nuclear pore complexes (NCPs) (Tamura and Hara-Nishimura 2014 and references therein) allowing RNA, nuclear proteins transport from nucleus into cytoplasm in response to various stress signals. Dong et al. (2006) reported involvement of *AtNUP160* in LT stress tolerance in *Arabidopsis*.

At post-translational level, the stabilization and regulation of ICE1 is controlled by ubiquitination [initiated by "*HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENE 1*" (HOS1)] (Dong et al. 2006; Chinnusamy et al. 2007; Zhu et al. 2007) and sumoylation (mediated by SIZ1) (Chinnusamy et al. 2007; Miura et al. 2007) (for details see Lissarre et al. 2010; Miura and Furumoto 2013). Thus, positive regulation of ICE1 via sumoylation and negative regulation of ICE1 via ubiquitination influence the expression of *COR* gene during LT stress (Dong et al. 2006; Miura et al. 2007).

In addition, participation of epigenetic reprogramming or modification encompassing histone modification covering histone methylation and histone acetylation dynamics has received serious attention for its underlying significant role in regulating transcriptional outcome of cold-responsive genes (Hu et al. 2011; Ji et al. 2015; Kim et al. 2015). Instances of histone acetylation in *COR* genes viz., *ZmDREB1* and *ZmCOR413* in maize (Hu et al. 2011) and *OsDREB1b* in rice (Roy et al. 2014) causing LT adaptation are remarkable, while reduction of H3K27me3 in *COR15A* and *ATGOLS3* genes were noted under LT in *Arabidopsis* (Kwon et al. 2009). Further, activation of heterochromatic tandem-repeat sequence regions in association with increase in H3K9ac acetylation plays important role in cold acclimation under LT stress in *Arabidopsis* (To et al. 2011), maize (Hu et al. 2012) and in rice (Roy et al. 2014). In this context, Ji et al. (2015) reported that TCF1 protein regulates LT tolerance in *Arabidopsis* via modification of histones in *BCB* gene resulting in lower lignin synthesis and, thus, causing LT tolerance.

Crop genetic resources and breeding for cold tolerance

Genetic resources are crucial to plant breeding as these allow access to the allelic diversity for improving the desired traits. According to Mickelbart et al. (2015), these serve as the valuable reservoir of 'stress adaptation loci' including LT stress. For instance, important sources of LT tolerance viz., Silewah (Satake and Toriyama 1979), Koshihikari (Sasaki 1981), Chhomrang (Sthapit 1987) and Jumli Marshi (Lindlöf et al. 2015) were reported in japonica rice. In general, japonica rice grown in temperate regions shows higher LT tolerance than the indica types (Glaszmann et al. 1990; Mackill and Lei 1997). However, few indica-type rice also show tolerance to LT viz., BR-IRGA 410 and IRGA 416 (da Cruz and Milach 2004).

Jeong et al. (2000) reported lower cold tolerance in Korean Tongil rice than the japonica-type rice.

Selection using different parameters led to the discovery of LT-tolerant genotypes such as HSC55, M103 and Jyoudeki in rice based on low spikelet sterility under LT stress (Farrell et al. 2006; Ye et al. 2009), cultivar 996 based on better pollination and pollen germination (Deng et al. 2011), NERICA rice genotypes based on higher filled-grain ratio (FGR) (51.9–57.9%) at reproductive stage (Wainaina et al. 2015) and 12 USDA minicore genotypes based on root and shoot length reduction under LT stress (Moraes de Freitas et al. 2016). The genotype Norin PL 8 containing an introgressed gene from Silewah showed tolerance to LT stress at booting stage. The LT stress tolerance of *Oryza rufipogon* Griff. at both flowering and booting stages highlights the importance of the crop wild relative in addressing the stress problem (Liu et al. 2003). Also, the introgression lines (ILs) derived from *O. rufipogon* are considered to be important sources of LT tolerance in rice (Tian et al. 2006). Likewise, a rice landrace KMXBG possesses LT stress tolerance for all vital growth stages vulnerable to LT (Cheng 1993). Chinese rice varieties B55, Bangjiemang, Lijiangheigu and one Hungarian rice variety HSC55 were recorded to be LT-tolerant in all key growth stages under field condition (Ye et al. 2009). Similarly, LT tolerance at reproductive stage was evident in field condition screening of rice cultivars HSC55, M103 and Jyoudeki (Farrell et al. 2006).

Considering better photosynthetic activity under LT stress, semi-winter wheat genotype Yannong 19 was reported to be having higher photosynthetic activity under LT stress (Guan et al. 2013a, b). Significant variation for thousand kernel weight and yield was recorded across more than 600 durum wheat cultivars under LT stress (Mohammadi et al. 2015). Importantly, winter wheat cultivar Norstar was reported to carry combination of frost-tolerant genes (*Vrn-A1w* + *Fr-A2T* + *Fr-B2WT* alleles), thus offering LT tolerance at vegetative stage in wheat (Eagles et al. 2016).

Kolar et al. (1991) recorded higher cold tolerance in winter barley than the facultative cultivars from a panel comprising eight winter and two facultative barley cultivars, while Franklin, Amagi Nijo and Haruna Nijo genotypes were found to be frost-tolerant at post-head-emergence stage in southern region of Australia (Frederiks et al. 2011).

In case of maize, cold tolerance of Swiss landraces was evident from examination of early vigor under LT stress (Peter et al. 2006, 2009). Therefore, utilization of genetic resources will allow plant breeders to siphon the hitherto unexploited genetic variation into breeding programmes from diverse gene pools.

Conventional breeding has been instrumental in developing LT-tolerant cultivars in various crops. For example, EP80 × Puenteareas population in maize was reported to be important source of LT tolerance based on both field and controlled conditions (Rodriguez et al. 2007). In wheat, Tiber (Kisha et al. 1992) derived from Redwin had good winter hardiness. OAC Elmira in barley was obtained as an outcome of conventional breeding (Falk et al. 1997). Attempts were made to introduce LT tolerance traits from landraces and crop wild relative into high-yielding yet sensitive rice varieties such as Guichao 2 (Liu et al. 2003), Towada (Xu et al. 2008; Zhou et al. 2012), Hitomebore (Shirasawa et al. 2012), HJX74 (Zhang et al. 2004), Norin-PL11 (Kuroki et al. 2007), Norin-PL8 (Saito et al. 1995; Dai et al. 2004), Milyang 23 (Oh et al. 2004), Plaisant in barley (Casao et al. 2011) and in tomato (Vallejos and Tanksley 1983) through back-cross breeding procedure. Nevertheless, genomics approaches have emerged in recent years to enhance the efficacy of traditional breeding protocols.

Understanding the genetic architecture of cold tolerance in crop plants

Enabling access to the precisely delineated chromosomal segments in genome that contain gene (s)/QTL (s) controlling important traits is a prerequisite for undertaking molecular breeding to accelerate trait improvement. Genotypic and phenotypic records of mapping populations or diversified panel are combined to establish significant marker–trait associations (MTAs), referred to as linkage-map-based QTL mapping and association analysis, respectively. In this section, we briefly describe about the QTLs for LT stress tolerance discovered across different crops using both conventional QTL mapping and association mapping approaches.

Linkage-map-based QTL analysis

DNA marker technology has been effectively exploited to map the QTLs that are associated with the traits contributing towards cold tolerance in plants (Table 2).

Rice

Several reports on QTLs controlling cold tolerance at germination stage were published in rice (Fujino et al. 2004; Hou et al. 2004; Han et al. 2006; Long-Zhai et al. 2006; Fujino et al. 2008; Ji et al. 2009; Fujino and Matsuda 2010; Iwata and Fujino 2010; Fujino and Iwata 2011; Fujino and Sekiguchi 2011; Li et al. 2013; Ranawake et al. 2014). Initially, Miura et al. (2001) reported five QTLs conferring LT tolerance at germination stage. In the same

Table 2 List of QTLs contributing in LT stress tolerance in plants

Crop	Mapping population	Type and size	Locus/QTL	Type of marker	Chromosome/ LG group	Major QTL and important linked marker and their map position	PV%	References
Arabidopsis	Ler × Cvi	RIL (132)	7 QTLs, *FTQ1* to *FTQ7*	AFLP	1, 4, 5	–	3–19.5	Alonso-Blanco et al. (2005)
Arabidopsis	Bay-0 × Shahdara	RIL	*CDG1*, *CDG2*, *CDG3*	SSR	1, 2, 4	MSAT1-10, MSAT2-36, MSAT4-15	17–25	Meng et al. (2008)
Arabidopsis	C24 × Tenela,	RIL (250)	*QTLc2, QTLc4* and *QTLc5*	SNP	2, 4, 5	snp142, snp306, snp307, snp350	6.8–9.2	Meissner et al. (2013)
Barley	Dicktoo × Morex	DH (100)	*HvCbf3*	–	5H	WG364b and saflp58	–	Choi et al. (2002)
Barley	Franklin × Arapiles, Galleon × Haruna Nijo, Amagi × WI2585	DH (225), DH (112), DH (139)	QTLs for frost tolerance	SSR	2HL, 5HL	Hv635P2.4f, Hv635P2.4f	–	Reinheimer et al. (2004)
Barley	DH, ‘Nure’ × ’Tremois’	–	2 Loci	–	5H	–	–	Francia et al. (2004)
Barley	Dicktoo × Morex (DxM)	–	3 QTLs	–	1H-L, 4H-S, and 4H-L	saflp164, saflp176, Bmy1	–	Skinner et al. (2006)
Barley	‘Nure’ × ’Tremois’, ‘Proctor’ × ’Nudinka’, ‘Steptoe’ × ’Morex’	DH (136), DH (113), DH (150)	6 HvCBF genes, ICE1 and FRY1, *Fr-H2* QTL	STS, SNP, SSCP	5H, 7H	ABC154B, ABG380	–	Tondelli et al. (2006)
Barley	Nure’ × ’Tremois	–	*VRN-H1/Fr-H1* and *Fr-H2*	–	–	–	–	Stockinger et al. (2007)
Barley	‘Nure’ × ‘Tremois’’	F_2 (1849), F_3	*Fr-H1* and *Fr-H2*,	RFLP, CAPS	5H	Bmag0223, MWG583, HvCBF4B (4.6 cM), HvMYB1	–	Francia et al. (2007)
Barley	Amagi Nijo × WI2585 and Haruna Nijo × Galleon	–	LTR tolerance QTL		2HL, 5HL	–	–	Chen et al. (2009)
Barley	NB3437f × OR71, NB713 × OR71	DH	*VRN-H3*, FR-H3	SNP	1H	–	48	Fisk et al. (2013)
Brassica	*Brassica rapa* × Brassica napus,	F_2, DH	2 QTLs	RFLP	–	–	–	Teutonico et al. (1995)
Brassica	SLMO46 × Quantum,	$F_{2:3}$ (200)	8 putative QTLs	RAPD, SSR	4, 7, 9	–	6–23	Asghari et al. (2007)
Faba bean	Côte d’Or 1 × BeanPureLine 4628	RIL (106)	5 Putative QTLs	RAPD	10	U09_1499/B20_803 F15_476/I10_661 O18_715/O18_737	21.8–40.7	Arbaoui et al. (2008)
Festuca pratensis	B14/16 × HF2/7	F1 (138)	*QFt5F*-1, *QFt5F-2* and *QFt6F* *QFt7F*, 6 QTLs for winter survival	–	1, 4, 5, 6, 7	P77M76_92 (10.9 cM), Xrz141b (26.5 cM), Xcdo678b (46 cM)	–	Alm et al. (2011)

Table 2 continued

Crop	Mapping population	Type and size	Locus/QTL	Type of marker	Chromosome/ LG group	Major QTL and important linked marker and their map position	PV%	References
Lentil	WA8649090 × Precoz,	RIL (106)	7QTLs	RAPD, ISSR, AFLP	LG4	ubc808-12 ubc840-3	22.9–42.7	Kahraman et al. (2004)
Medicago truncatula	–		4 QTLs	–	LG1, LG4 and LG6		40	Avia et al. (2013)
M. truncatula	F83005-5 × DZA045-5,	RIL (F_7, F_8)	*Mt-FTQTL6*		LG6		–	Tayeh et al. (2013)
Maize	Ac7643 × Ac7729	RIL (233)	8QTLs	RFLP	1, 2, 3, 9	bnl3.06 (62 cM), umc10 (70 cM)	28	Fracheboud et al. (2002)
Maize		$F_{2:3}$	4QTLs	–	2, 6		37.6	Fracheboud et al. (2004)
Maize	Lo964 × Lo1016,	$F_{2:4}$ (168)	20QTLs	–	1, 3, 4, 5, 6, 8, 10		10–37.1	Hund et al. (2004)
Maize	ETH-DH7 × ETH-DL3	$F_{2:3}$	–	SSR	1, 2, 3, 4, 6, 8, 9, 10		–	Jompuk et al. (2005)
Maize	–	$F_{2:3}$ (214)	*QTL 3.096*, *QTL 8.025*, *QTL 4.136*	RFLP	3, 4, 8		10	Pimental et al. (2005)
Maize	–	DH (720)	7 QTLs	SSR	–		–	Presterl et al. (2007)
Maize	EP42 × A661	$F_{2:3}$ (210)	10 QTLs	SSR	2, 4, 8	umc1823,umc1185 (69-104 cM) umc2150, bnlg1318 (8-41 cM) bnlg1318,umc1963 (45-87 cM)	5.5–19	Rodriguez et al. (2014)
Maize	B73 × Mo17	243 IBM Syn4 lines	6 QTLs	–	4, 5, 6, 7 9		3.9–8.4	Hu et al. (2016)
Oat	Kanota' × 'Ogle'	RIL (135)	7 QTLs		7, 17	waaccac273,UMN433	56	Wooten et al. (2008)
Oat	–	138accessions	3 robust QTLs	SNP	5C,1C	GMI_ES01_c1416_473 (101 cM) GMI_ES01_c30278_396 (8.8 cM) GMI_ES05_c13603_259 (9.8 cM)	–	Tumino et al. (2016)
Pisum sativum	Champagne × Terese,	RIL (164)	*Hr* locus, 6 QTLs	–	–		–	Lejeune-Henaut et al. (2008)
Pisum sativum	Champagne × Terese	–	Two raffinose QTL one RuBisCO activity		5 and 6		6.5–46.5	Dumont et al. (2009)

Table 2 continued

Crop	Mapping population	Type and size	Locus/QTL	Type of marker	Chromosome/ LG group	Major QTL and important linked marker and their map position	PV%	References
Pisum sativum	Champagne × Terese	RIL (164)	3 QTLs and 5 candidate genes	SSCP	3, 6, 7	AD60 and AD59 D24 and AB136	–	Legrand et al. (2013)
Pisum sativum	JI1491 x Cameor	RIL(129)	161putative QTLs	–SNP, SSR	LGIII and VI		9–71	Klein et al. (2014)
Rice	Norin-PL8 × Silewah	BC (92)	Chromosomal segment 3, 4	RFLP	3, 4	XNpb379	–	Saito et al. (1995)
Rice	Hokuriku 142 × Hyogo-Kitanishiki,	F_2 (69) and F_3	13 QTLs	RFLP	1, 3, 9, 11		–	Misawa et al. (2000)
Rice	Akihikari × Koshihikari,	DH (212)	*qCT-7*,*qCT-1* and *qCT-11*	RFLP, RAPD	1, 7, 11	R1545, S778, C83	5–22.1	Takeuchi et al. (2001)
Rice	Nipponbare × Kasalath	BIL (98)	*qLTG-2*, *qLTG-4-1*,*qLTG-4-2* *qLTG*-5 and *qLTG-11*	RFLP	2, 4, 5, 11	G1327,C946 and C513,R830	40.7	Miura et al. (2001)
Rice	Guichao 2 × Dongxiang	BC	3QTLs	–	1, 6, 11		–	Liu et al. (2003)
Rice	M-202 × IR50	RIL (191)	*qCTS12a* +6 minor QTLs	SSR	1, 3, 4, 6, 8, 10, 11, 12	RM101-RM292, 3.8 cM	8.7–46	Andaya and Mackill (2003b)
Rice	M-202 × IR50	RIL (1954)	*qCTS12*	SSR	12	RM5746-RM7003, 1.5 cM	41	Andaya and Mackill (2003a)
Rice	Kunmingxiaobaigu × Towada	F_2 (250)	9 QTLs	SSR	1, 3, 4, 6, 7, 10, 12	S1563 and R1789, 16.9 cM	–	Dai et al. (2004)
Rice	Milyang 23 × Jileng 1	$F_{2:3}$ (200)	12 QTLs	SSR	1, 2, 3, 5, 7, 9, 11, 12	RM265–RM104 (22.9 cM)	5.6–42.9	Long-zhi et al. (2004)
Rice	Italica Livorno × Hayamasari	BIL (122)	*qLTG-3-1*,*qLTG-3-2*, *qLTG-4*	RFLP, SSR	3, 4	GBR3001-GBR3002 (3, 7 cM) RM3436, R1854	35	Fujino et al. (2004)
Rice	Kinmaze × DV85	RIL (81)	*qLTG-2*, *qLTG-6*, *qLTG-7* *qLTG-LTG*-11 and *qLTG-12*	–	2, 6, 7, 11 and 12		–	Hou et al. (2004)
Rice	Milyang23 × Hapcheonaengmi3,	RIL (80)	14 QTLs	SSR	1, 3, 5, 6, 7, 8, 9, 11	RM128, RM85, RM552	5.8–32.8	Oh et al. (2004)
Rice	Lemont × Teqing,	RIL (269)	3 main effect QTLs, *qSCT-11*	SSR	3, 7, 11	RM156–RM16 RM336–RM10 RZ53–RM202	30	Zhang et al. (2005)

Table 2 continued

Crop	Mapping population	Type and size	Locus/QTL	Type of marker	Chromosome/ LG group	Major QTL and important linked marker and their map position	PV%	References
Rice	Milyang 23 × Jileng 1	$F_{2:3}$ (200)	*qLVG2*, *qLVG7*-2 and *qCIVG7-2* *qCIVG2*	SSR	2, 7	RM29-RM262,RM336-RM118	–	Han et al. (2006)
Rice	M202 × IR50	RIL, F_5-F_{10} (1954)	*qCTS12*	SSR	12	RM7003	40	Andaya and Tai (2006)
Rice	Milyang 23 × Jileng 1	$F_{2:3}$ (200)	12 QTLs	SSR	1, 2, 7, 8, and 12	RM262-RM263,RM270-RM17 RM19-RM270, RM129-RM9	5.2–17.9	Han et al. (2007)
Rice	AAV002863 × Zhenshan97B	DH (193)	One major effect and 5 minor effect QTLs	SSR	1, 2, 8	RM561-RM341	27. 4	Lou et al. (2007)
Rice	Hokkai-PL9 × Hokkai287	F_2, F_3, and F_7	*qCTB8*	SSR	8	RM5647 and PLA61 (1.7 cM)	26.6	Kuroki et al. (2007)
Rice	Kunmingxiaobaigu × Towada	BC_5F_2 (1557)	8 QTLs *qCTB-1-1*, *qCTB-4-1*, *qCTB-4-2*, *qCTB-5-1*, qCTB-5-2, qCTB-10-1, *qCTB-10-2* and *qCTB-11-1*	SSR	1, 4, 5, 10, 11	RM335, RM518, RM1282 RM31, RM7217	0.90–14.9	Xu et al. (2008)
Rice	Italica Livorno × Hayamasari	–	*qLTG3-1*	FNP	3	SSR118673–13.1, STS73–28	–	Fujino et al. (2008),
Rice	Asominori' × IR 24	CSSL	*qGR-2* and *qGR-11*	–	2, 11		–	Ji et al. (2009)
Rice	W1943 × Guang-lu-ai 4	F_2, (184)	*qCtss11*	SNP	3, 10, 11	AK24 and GP0030	40	Koseki et al. (2010)
Rice	TN1 × Chunjiang 06	DH, (120)	5QTLs	SSR	1, 2, 4, 8, 9, 10, 11	RM286–RM1812	14.1–21.5	Ji et al. (2010)
Rice	Reiziq × Lijiangheigu	BC (84), F_2 (282)	*qLTSPKST10.1*	SSR, STS	10	S10010.9 and S10014.4 (3.5 cM)	20.5	Ye et al. (2010)
Rice	Silewah × Hokkai241	BC	*Ctb1*	SSLP	4	PNK5, PNK7, and PNK10	–	Saito et al. (2010)
Rice	ZL1929-4 × Towada	F_2, F_3	*qCTB7* and 12 candidate genes	SSR	7	RI02905 and RM21862	9–21	Zhou et al. (2010)
Rice	Kasalath × Hoshinoyume Kasalath × Hayamasari Kasalath × Koshihikari	BC BC BC	*qLTG3-1* and *qLTG11*	–	3, 11		–	Iwata and Fujino (2010)
Rice	J502 × Hoshimaru	F_2 (150)	*qCTB3*	SSR	3	RM6974	–	Mori et al. (2011)

Table 2 continued

Crop	Mapping population	Type and size	Locus/QTL	Type of marker	Chromosome/ LG group	Major QTL and important linked marker and their map position	PV%	References
Rice	Dasanbyeo × TR22183	RIL (152)	56QTLs and 76 E-QTLs	SSR	1.- 12	QTL 8.1 near centromeric region (52-55 cM)	13.2–29.1 and 10.6–29	Jiang et al. (2011)
Rice	–	–	*qLTG3-1*		3		–	Fujino and Iwata (2011)
Rice	Italica Livorno × Hayamasari		*qLTG3-1*	FNP, InDel	3	–	–	Fujino and Sekiguchi (2011)
Rice	Ukei 840' × 'Hitomebore'	F_2, BC	1.2-Mb genomic region on chrom3	SSR	3	RM3719 and RM7000	–	Shirasawa et al. (2012)
Rice	Geumobyeo × IR66160-121-4-4-2	RIL (153)	*qCTS4a* and *qCTS4b*	SSR		RM3648-RM2799 RM3375a-RM558	7.8–8.3	Suh et al. (2012)
Rice	GC2 × IL112	$F_{2:3}$ (394)	*qCST1-1*,*qCST1-2*,*qCST2*,*qCST5* *qCST6*,*qCST7*,*qCST10*	SSR	1, 2, 5, 6, 7, 10		8–20	Liu et al. (2013)
Rice	USSR5 × N22	RIL, BC	*qLTG-7*, *qLTG-9* and *qLTG-12*	–	7, 9, 12	L9-25D and ID-1	7.08–12.12	Li et al. (2013)
Rice	Nipponbare × LPBG,	F_3 (10,800)	*qCTSS-1*, *qCTSS-2a*, *qCTSS-2b* *qCTSS-5*,*qCTSS-8*,*qCTSS-10*	SNP	1, 2, 5, 8, 10		–	Yang et al. (2013a, b)
Rice	Eikei88223 × Suisei,	BC_1F_5 (77)	*qCTF7*, *qCTF12* and *qCTF8*	SSR	7, 8, 12	RM28661, RM22613	7.9–19.2	Shinada et al. (2013, 2014)
Rice	Lijiangxintuanheigu × Sanhuangzhan-2	RIL	9 QTLs and *qCTS-9* and *qCTS-12 QTLs*	–	1, 6, 7, 8, 9, 10, 11, 12		–	Zhang et al. (2014a)
Rice	*Oryza rufipogon* Griff., Dongxiang × Nanjing 11,	BC (151)	*qRC10-1* and *qRC10-2*	SSR, InDel	10	RM171-RM1108, (148.3 cM) RM25570-RM304, (163.3 cM)	9.4–32.1	Xiao et al. (2014)
Rice	Jinbu × BR29	RIL (123)	*qSCT1a*, *qSCT2*,*qSCT10* *qSCT11*,*qSCT1b*, *qSCT4*	SSR	1, 2, 4, 10, 11	RM3602–RM8236, (3.7 cM) RM3602–RM5310, (11.3 cM)	6.1–16.5	Kim et al. (2014)
Rice		$F_{2:3}$		SSR		RM22034, RM6547 RM14978,RM144	–	Bonnecarrère et al. (2014)
Rice	HGKN × HOK	RIL (162)	5QTLs + 9QTLs	SSR	2, 5, 6, 7, 8, 11	RM125, RM214, RM21, RM206	5.7–35.6	Ranawake et al. (2014)
Rice	(Xiang 743 × Katy), (Xiang 743 × Dular)	$F_{2:3}$	7QTLs	SSR	–		47.26	Liu et al. (2015a)

Table 2 continued

Crop	Mapping population	Type and size	Locus/QTL	Type of marker	Chromosome/ LG group	Major QTL and important linked marker and their map position	PV%	References
Rice	*Oryza rufipogon* Griff × *O. indica*	RIL	*2 QTLSqLOP2* and qPSR2-1 gene *Os02g0677300*	SSR	2	RM221 and RS8	10.1–12.3	Xiao et al. (2015)
Rice	DXWR	–	13 QTLs	InDel	–		–	Mao et al. (2015)
Rice	NIP 3 × 93-11	F_2, RIL, BC	*COLD1*	SNP	4	AL606683-2 (1.8 cM) and RM5503 (0.8 cM)	–	Ma et al. 2015)
Rice	–	174 diverse accessions	51 QTLs	SSR	1-12.	RM528, RM160, RM4B, RM235	–	Pan et al. (2015)
Rice	Huanghuazhan × Eight donor parents	BC,	6 QTLs	SNP	3, 4, 12		4.2–9.5	Zhu et al. (2015)
Rice	Maratteli × Akitakomachi	F_2 (120), NIL	*qLTG1-1*, *qLTG3-1*, *qLTG3-2*, *qLTG11-1*	SSR	1, 3, 11	RM5914 (6 cM), RM338792 cM) RM3436 (6 cM) AC104484	5.8–22.1	Satoh et al. (2016)
Rice	–	420 acessions	11 loci	SNP	1, 7		–	Eizenga et al. (2015)
Rice	Hitomebore × Kuchum	BC	*qCT-4*	SSR, InDel	4	(RM3658, S72D21-1)	–	Endo et al. (2016)
Rice	Hitomebore × Lijianxintuanheigu	BC	One QTL	SSR, SNP	3	NLSNP3-12 and RM7000	–	Ulziibat et al. (2016))
Rice	Junam × IR72,	Advanced backcross inbred (132)	*qCT11*	InDel	11	RM224	–	Hur et al. (2016)
Rice	Nan-yang-zhan × Hua-jing-xian 74	SSSL (32)	*qCTBB-5* and *qCTBB*-6 *qCTS-6* and *qCTS-12*	SSR	5, 6, 12	RM6015, RM170, RM589 RM28828	–	Yang et al. (2016)
Rye	Annual × perennial ryegrass (152)	–	39 QTL	–	LG4, and 5		10.4–22.1	Xiong et al. (2007)
Sorghum	Shan Qui Red × SRN39	RIL (153)	2 QTLs		SBI-03a, SBI-07b		–	Knoll et al. (2008)
Sorghum	RTx430 × PI610727	RIL (171)	14 QTLs	SSR	1, 7, 9	0–16 cM	3.1–20	Burow et al. (2010)
Sorghum	*S. bicolor* × *S. propinquum*	F $_{3:4}$ (130)	2QTLs	SSR	SBI-01	SBL1B5H (4 cM) SB050A (4.5 cM)	11.53–25.32	Washburn et al. (2013)
Soybean	Hayahikari × Toyomusume	RIL (104)	*qCTTSW1* and*qCTTSW2* *qCTTSW3*	–	–		–	Funatsuki et al. (2005)
Soybean	Toyomusume × Toyoharuka	RIL (192)	a large effect QTL	SSR	A2	Sat_162	–	Ikeda et al. (2009)

Table 2 continued

Crop	Mapping population	Type and size	Locus/QTL	Type of marker	Chromosome/ LG group	Major QTL and important linked marker and their map position	PV%	References
Tomato	NC84173 × LA722	BC (119)	3-5 putative QTLs	RFLP	1 and 4		11.9–33.4	Foolad et al. 1998)
Tomato	*Lycopersicon esculentum* Mill. cv T5 × *Lycopersicon hirsutum* f. *typicum* accession LA1778,	BC (196)	8 QTLs	RFLP	5, 6, 7, 9, 12		–	Truco et al. (2000)
Tomato	*L. esculentum* × *L. hirsutum, BC*	NIL	*stm9*	–	9	–	–	Goodstal et al. (2005)
Tomato	–	–	*stm9*	–	9	–	–	Arms et al. (2015)
Triticale	DH06, DH07, EAW74, EAW78 families	DH,647	9 main effect QTLs	DArT	5A, 1B and 5R	52.5 (cM), 54.1 (cM), 55.6 (cM)	–	Liu et al. (2014)
Wheat	–	–	*Fr1*	–	5A	Xwg644 (2 cM)	–	Sutka (1994), Galiba et al. (1995)
Wheat	–	–	*Fr1*	–	5A	–	–	Sutka and Snape 1989)
Wheat	–	–	(*Wrab19* and *Wrab17*) *Cor* gene family	–	5A, 4B or 4D	–	–	Tsuda et al. (2000)
Wheat	–	–	*wcor14*	–	–	–	–	Tsvetanov et al. (2000)
Wheat	*Triticum spelta* 5A × Cheyenne 5A	–	2 loci	RFLP	5A and 2Am	Fr-A1 (35 cM), Xpsr911	–	Vágújfalvi et al. (2000)
Wheat	–		*Fr1*	RFLP, AFLP	5A	*Xpsr426* and *Xwg644*	–	Sutka (2001)
Wheat	Vrn-A1 × Norstar, NIL	–	*Vrn-A1*	–	–		–	Limin and Fowler (2002)
Wheat	Cheyenne' 5B × 'Chinese Spring'	RIL	*Fr-B1*	SSR	5B	From Vrn-B1 (40 cM)		Toth et al. (2003)
Wheat	DV92 × G3116	RIL (74)	*Fr-A2locus* and *Cbf3* gene	RFLP	5A	VRN-1 (30 cM)	–	Vágújfalvi et al. (2000)
Wheat	Triple Dirk	NIL	*Fr-A1*, *Cor/Lea gene*	–	5		–	Kobayashi et al. (2005)
Wheat	–		*Fr-A* (*m*)2	–	5A		–	Miller et al. (2006)
Wheat	Norstar × Winter Manitou	DH (107)	One major QTL	AFLP, SSR	5A, 1D	46 cM from *vrn-A1* locus	40	Båga et al. (2007)

Table 2 continued

Crop	Mapping population	Type and size	Locus/QTL	Type of marker	Chromosome/ LG group	Major QTL and important linked marker and their map position	PV%	References
Wheat	G3116 × DV92	F_2 (374)	*Fr-Am2*, 2QTLs	CAPS	5	–		Knox et al. (2008)
Wheat	Norstar × Zagros	F_2 (280)	–	SSR	2B, 5A		27	Sofalian et al. (2008)
Wheat	Durelle × Kronos	BC	*Frost Resistance*-B2 (*Fr*-B2)	SNP	5B	–	–	Pearce et al. (2013)
Wheat	–	1064 hybrids and 135 parental lines	One major locus	SNP	5B	41 SNPs	–	Zhao et al. (2013)
Wheat	M808 × CS	RILs (210)	*WCBF2*, *TaCBF12*, *Wlt10*, *Wdhn13*	SSR	1D, 2A, 4B and 5A	Xbarc330 (49.8 cM)		Motomura et al. (2013)
			Wcor14			Xhbg406 (48.8 cM)		
Wheat	Brundage × Coda	RIL	6 QTLs	SSR, DArT, SNP	5AL, 2A, 3A, 5B, and 6D		–	Case et al. (2013)
Wheat	Eltan × ORFW	$F_{4:5}$, spring panel (81)	*FR2* (*FR-A2-S*, *FR-A2-T*)	InDel, SNP	–	2InDels (*FR-A2-S* and *FR-A2-T*)	–	Zhu et al. (2014)
		winter panel (65)				10 SNPs (*CBF-A12*, *CBF-A15*)		
Wheat	–	170 winter and 14 spring wheatgenotypes	One QTL, *Fr-A2* locus	SNP	5A		–	Sieber et al. (2016)

BC back cross, *RIL* recombinant inbred line, *FNP* functional nucleotide polymorphism, *DArT* Diversity Arrays Technology genomic region on chromosome 4, the QTL *qLTG-4* was later discovered (Fujino et al. 2004). The QTL *qCTBB-6/qCTS-6* reported by Yang et al. (2016) coincided with the QTL *qCTG6* (Ranawake et al. 2014) controlling LT tolerance at germination stage. Using a map-based cloning approach, Fujino et al. (2008) elucidated the candidate gene "*Os03g0103300*" underlying the QTL (*qLTG3-1*) that imparts cold tolerance at germination stage. Concerning LT tolerance at seedling stage, a range of QTLs were detected in rice exerting substantial impact on the tolerance level (Qingcai et al. 2004; Han et al. 2007; Lou et al. 2007; Koseki et al. 2010; Suh et al. 2012; Liu et al. 2013; Yang et al. 2016). Five QTLs discovered by Ji et al. (2010) conferring LT tolerance at plumule stage explained phenotypic variation (PV) up to 21%. Regarding seedling-stage tolerance, chromosomal region harboring the QTL *qCTS1* was reported to be in the close proximity of the QTLs *qCTS1* (Andaya and MacKill 2003b), *qCTs-1-c* (Han et al. 2007) and *qCSH1* (Lou et al. 2007). Zhang et al. (2005) reported three QTLs with a major one (*qSCT-11*) explaining 30% PV for cold tolerance at seedling stage. This chromosomal region corresponded with the chromosomal region containing QTLs *qSCT11* (Kim et al. 2014), *qCTS11-2* (Andaya and MacKill 2003b) and *qCtss11* (Koseki et al. 2010). Subsequently, fine-mapping of *qCtss11*QTL unfolded the two important candidate genes "*Os11g0615600*" and "*Os11g0615900*" (Koseki et al. 2010). In a similar way, sets of candidate genes *LOC_Os01g69910*, *LOC_Os01g69290*, *LOC_Os01g69900* and *LOC_Os11g37730*, *LOC_Os11g37720* were obtained for the respective QTLs *qSCT1* and *qSCT11* through fine-mapping (Kim et al. 2014). The QTL *q14d-11* (Ji et al. 2010) flanked by RM286–RM1812 marker was found to be different from the QTL reported by Zhang et al. (2005) on chromosome 11. One major QTL *qCTS12a* on chromosome 12 explaining 41% PV (Andaya and MacKill 2003b) corresponded to the chromosomal region harboring *qCTS12* reported by Andaya and Tai (2006) for vegetative LT tolerance. Candidate gene (s) *OsGSTZ1* and *OsGSTZ2* were suggested to be lying under the QTL *qCTS12* (Andaya and Tai 2006). Interestingly, QTL *qCTB-4-1* contributing to LT tolerance at booting stage overlapped with the chromosomal region harboring QTL *qCTS4* for vegetative LT tolerance (Andaya and Tai 2007) on chromosome 4. Two QTLs *qRC10-1* and *qRC10-2* reported recently by Xiao et al. (2014) coincided with the chromosomal region containing *qCST10* (Liu et al. 2013) and *qCTSS-10* (Yang et al. 2013a, b). Fine-mapping of *qCST10* revealed *LOC_Os07g22494* as the causative locus for LT tolerance (Liu et al. 2013). Similarly, fine-mapping of *qRC10-2* by Xiao et al. (2014) led them to advocate gene (s) *Os10g0489500* and *Os10g0490100* as the prime candidates for the given QTL. Similarly, QTL *qCTS7* (*2*) (Ranawake et al. 2014) controlling LT tolerance at seedling stage coincided with earlier known QTLs *qSES7-1* and *qSES7-2* (Iwata et al. 2010). Notably, the QTLs *qCTS11* (*1*)-*2* and *qCTS11* (*2*)-*2* (Ranawake et al. 2014) were mapped in the same genomic region reported by Misawa et al. (2000). Likewise, QTL *qCTS8* (*2*) (Ranawake et al. 2014) overlapped with the QTL *qCTS8.1* reported previously by Wang et al. (2011). Five QTLs for leaf rolling and seedling survival under two different LT conditions were discovered in a recent work (Zhang et al. 2014a). Combining bulk segregation analysis (BSA) with next-generation sequencing (NGS) technique has enabled the identification of six QTLs contributing to LT tolerance at seedling stage in rice (Yang et al. 2013a).

Concerning LT tolerance at booting stage, Saito et al. (1995) discovered two genomic regions on chromosomes 3 and 4 that were associated with LT tolerance at booting stage. Later, two QTLs were reported on chromosome 4 governing LT stress tolerance at booting stage (Saito et al. 2001) and three QTLs viz. *qCT-7*, *qCT-1* and *qCT-11* were detected using RFLP and RAPD markers (Takeuchi et al. 2001). Subsequently, several QTLs were reported for LT tolerance at booting stage (Andaya and Mackill 2003a; Liu et al. 2003; Xu et al. 2008; Mori et al. 2011; Shirasawa et al. 2012; Xiao et al. 2014; Zhu et al. 2015). The QTLs *qCTB-4-1* and *qCTB-4-2* on chromosome 4 (Xu et al. 2008) did not coincide with the QTL region suggested by Saito et al. (2001) on chromosome 4. The QTL region containing *qCTB-11-1* (Xu et al. 2008) on chromosome 11 was different from the QTL obtained by Liu et al. (2003). Likewise, the markers reported by Dai et al. (2003) for LT tolerance at booting stage did not map in the same position on chromosomes 4, 5 and 11 as reported by Xu et al. (2008). Difference was also observed in the mapping position of *QTL 8.1* for spikelet fertility under LT (Jiang et al. 2011) on chromosome 8 with previous QTLs *qCTB8* (Kuroki et al. 2007) and *qCTF8* (Shinada et al. 2013) detected on the same chromosome. However, the QTL *qLTSPKST10.1* reported by Ye et al. (2010) on chromosome 10 harbored within the same region that harbours *QTL 10.1* (Jiang et al. 2011) and *qCTB-10-2* (Xu et al. 2008) (Tables 3, 4).

The QTL *qCTF7* (Shinada et al. 2013) explaining 33.5% PV was different from the QTL region reported by Zhou et al. (2010) and Takeuchi et al. (2001). But the QTL *qRCT7* (Dai et al. 2004)-containing region remained close to the QTL *qCT-7* on chromosome 7 reported by Takeuchi et al. (2001). The QTL *qCTB-11-1* (Xu et al. 2008) shared the genomic region harboring the QTL *qCT11* as reported by Takeuchi et al. (2001). Similarly, *fer11* QTL offering spikelet fertility tolerance at LT (Oh et al. 2004) was located in the same region on chromosome 11 as *qCT11* (Takeuchi et al. 2001). Though the QTL *qRCT6b* reported

Table 3 List of fine-mapped QTLs contributing in cold tolerance in various crop plants

Crop	Type of population	Marker	Fine-mapped QTL	Chromosome	Candidate gene	Putative function	References
Arabidopsis	RIL (132)	AFLP	*FTQ4*	4	*CBF2*	Encode transcriptional activators for cold acclimation response	Alonso-Blanco et al. (2005)
Arabidopsis	RIL (250)	SNP	*QTLc2*, *QTLc4* and *QTLc5*	5	*REVEILLE1* (*At5g17300*)	Hormonal control	Meissner et al. (2013)
Hordeum vulgare	F_2 (1849)	Bmag0223, MWG583, HvCBF4B, HvMYB1	*Fr-H1* and *Fr-H2*	5	CBF transcription factor	–	Francia et al. (2007)
Festuca pratensis	F_1 (138)	P77M76_92	*QFt5F-1*	5	*FpIRI1*	–	Alm et al. (2011)
Zea mays	RIL (243)	umc1	*qOTGR5-1*, *qLTGR5-1*	5, 4, 6, 9	*GRMZM2G325653*	Mildew resistance locus (MLO)-like protein, C2H2 zinc-finger family protein, cortical cell-delineating protein, non-phototropic hypocotyl 3 family protein	Hund et al. (2016)
		umc1303	*qLTPRL5-1*		*GRMZM2G377165*		
		umc1303, umc62	*qLTGR4-1*, *qLTPRL4-1*		*GRMZM2G398807*		
		bnl14.28a	*qLTGR6-1*, *qLTPRL6-2*		*GRMZM2G154595*		
			qLTPRL9-1, *qLTGR9-1*		*GRMZM2G154149*		
Oryza sativa	F_2 (2008)	–	*Ctb1*	4	–	Ubiquitin–proteasome pathway	Saito et al. (2004)
	F_3 and F_7 substitution line	RM5647 and RM6670	*qCTB8*	8	Monodehydroascorbate reductase	–	Kuroki et al. (2007)
	NIL, 12-195-1 and 27-355-3	PNK5, PNK7, and PNK10	*Ctb 1*		Two genes encoding	Contributing in cold tolerance	Saito et al. (2010)
	NILs 18-170-2, 29-279-6				F-box protein	ubiquitin–proteasome pathway	
					ser/thr protein kinase		
	BC_1F_2 (3200)	SSR118673–13.1	*qLTG3–1*	3	"*Os03g0103300*"	Protein of unknown function	Fujino et al. (2008)
		STS73–28					
	F (5) and F (10)1954	RM7003	*qCTS12*	12	*OsGSTZ1* and *OsGSTZ2*	Encode	Andaya and Tai (2006)
						zeta class glutathione S-transferases	
	–	–	*qCTS4*	4	–	–	Andaya and Tai (2007)
	F_2, (2810)	RI02905 and RM21862	*qCTB7*	7	12 putative candidate genes	–	Zhou et al. (2010)
	F_2 (184)	AK24 and GP0030	*qCtss11*	11	*Os11g0615600* and/or *Os11g0615900*	–	Koseki et al. (2010)
	$F_{2:3}$ population 394	–	–		*LOC_Os07g22494*	Involved in DREB/CBF pathway	Liu et al. (2013)
	RIL, (123)	In1-c3, In11-d1	*qSCT1* and *qSCT11*	1, 11	*LOC_Os01g69910*	Calmodulin-binding	Kim et al. (2014)
					LOC_Os11g37720	transcription activator	
	11,326 BC_4F_2	RM221 and RS8	*qLOP2* and *qPSR2-1*	2	*Os02g0677300*	–	Xiao et al. (2015)
	8642 BC_4F_3						
	BC_5F_2 (13,324)	RM171-RM1108	*qRC10-1* and *qRC10-2*	10	*Os10g0489500* and *Os10g0490100*	–	Xiao et al. (2014)
		RM25570-RM304					
	F_2 (8368)	AL606683-2 and RM5503	*COLD1*	4	–	Regulator of G-protein signaling on plasma membrane and endoplasmic reticulatum	Ma et al. (2015)

Table 3 continued

Crop	Type of population	Marker	Fine-mapped QTL	Chromosome	Candidate gene	Putative function	References
	BC	NLSNP3-12 and RM7000	QTL remaing in 35 kb region	3	*Os03g0789800* *Os03g0790700* *Os03g0793500* *Os03g0793700* *Os03g0806700*	–	Ulzibat et al. (2016)
Capsicum chinense	F_2	SNP 5-5 and SNP 3-8	*sy-2*	1	*ORF10* and *ORF20*	Encode F-box proteins	Liu et al. (2016)
Triticum aestivum	DH (150)	*wmc156* and *P3346-183*	*TaSnRK2.3*	1B	3 candidate genes	–	Tian et al. (2013b)

by Dai et al. (2004) remained in close proximity with the QTL *qCTB6* (Andaya and Mackill 2003a), this QTL was not related with LT tolerance at booting stage. Mori et al. (2011) established a novel QTL *qCTB3-Silewah* on chromosome 3 that differed from the QTL reported by Saito et al. (1995) on the same chromosome. Concerning LT tolerance at booting stage, physical mapping of the QTL *Ctb1* by Saito et al. (2004) was followed by the successful cloning of this QTL (Saito et al. 2010). Notably, the authors recorded two genes encoding F-box protein and a Ser/Thr protein kinase, thereby suggesting the possible role of ubiquitin–proteasome pathway in LT tolerance in rice. More recently, fine-mapping of one QTL (*qCT-3-2*) using SNP markers precisely delineated a 192.9-kb region on the reference genome sequence (Zhu et al. 2015). The readers are referred to the recently published reviews for greater details on QTLs for LT stress tolerance in rice (da Cruz et al. 2013; Zhang et al. 2014c).

Wheat

A regulated expression of *VRN1* and *CBF* genes is reported to allow temperate cereal crops, especially wheat and barley, to withstand LT stress (Francia et al. 2004, 2007; Stockinger et al. 2007; Dhillon et al. 2010; Knox et al. 2010; Pearce et al. 2013; Zhu et al. 2014; Mickelbart et al. 2015). Importantly, chromosomal synteny/colinearity of LT tolerance loci/QTL (s) belonging to the Triticeae family has been discussed (Cattivelli et al. 2002). Adaptive mechanism of winter wheat to acclimatize with freezing tolerance via higher expression of *CBF* genes and limiting *VRN1* transcripts till vernalization (Dhillon and Stockinger 2013; Pearce et al. 2013; Zhu et al. 2014; Mickelbart et al. 2015) remains in sheer contrast to spring wheat which shows freezing tolerance due to deletion or lower expression of *CBF* genes (at *FR2* locus) and enhanced expression of *VRN1* transcript (at *FR1* locus) (Pearce et al. 2013; Zhu et al. 2014; Mickelbart et al. 2015).

While working out the genetics of frost-tolerance gene (*Fr1*), Sutka and Snape (1989) established its linkage with *Vrn1* gene on chromosome 5A. Two loci with additive effect orchestrating the expression of *cor14b* gene describing LT tolerance were reported (Vágújfalvi et al. 2000). Three genes viz. *Fr-A1*, *Fr-B1* and *Fr-D1* accounting for LT stress tolerance were mapped on chromosomes 5A, 5B and 5D, respectively (Galiba et al. 1995; Snape et al. 1997; Toth et al. 2003). Later, the *XCbf3* was identified as a causative gene underlying *Fr-A2* locus on 5A chromosome and this contributes to frost tolerance in diploid wheat (*Triticum monococcum*) (Vágújfalvi et al. 2003). It is important to note that the LT-related genomic region on 5A chromosome reported by Båga et al. (2007)

Table 4 LT stress tolerance in plants obtained thorugh transcriptome sequencing

Crop	Genotype name	Stage	Platform used	Candidate gene/differentially expressed gene(DEG)/miRNA	Function	References
		–			–	
Alfalfa	Zhaodong	Seedling	Illumina GAII	35 cold-responsive miRNA recovered	–	Shu et al. (2016)
Alfalfa	Zhaodong	Crown buds	–	5605 differentially expressed genes	–	Song et al. (2016)
Anthurium andraeanum	Alabama	Stem and leave	Illumina HiSeq^{TM} 2000	39 cold-inducible TFs, 4363 DEGs	LT tolerance	Tian et al. (2013a)
Apple	–	Leaves	Illumina sequencing	Upregulated gene MDP0000198054	LT stress response	Du et al. (2015)
Brassica juncea	Varuna	Sliqua	Illumina HiSeq 2000	283 commonly cold induced transcripts	LT stress signaling	Sinha et al. (2015)
Banana	Musa spp. Dajiao Musa spp. Cavendish	Seedling	Illumina TruSeq^{TM}	Twelve early responsive genes and *ICE1* and *MYBS3*, 10 and 68 DEGs	LT tolerance	Yang et al. (2015)
Lotus japonicus	Gifu B-129	Seedling	Illumina HiSeq 1500	1077 DEG,41 cold-inducible TFs	Cell wall, phenylpropanoid proline regulation, and affecting photosynthetic process	Calzadilla et al. (2016)
Potato	10908-06, ED25	Tuber	Illumina HiSeq 2000	11 cold-responsive miRNA	Adaptive response to LT stress	Ou et al. (2015)
Prunus persica	Lovell	Buds and young leave	SOLID Platform	miR5021, miR2919, and miR414	–	Barakat et al. (2012)
Rice	IRGA959-1-2-2F-4-1-4-A and IRGA959-1-2-2F-4-1-4-D-1-CA-1	Seedling 7 days after germination at 13 °C	Illumina HiSeq 2000 technology	1361 DEGs	Fatty acid desaturase, Antioxidant activity, Cell wall structural proteins Cold signaling	Dametto et al. (2015)
Rice	3 genotypes	–	–	2242 DEGs and 318 common DEGs	Involved in chilling stress adaptation	Shen et al. (2014)
Rice	Y58S and P64S	–	Illumina HiSeq^{TM} 2000 platform	1497 and 5652 DEGs	LT stress signaling	Bai et al. (2015)
Soybean	Williams 82	Mature nodules	Illumina-Solexa 1 Genetic Analyzer	11 cold-responsive miRNAs including gma- miR166u, gma- miR171p, miR2111f and miR169c	Protection of nodule from cold stress	Zhang et al. (2015)
	PC17-109	Leaf tissues			–	

Table 4 continued

Crop	Genotype name	Stage	Platform used	Candidate gene/ differentially expressed gene(DEG)/miRNA	Function	References
Spartina pectinata Link			Illumina HiSeq 2500	Cold-responsive DEGs		Nah et al. (2016)
Tea	Yingshuang, Baiye 1	–	Illumina sequencing	77 upregulated and 88 downregulated cold-responsive miRNA	LT stress tolerance	Zhang et al. (2014b)
Tea	Longjing 43	Leaves	Illumina Hiseq 2000	DREB1b/CBF1 TFs and cold-responsive miRNAs	Cold tolerance	Zheng et al. (2015b)
Tomato	LA1777	–	–	161 conserved miRNA and 236 novel miRNA recovered	Involved in chilling response	Cao et al. (2014)
Tomato	*Solanum lycopersicum* and *Solanum habrochaites*	–		89 miRNA miR159, miR319, and miR6022	LT response	Chen et al. (2015b)
Tripsacum dactyloides	Pete	–	–	Sequence variation in known cold tolerance gene		Gault et al. (2016)
Tripsacum floridanum	–	–	–		–	
Wheat	Winter Norstar and winter Manitou	Crown stage		–	LT acclimation	Laudencia-Chingcuano and Fowler (2015)

coincided with *Fr-A2* locus in diploid wheat (Vágújfalvi et al. 2000, 2003, 2005). Furthermore, the sequences pertaining to two CBF genes identified by Båga et al. (2007) showed similarity with the genes *Cbf14* and *Cbf15* underlying the *Fr-2* locus, which was reported by Miller et al. (2006) in *T. monococcum*. In winter durum wheat, genotyping by sequencing (GBS) has recently allowed researchers to locate one major QTL (for frost tolerance) on chromosome 5 in close proximity of *Fr-A2* locus (Sieber et al. 2016). Importantly, the *Fr-A* (^{m})*2* (harboring clusters of CBF genes) loci orthologous to barley *HvCBF* gene were mapped on chromosome 5 in *T. monococcum* (Miller et al. 2006). Later, the candidate gene underlying *Fr-A*^{m}*2* locus was reported to be a *CBF* gene in *T. monococcum* (Knox et al. 2008). Two important SSR markers on chromosomes 2B and 5A were found to be linked with cold tolerance through improved heading time under LT stressed conditions (Sofalian et al. 2008). In a recent study, significance of the loci *VRN1* and *FR2* (harboring *CBF* copies) with respect to cold tolerance was demonstrated (Zhu et al. 2014). Importantly, the authors identified two haplotypes of *FR-A2* viz. 'FR-A2-S' and 'FR-A2-T' associated with cold tolerance in wheat. Earlier, Pearce et al. (2013) reported deletion of *CBF* gene clusters in '*Fr-B2*' locus leading to a marked reduction in LT tolerance in both tetraploid and hexaploid wheat.

Barley

At least 20 HvCBF genes are known to reside in barley genome, which can be phylogenetically classified into three subgroups, i.e., HvCBF1, HvCBF3, and HvCBF4 (Skinner et al. 2005). Barley *CBFs* viz. *HvCBF3*, *HvCBF4* and *HvCBF8* were assigned to chromosome 5H (Choi et al. 2002; Francia et al. 2004). On chromosome 5H, Francia et al. (2004) reported two QTLs *Fr-H1* and *Fr-H2* for frost tolerance (harboring *HvCBF4* gene). The *11HvCBF* genes discovered later (Skinner et al. 2006) overlapped with the genomic region harboring QTL *Fr-H2* reported earlier by Francia et al. (2004). Co-localization of QTLs associated with cold tolerance and vernalization was also reported on chromosome 5H (Francia et al. 2004). In addition, QTLs were detected on chromosomes 2HL and 5HL to elucidate frost tolerance at vegetative and reproductive stages in barley (Reinheimer et al. 2004). Notably, three LT-tolerance-related QTLs in barley were reported to manifest homology with *CBFs*, *ICE1*, and *ZAT12* genes involved in regulation of cold tolerance in Arabidopsis (Skinner et al. 2006). Recently, a novel QTL *FR-H3* governing 48% PV for LT tolerance was reported in barley mapping populations (NB3437f × OR71 and NB713 × OR71) (Fisk et al. 2013). Stockinger et al. (2007) reported the regulatory role of *VRN-H1/Fr-H1* locus on chromosome 5, controlling *Cbf* gene expression localizing with *Fr*-2locus in barley under cold stress. High-resolution mapping of *Fr-H2* locus in barley revealed seven CBF sub-clusters involved in frost tolerance (Francia et al. 2007). Cluster of six *HvCBF* genes was reported to co-localize with *Fr-H2* QTL on 5H (Tondelli et al. 2006). Role of CBF copies localizing with *FR-1* and *FR-2* loci in cold tolerance and acclimatization in cereals and in barley has been recorded (Knox et al. 2010; Tondelli et al. 2006). Subsequently, alleles of *Vrn-H1* locus on 5H chromosome were identified to be linked with early-flowering trait, providing low-temperature tolerance at reproductive stage, whereas frost-tolerance loci on 2HL were associated with late-flowering alleles governed by *Flt-2L* gene in barley (Chen et al. 2009). It is important to note that higher copy number of *HvCBF4* and *HvCBF2* delivered greater frost tolerance (Francia et al. 2016) and the authors also developed cleaved amplified polymorphic sequence (CAPS) assay to distinguish between *CBF2A* and *CBF2B* genes. Based on comparative analysis, it was inferred that the position of CBF clusters underlying *Fr-H2* locus in Morex × Dicktoo barley population (Skinner et al. 2006) had synteny with the genomic region containing *Fr-A*^{m}*2locus* (on chromosome 5A) in winter × spring *T. monococcum* diploid wheat mapping population (Vágújfalvi et al. 2000). Equally important, in *Festuca pratensis* belonging to the Triticeae family, two QTLs *QWs5F-2* corresponding to wheat *Fr-A1/Fr-H1* and the *QFt5F-2/QWs5F-1* QTL corresponding to *Fr-H2/Fr-A*^{m}*2* locus have been reported (Alm et al. 2011). The synteny of *FR-H2* locus harboring *CBF* genes in barley (Francia et al. 2007) with *Fr-A2*^{m}*2* locus in diploid wheat *T. monococcum* (Knox et al. 2008; Tondelli et al. 2006; Miller et al. 2006) has been thoroughly discussed by Galiba et al. (2009).

Maize

In maize, QTLs for various traits such as early seedling vigor, root, leaf and shoot traits were registered under LT stress condition (Hund et al. 2004; Presterl et al. 2007). One major QTL contributing to photo-inhibition tolerance under LT was disclosed residing on chromosome 6 (Fracheboud et al. 2004). Notably, three genomic regions located on 2, 4 and 8 chromosomal regions, contributing to seedling LT tolerance have been registered (Rodriguez et al. 2014).

Sorghum

In sorghum, two QTLs conferring LT tolerance at germination stage were detected each on LGs SBI-03a and SBI-07b using a mapping population derived from the cross Shan Qui Red × SRN39 (Knoll et al. 2008), whereas considering LT tolerance at emergence stage, QTL-containing regions were identified on different LGs viz. SBI-01, SBI-03, SBI-04, SBI-06, SBI-08 and SBI-09 (Fiedler et al. 2012).

Pea

Based on data recorded over multiple years and multiple locations, three promising frost-tolerance-related QTLs were reported, which also exhibited co-localization with *Hr* flowering locus (Lejeune-Henaut et al. 2008). Similarly, Klein et al. (2014) discovered a QTL cluster LG IV which could be accounted for 70% PV for frost tolerance damage in pea. On the other hand, the QTL clusters on LGIII were associated with *Hr* and *Le* loci. Two consistent QTLs for cold tolerance were reported on LG V and LG VI. Interestingly, these QTLs coincided with the genomic segments related to raffinose and RuBisCO activity (Dumont et al. 2009).

Other crops

In Triticale, nine main-effect QTLs accountable for both winter hardiness and LT tolerance were recovered from more than 600 double haploid (DH) lines (Liu et al. 2014). In case of soybean, three QTLs (*qCTTSW1*, *qCTTSW*2, and *qCTTSW3*) were detected that controlled LT tolerance at reproductive stage (Funatsuki et al. 2005), while a major QTL discovered by Ikeda et al. (2009) maintained seed development under LT stress. In *Medicago truncatula*, QTLs that define leaf shoot and root orientation under LT stress conditions were discovered (Avia et al. 2013). The entire trait QTLs viz, number of leaves, leaf area, electrolyte leakage, and other shoot and root QTLs were assigned on chromosomes LG1, LG4 and LG6 (Avia et al. 2013). In *B. napus*, a total of six significant QTLs conferring LT tolerance were reported under more than one winter season (Kole et al. 2002). In tomato, wide cross involving NC84173 (*Lycopersicon esculentum*) and LA722 (wild *L. pimpinellifolium* accession) served for the delivery of QTLs that impart tolerance to LT stress during germination stage (Foolad et al. 1998). Similarly, Truco et al. (2000) reported three QTLs derived from *L. esculentum* × *L. hirsutum*, that were found to be controlling wilting and root ammonium uptake under chilling stress. One QTL for shoot turgor maintenance (designated by *stm9*) was introgressed into *L. esculentum* from wild

L. hirsutum, which eventually conditioned chilling tolerance in tomato (Goodstal et al. 2005).

Incorporating LT tolerance into susceptible genetic backgrounds using molecular breeding techniques

The robust QTLs/markers described in the preceding section hold great potential to accelerate the progress of traditional breeding. These DNA markers permit precise selection of the desirable genotypes in a time-saving and environment-independent manner. As suggested by Cui et al. (2013), the marker-assisted selection (MAS) becomes crucial in a situation that demands accumulation of favourable alleles to enhance the intensity of tolerance level. Besides favourable allele, the allele that exerts strong negative impact on the performance should also be taken into account while breeding for cold tolerance. Marker genotypes that exert negative impact on cold tolerance were discovered in both indica and japonica rice by Pan et al. (2015).

Marker-assisted back-crossing (MABC) is the simplest form of marker-assisted selection (MAS) that seeks targeted transfer/incorporation of QTL/gene-containing genomic segments to elite yet susceptible genetic bases. This approach has been found particularly suitable for introgressing QTL having large effect on the phenotype of interest (Varshney et al. 2012). More importantly, MABC remains the most efficient way to pyramid different gene (s)/QTL (s) into a single genotype (Collard and Mackill 2008). MABC has been successfully implemented to introgress as well as pyramid different LT-tolerance-related QTL (s) into sensitive genetic backgrounds. Two QTLs (*qCTBB-5* and *qCTBB*-6) and two QTLs (*qCTS-6* and *qCTS-12*) conferring tolerance at bud bursting and seedling stages, respectively, were pyramided into SC1-1, a single-segment substitution line (SSSL) were derived from the cross between Nan-yang-zhan and Hua-jing-xian 74 (Yang et al. 2016). Pyramiding of the QTLs (*qCTF7*, *qCTF8* and *qCTF12*) was attempted using SSR markers to enhance cold tolerance at fertilization stage in rice (Shinada et al. 2014). Co-segregating markers viz. In1-c3 and In11-d1 could be exploited in MABC scheme to transfer LT tolerance to high-yielding yet cold-sensitive rice cultivars (Kim et al. 2014). Likewise, MABC also permitted the transfer of QTLs *qRC10-2* (Xiao et al. 2014) and *qCTB3-Silewah* (Mori et al. 2011) controlling LT tolerance at seedling and booting stages, respectively, from Dongxiang wild rice and J501 to susceptible genotypes. Two near-isogenic lines (NILs) were recovered in the background of Towada, which contained QTL-containing region (LT tolerance genes) from Kunmingxiaobaigu (Zhou et al. 2012). As evident from the successful examples reported in rice, MABC holds great potential in enhancing the LT tolerance level of high-yielding yet susceptible cultivars, thus emerging as a promising breeding tool for food security in the face of increasing LT stress worldwide.

Association mapping/genome-wide association studies (GWAS)

Relying on a panel of unrelated individuals, the GWAS technique is quick-to-implement as it does not demand artificially created experimental populations and offers a high-resolution genetic dissection of the complex traits (Mitchell-Olds 2010; Ogura and Busch 2015). Moreover, the wide complementarily of GWAS with the linkage-map-based QTL analysis has been well accentuated by various researchers (Mitchell-Olds 2010; Korte and Farlow 2013; Huang and Han 2014). To illuminate the genetic landscape of LT tolerance at booting stage in rice, association analysis of 347 rice accessions using 148 SSR markers unearthed a set of 24 SSR markers that showed significant association with cold tolerance (Cui et al. 2013). The SSR markers corresponded with the QTL regions reported in earlier studies; for instance, RM252 was adjacent to *Ctb 2*, RM220 and RM 1 with *Ctb1* (Saito et al. 2001, 2004, 2010), and RM566 with *qCTB9* (Andaya and Mackill 2003a, b). Similarly, the DNA markers RM528, RM160, RM4B and RM 235 corresponded with *qLTSSvR6-1*, *qCTSSR9-1*, *qCTSSR11-1* and *qCTSSR12-1*, respectively, as reported more recently by Pan et al. (2015) based on GWAS of 174 rice accessions with 273 SSR markers. Of the 52 QTLs reported by Pan et al. (2015) for cold tolerance, 27 QTLs were mapped in the vicinity of known QTLs. An interconnected breeding (IB) population involving eight *indica* varieties as donors facilitated the identification of six QTLs on three chromosomes in rice (Zhu et al. 2015). One stable QTL *qCT-3-2* was detected in all four environments accounting R^2 up to 9.5%, and fine-mapping using NIL (derived from this IB) assigned *qCT-3-2* to a 193-kb genomic segment. This QTL (*qCT-3-2*) on chromosome 3 was also detected earlier in an RIL population and explained 7.1% PV (Suh et al. 2010). In a recent GWA study, a total of 132 loci were identified from 529 accessions to explain the genetic basis of natural chilling and cold shock in rice (Lv et al. 2016). Interestingly, 68 loci were previously registered for cold tolerance in rice, implying towards some overlap between cold tolerance at different growth stages. GWAS on panels of *japonica* and *indica* rice reconfirmed greater cold tolerance of *japonica* than the *indica* rice (Pan et al. 2015; Lv et al. 2016).

The QTL overlaps suggested by Lv et al. (2016) in rice remained in contrast with the observation in maize where 43 MTAs based on GWAS for cold tolerance did not show any overlap between seedling and booting stages (Huang et al. 2013). Huang et al. (2013) established correspondence of SNP11 and SNP19 with the QTL regions discovered earlier by Jompuk et al. (2005) for chilling tolerance in maize $F_{2:3}$. Based on GWAS of 306 dent and 292 flint inbreds with 49,585 SNPs, a recent study revealed the highest number of QTLs (275 SNPs) for cold tolerance in maize (Revilla et al. 2016). The candidate genes underlying these QTLs coincided with the genomic regions found by Strigens et al. (2013) including QTLs for SPAD and early vigor in dent and flint panels, respectively. Strigens and colleagues detected 19 QTLs for cold tolerance from 375 inbred lines belonging to three breeding groups (NA-D, EU-D and EU-F); majority of these QTLs (*QTL1_RGR* to *QTL10_RGR* with R^2 up to 52.49%) were associated with relative growth rate, and the authors proposed pleiotropy as the major reason to explain the overlapping of QTLs controlling multiple traits. In oat, GWAS of 138 accessions from 27 European countries using Infinium 6K Oat array led to the identification of three robust QTLs for frost tolerance (Tumino et al. 2016). Attempts to link these newly discovered QTLs with the known ones led the authors to propose *Mrg 11* as a new QTL, whereas two QTLs viz. *Mrg 20* and *Mrg 21* found resemblance with genomic regions harboring *Vrn1* locus (KO linkage group 24_26_34) and its second copy (KO linkage group 22_44_18). Similarly, in wheat, a major-effect locus different from *Fr-B1*/*Vrn-B1* and *Fr-B2* was detected on 5B through 9 K SNP array-based analysis of 1739 genotypes (Zhao et al. 2013). Given the 60% higher prediction accuracy of genomic selection (GS) over GWAS, the authors advocated embracing GS technique to offer an improved understanding of frost tolerance in wheat via capturing QTLs having small effect sizes. In sorghum, 194 breeding lines and two $F_{2:3}$ populations comprising 80 and 90 individuals were genotyped with 2620 SNPs. Association analysis uncovered 109 SMTAs, whereas 32 and 37 QTLs were detected from the two populations. The robust MTAs/QTLs were located on SBI-01, 02, 03, 04, 06 and 09 with the underlying candidate genes associated with SbCBF4, CSDP1, ICE1, and cytochrome P45. (Fiedler et al. 2016). A similar approach combining bi-parental population (BPP) and GWAS (Gottingen Winter Bean population: GWBP) was used recently in faba bean (Sallam et al. 2016a). This study yielded 17 QTLs and 25 MTAs in BPP and GWBP, respectively, with corresponding PVs lying in the range of 2.74–29.41 and 2.66–11.89%, and notably, a subset of five significant SNPs was found common to both methods. The SNP loci validated in this study viz VF_Mt5g026780, VF_Mt3g086600 and VF_Mt4g127690 showed association with winter hardiness and yield traits based on association mapping of GWBP (Sallam et al. 2016b).

New-generation omics technologies to illustrate plant LT stress response

Genome-wide expression profiling

Recent advances in functional genomics have deepened our knowledge about the key candidate gene (s), and regulatory network underlying LT stress signaling and tolerance mechanism (Winfield et al. 2010; Zhang et al. 2012b; Bai et al. 2015; Zhao et al. 2015a, b). In this regard, NGS-enabled digital gene expression (DGE) profiling has emerged as a sensitive and high-throughput approach to examine the gene expression that alters during physiological, morphological and molecular response under LT stress in plants (Herman et al. 2006; Fowler and Thomashow 2002). Expression analysis of *Cbf* gene transcripts in barley suggested that higher LT tolerance in recombinants derived from Nure × Tremois cross was due to higher accumulation of *Cbf2* and *Cbf4* gene transcript expression (Stockinger et al. 2007). In wheat, gene expression analysis in Triple Dark (without dominant *Vrn-1* alleles) and nearly isogenic lines (NILs) of Triple Dark (with *Vrn-A1* allele) suggested that the NILs without *Vrn-1* alleles had higher expression of *Wcbf2* and Cor/Lea genes eventually reflected as lower freezing damage than the NILs carrying *Vrn-1* allele (Kobayashi et al. 2005). A comparative expression analysis of rye *Cbf* genes (*ScCbf*s) and *Cor* gene with orthologous CBF and *Cor* genes of wheat *Wcor14b* and *Hvcor14b* genes from barley suggested their "temperature-dependent and light-regulated diurnal response" (Campoli et al. 2009). To elucidate the gene expression under LT stress conditions, expression profiling has witnessed a shift from conventional microarray analysis (Monroy et al. 2007; Cho et al. 2012; Zhang et al. 2012b) to DGE (Fowler and Thomashow 2002; Tian et al. 2013a; Shen et al. 2014; Yang et al. 2015). Microarray analysis revealed changes in the transcripts of 300 genes in spring and winter wheat under LT stress and the encoded proteins from most of the genes suggested their involvement in key metabolic process in wheat (Gulik et al. 2005). Similarly, transcript levels of 450 genes altered in response to cold treatment in contrasting wheat cultivars, thus implying towards the possible participation of 130 candidate genes in signaling and regulatory mechanism viz., TFs and protein kinases (Monroy et al. 2007). Under field and controlled conditions, transcriptome analysis of two cold-acclimated winter wheat lines differing in freeze survival suggested an increase in the expression of *Cbf-2*, *-A22* and *B-22* genes, while Cbf genes (*Cbf-3*, *5*, *6*, *12*, *14* and *19*) were differentially expressed in cold-acclimated higher-freeze-survival and lower-freeze-survival lines in comparison to non-acclimated controls (Sutton et al. 2009). Importantly, *Ta1-*

FFT and *Ta6-SF* fructan biosynthesis gene and *Cor*/*Lea* genes point to their relevance in cold acclimation in wheat (Yokota et al. 2015). To this end, changes in *COR* gene expression and CBF regulon under LT stress recruiting transcriptome study in wheat have been critically reviewed elsewhere (Winfield et al. 2010). In rice, mechanistic complexity of LT tolerance was reported to be higher in indica type than the japonica type given the fact that the former withstands LT stress by activating both CBF-dependent and CBF-independent pathways through recruiting various TFs (Bevilacqua et al. 2015). Comparative transcriptional profiling of two chilling-tolerant (LTH, JM) and two chilling-sensitive (IR29 and PB1) rice cultivars revealed differential expression of 182 genes by twofold, and the set of genes was referred to as Common Cold Induced (CCI). On the other hand, 511 genes termed as Cold Induced in Tolerant (CIT) were expressed in chilling-tolerant cultivars, whereas 2101 genes were expressed differentially only in the cultivar JM (Chawade et al. 2013). Participation of various regulatory genes involving antioxidant enzyme genes, genes associated with signal transduction of abscisic acid (ABA), salicylic acid (SA) regulatory phytohormones and *OsDREB2A* gene became evident by genome-wide expression profiling under LT stress (Zhao et al. 2015b). Differential expression of lipid transfer protein (LTP) genes was also reported in LT-tolerant and LT-sensitive genotypes in rice (Moraes de Freitas et al. 2016). Based on mRNA expression profiling, higher expression of plasma membrane intrinsic proteins (PIPs) in LT-tolerant rice in comparison to sensitive cultivar under LT stress highlighted their importance in LT stress, and it has been recorded through mRNA expression profiling (Yu et al. 2006). Analysis of rice genotypes IL112 and GC2 using Affymetrix GeneChip provided one candidate gene *LOC_Os07g22494* responsible for seedling LT tolerance (Liu et al. 2013). Employing Agilent Rice Gene Expression Microarray 4 × 44 K in two chilling-tolerant rice varieties, i.e., Sijung and Jumli Marshi led the authors to propose that genes confer chilling tolerance in Sijung largely through enabling protection of the cell wall and plasma membrane. On the other hand, Jumli Marshi exploits detoxification mechanism to withstand chilling stress through ROS scavenging and safeguarding chloroplast translation (Lindlöf et al. 2015). Based on a microarray analysis in barley, the role of *VRN1* was reconfirmed by Greenup et al. (2011) as the contig corresponding to *HvVRN1* remained upregulated in prolonged cold and vernalized plants. Authors also observed increased transcript levels for two genes *HvCOR14B* and *WSC19* in both short-term and prolonged cold treatments and in vernalized plants. By contrast, HvCBF9 showed upregulation in response to short-term LT stress. Some genes reported to be significant for cold tolerance in wheat (associated gibberellin biosynthesis pathway) did not register any response in this study. Expression level of 102 genes was showing up to eightfold difference under freeze stress at −5 °C based on Affymetrix Wheat GeneChip microarray in wheat genotype Yumai 34 (Kang et al. 2013); the authors obtained a set of genes viz., WCOR413, LEA, aquaporin 2 showing expression levels similar to those recorded previously in wheat and barley for spring freeze stress. By employing GeneChip Wheat Genome Array, Skinner (2015) recorded more than twofold upregulation of 2000 genes in Tiber wheat cultivar under freezing (−3 °C for 24 h) and thawing (+3 °C for 24 or 48 h) treatment, suggesting the involvement of genes participating in cell signaling, and activating stress responsive mechanism. Likewise, Arabidopsis NimbleGen ATH6 Microarrays analysis of 10 *Arabidopsis* ecotypes collected from different geographical regions revealed ecotype-specific regulatory TFs that respond to LT stress (Barah et al. 2013). Based on a microarray analysis in *Festuca pratensis*, Rudi et al. (2011) found two candidate genes *FpQM* and *FpTPT* contributing to LT tolerance. Genome-wide transcriptome analysis in tolerant and wild lines of rice delivered a set of 78 genes related to chilling stress(Cho et al. 2012). In another study, differentially expressed genes involved in *OsDREB1* and *OsMyb4* regulons were found to be contributing to LT stress tolerance in rice (Zhang et al. 2012a). The study established genes encoding membrane fluidity and defensive proteins as instrumental in conferring LT tolerance in the line K354. Notably, Zhang et al. (2012b) found a common set of genes associated with cold signaling and transcription regulation, which showed upregulation in contrasting rice genotypes LTH and IR29 under early chilling response. Whereas, the given genotypes differed in regulatory gene expression, thus offering adaptation ability to the chilling-tolerant genotype under late phase of chilling stress. Considerable transcriptional variation was observed between *Solanum commersonii* and *S. tuberosum* concerning genes involved in CBF regulons, and importantly, putative orthologous LT regulatory genes common to *S. commersonii*, *S. tuberosum* and *A. thaliana* were recovered (Carvallo et al. 2011). Transcriptome analysis in contrasting lines Champagne (freezing tolerant) and Terese (freezing sensitive) in pea suggested that the chilling tolerance was induced comparatively early in Champagne than in Terese via expressing *CBF*, *COR* and *LEA* genes; however, freezing tolerance of Champagne was due to orchestrating safeguard mechanism of antioxidant production, and cell wall modification (Lucau-Danila et al. 2012). While molecular markers developed from the differentially expressed genes obtained from quantitative polymerase chain reaction (qPCR) led to the detection of five candidate genes conferring LT tolerance existing in previously reported three LT-tolerant QTLs (Legrand et al. 2013).

RNA-seq has shed light on a variety of genes showing differential expression in response to LT stress tolerance (Bai et al. 2015; Chen et al. 2015b). For example, more than 300 differentially expressed genes under LT stress were discovered in rice using RNA-seq analysis of three LT-tolerant and one LT-sensitive genotypes (Shen et al. 2014). In another study, RNA-seq analysis of *indica* rice at germination stage under LT stress indicated marked changes in cellular response encompassing cell division, Ca^{2+} signaling, sucrose synthesis and antioxidant activity (Dametto et al. 2015). Anther transcriptome analysis in rice revealed 1497 and 5652 differentially expressed genes, thus suggesting their role in signal transduction and transcription regulation of cold tolerance, respectively (Bai et al. 2015). RNA-seq driven by Illumina sequencing aided in disclosing 39 TFs viz., AP2/ERF, zinc finger, NAC, MYB involved in LT stress in *Anthurium andraeanum* (Tian et al. 2013a). A recent RNA-seq based comparative transcriptome analysis in banana and plantain elucidated significant difference in expression levels of several genes including ICE1 and MYBS3 under different LT stress treatments (Yang et al. 2015). Similarly, RNA-seq analysis of LT-treated leaf tissue of *Spartina pectinata* revealed active involvement of genes ranging from transcription regulators, anti-freezing proteins to epigenetic regulatory genes providing freezing stress tolerance (Nah et al. 2016). The recent transcriptomic studies provide valuable insights on genome-scale expression profiling of various genes including regulatory genes involved in key metabolisms and development pathways under LT.

Non-coding RNAs, their targets and LT stress

The NGS technology has offered unprecedented opportunity to capture non-coding RNA (ncRNA) molecules including miRNA, siRNA and lncRNA that make significant contribution to abiotic stress tolerance in plants (Khraiwesh et al. 2012; Matsui et al. 2013). Recent studies have facilitated discovery and functional characterization of cold-responsive ncRNAs and their possible targets (Chen et al. 2012; Thiebaut et al. 2012; Niu et al. 2016). In this context, the role of miR-167 and miR-319 in response to cold stress in rice is worth mentioning (Lv et al. 2010). Examination of Osa-miR319b (a family of miRNA319 in rice) to find the contribution towards LT tolerance unearthed targeting of TFs like *OsPCF6* and *OsTCP21*) Wang et al. 2014). Moreover, overexpression of Osa-miRNA319 targeting *OsPCF5* and *OsPCF8* genes conferring LT in transgenic rice could be potentially harnessed to develop LT-tolerant rice cultivar (Yang et al. 2013b). NGS analysis of small RNA libraries in poplar (*Populus tomentosa*) provided set of cold-responsive miRNAs showing down- (21) and up-regulation (9) (Chen et al. 2012). Likewise, role of miR475b in freezing tolerance has been unfolded via cloning *MIR475b* gene in *Populus suaveolens* (Niu et al. 2016). Likewise, in tea, RNA-seq analysis using Solexa sequencing led to the identification of 31 upregulated and 43 downregulated miRNAs in Yingshuang genotype and 46 upregulated and 45 downregulated miRNAs in Baiye 1 genotype, respectively, under LT stress (Zhang et al. 2014b). Interestingly, from this study, a total of 763 related target genes were recovered via degradome sequencing. In tomato, cold-responsive miRNAs were obtained under LT stress such as miR159, miR319, and miR6022 from *Solanum lycopersicum* and *S. habrochaites* (Chen et al. 2015b) and miR167, miR169, miR172, miR 393 and miR397 (Koc et al. 2015). Interestingly, conservative role of these non-coding molecules in conferring LT stress tolerance across different plant species has been supported by various studies. The recent examples include miR319 and its putative targets *GAMyb*, and *PCF6* in sugarcane (Thiebaut et al. 2012) and miR156, miR159, miR167, miRNA172, miRNA396 and miRNA398 in alfalfa (Shu et al. 2016). Further exploration of non-coding RNA world will assist in unraveling novel ncRNAs and their targets that participate in LT signaling and crosstalk in plants. Recently, microRNA (miRNA) and small interfering RNA (siRNA) functioning at post-transcriptional level are receiving attention owing to their significant contribution in both biotic and abiotic stress tolerance (Ariel et al. 2015; Liu et al. 2015b). Evidences of miRNA contributing in LT stress in *Arabidopsis* (Zhou et al. 2008), rice (Wang et al. 2014), *Populous* (Chen et al. 2012), *Brachypodium*) Zhang et al. 2009), tea (Zhang et al. 2014b), and tomato (Chen et al. 2015b) have been recorded.

Analyzing proteomes to describe plant LT stress tolerance

As a complement to transcriptomics, proteomics allows characterization of the gene product at both translational and post-translational levels, thus revealing the complete landscape of the proteins involved in LT acclimatization in plant (Janmohammadi et al. 2015). In this section, we summarize the role of proteomics in understanding LT stress in crop plants. Role of proteomics in deciphering LT stress tolerance lies at various levels ranging from cellular metabolism and energy production, oxidative stress damage, cold acclimation to cellular signaling (Cui et al. 2005; Hashimoto and Komatsu 2007; Neilson et al. 2011; Dumont et al. 2011; Sandve et al. 2011; Kosová et al. 2013). Proteins participating in energy metabolism might play crucial roles in providing LT stress tolerance. For example, alteration in proteins involved in photosynthesis, transport and energy metabolism was recorded in LT-treated rice at seedling stage by iTRAQ assay (Neilson et al. 2011). Proteins contributing to sugar synthesis, regulating transcription and translation activity in chloroplast might cause LT acclimation in pea (Grimaud et al. 2013). Likewise, to elucidate the role of proteins contributing in LT tolerance at germination stage, expression of 85 and 196 proteins was examined, respectively, in tolerant and sensitive rice cultivars with shotgun proteomics analysis under LT stress (Lee et al. 2015). The expressed proteins obtained in tolerant cultivars suggested their participation in gibberellin and ABA-mediated signaling in LT tolerance. In addition, various proteins involved in protection mechanism from oxidative stress under LT stress were found. The LT imposed on winter and spring wheat cultivars caused an increase in stress and development proteins in winter wheat line, and an increase in proteins contributing in cell division re-establishment in spring wheat line (Kosová et al. 2013). Proteomics study in LT-treated cold-tolerant and cold-sensitive wheat cultivars suggested an increase in antioxidant-related proteins in LT-tolerant cultivar and an abundance in proteins involved in carbohydrate metabolism in LT-sensitive cultivar (Xu et al. 2013). While investigating proteins contributing to LT acclimation in alfalfa, proteomic study revealed greater insight into the changes of key proteins involved in cellular metabolism ranging from photosynthesis to stress-alleviating proteins. In this context, ‘autologous metabolism and biosynthesis’ halted in freezing-tolerant ZD cultivar, while W5 freezing-sensitive cultivar activated the proteins associated with protection mechanism against cold stress (Chen et al. 2015a). In pea, higher adaptation of Champagne genotype for chilling stress was elucidated owing to the presence of higher proteins involved in photosynthesis and protection mechanism (Dumont et al. 2011). In addition, dehydrins and late embryogenesis abundant proteins participate in conferring chilling tolerance in plant (Hanin et al. 2011). Greater accumulation of dehydrin 5 (DHN5) protein in winter barley lines in comparison to spring lines adequately explained the enhanced LT acclimation of winter barley (Kosová et al. 2010). The dynamics of dehydrin especially Wcs120 and Dhn5 in cold acclimation in barley and wheat, respectively, has been reviewed elsewhere (Vítámvás and Prásil 2008; Kosová et al. 2011). Furthermore, the role of proteins associated with “cell signaling, cellular transport and cell membrane” in response to LT stress in perennial grasses has been reviewed (see Sandve et al. 2011). Therefore, efforts are needed to combine proteomic and transcriptome data to gain deeper insight into the ‘gene regulatory network’ associated with LT stress tolerance in plants.

Conclusion and future prospects

Given the current trajectory of population growth worldwide that projects 9 billion people by 2050 (Godfray et al. 2010), LT stress can further aggravate the growing problem of food insecurity. To meet this challenge, plant breeding requires to efficiently tap the rich gene/allelic diversity contained in crop germplasm resources. This in turn paves the way for introducing unexploited genetic resources including wild crop relatives, landraces and advanced breeding lines into existing crop improvement schemes. Recent advancements in genomics can significantly underpin crop improvement to develop LT stress-tolerant crops. The QTLs controlling LT tolerance-related traits could be immediately deployed in breeding schemes through MAS or MABC. Alternatively, the QTL-containing segment may be targeted for fine-mapping or map-based cloning. Emerging QTL discovery methods such as GWAS make best use of the available phenotypic records and high-density DNA marker systems. As QTLs with small effect sizes substantially contribute to cold tolerance, genomic selection that adequately captures these minor QTLs holds greater relevance. In parallel, consolidating the information emanating from multiple omics platforms viz. transcriptomics, and proteomics would allow researchers to pinpoint the causative gene (s) involved in LT signaling and cold acclimation in plants. To this end, the reference genome sequences established in major crops open up opportunities for identification of specific DNA sequences that are involved in plant LT tolerance. We envisage that the modern omics technologies can significantly support conventional breeding to ensure sustainable crop production under LT stress.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest. No financial help is taken for writing this manuscript.

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