RESEARCH NOTE

Genetic dissection of seed vigour traits in maize (*Zea mays* L.) under low-temperature conditions

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Introduction

Seed vigour, an important factor governing the seed quality, reflects potential seed germination, seedling growth, seed longevity and tolerance to adversity (Sun *et al.* 2007). Maize plants grown in subtropical and temperate regions are often subjected to cold stress and frequently exhibit poor early-season vigour that leads to delayed seedling development and poor stand establishment (Hope *et al.* 1992). Many studies have uncovered various quantitative trait loci (QTL) associated with the chilling tolerance of maize seedlings (Frachebound *et al.* 2004; Jompuk *et al.* 2005; Presterl *et al.* 2007; Rodriguez *et al.* 2008; Marcelo 2012). However, the physiological mechanisms and genetic basis of seed vigour-related traits remain unknown. Here, we evaluated five seed vigour traits in two connected recombinant inbred lines (RIL) populations under low-temperature conditions. A total of 26 QTL were identified. Fourteen initial QTL were integrated into five meta-QTL (mQTL) in a meta-analysis. Our results provide an important reference for facilitating indirect selection for cold tolerance in maize breeding.

Materials and methods

Plant materials

Two sets of connected RIL populations consisting of 208 and 212 F_{10} RILs derived from two crosses (Yu82 × Shen137 and Yu537A × Shen137) using the single-seed descent method were used to identify QTL for seed vigour traits under low-temperature conditions. The population from Yu82 × Shen137 is designated as Pop. 1, and the population from Yu537A × Shen137 is referred to as Pop. 2. Parents Yu82 and Yu537A were derived from a synthetic population with Stiff Stalk germplasm, while Shen137 was selected from tropical germplasm.

Seeds of the two populations (F_9 RILs) and three parental lines were produced in the winter of 2010 in Hainan Province, China (18°45′N, 109°30′N). The seeds were completely dried after being harvested under natural conditions for the construction of a genetic linkage map and evaluation of low-temperature germination ability. For low-temperature measurements, the seeds of each genotype were divided into three portions, each consisting of 50 seeds, selected to ensure sowing quality.

Evaluation of low-temperature seed vigour

The germination experiment followed a complete randomized block design with three replications and was conducted at 18 ± 1°C in a growth chamber in 2011. A sprouting bed was established with 0.05–0.2 mm diameter fine sand. The sand was heated at 120°C for 2 h in a high-handed sterilization pan containing a 16 × 8 array of 40-mm diameter cells. In each cell, two seeds were placed on top of 3.5 cm of sand and then covered with 1.5 cm of sand. Fifty seeds were selected from each parental line and each RIL to ensure good sowing quality for each replicate. The seeds were incubated in a growth chamber at 18 ± 1°C (Chen *et al.* 2007), 60% relative humidity and illumination conditions of 4000 lx and a 14/10 (day/night) photoperiod with three replications. Vigour-related data were collected over an 8-day period after sowing and were used for QTL analysis. After 8 days data collection period was completed, five plants of each RIL were randomly selected for measurement

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of seedling length. Germination percentage (GP) was calculated as GP $= n/N \times 100$, where n is the total number of germinated seeds and N is the total number of seeds. Germination index (GI) was calculated as GI $= \sum G_t/D_t$, where D_t(d) is germination time, and G_t(d) is the number of germinated seeds during that time. Simple vigour index (SVI) was calculated as VI = GP × SL, where SL (cm) is the seedling length on the 11th day. Mean germination time (MGT) was calculated as MGT $= \sum(G_t \times D_t)/$GP. Finally, broad-sense heritability (h^2) for each trait was calculated as follows: $h^2 = \sigma_g^2/(\sigma_g^2+\sigma_{gy}^2/n+\sigma_e^2/nr)$, where σ_g^2 denotes the genetic variance, σ_{gy}^2 denotes the interaction variance of genotype and environment, σ_e^2 denotes the error variance, n denotes the number of environment and r denotes the replication number. σ_g^2, σ_{gy}^2 and σ_e^2 were estimated by analysis of variance (ANOVA) using the general linear model procedure of the statistical software SPSS 12.0. Descriptive statistics and simple Pearson correlation coefficients (r) were calculated between the traits using the above statistical software.

Genetic linkage map construction

To genotype 420 RILs and three parental lines, 3072 pairs of single-nucleotide polymorphism (SNP) markers were selected from more than 800,000 SNPs (Ganal *et al.* 2011). Polymorphisms were analysed in 3072 SNP markers between two parental pairs, Yu82/Shen137 and Yu537A/Shen137. Ultimately, 1397 and 1371 SNP markers were found to be polymorphic between the Yu82/Shen137 and Yu537A/Shen137 parents, respectively. Serious segregation distortion ($P < 0.05$) was exhibited by 225 Yu82/Shen137 markers and 232 Yu537A/Shen 137 markers. Two genetic linkage maps were constructed using JoinMap ver. 4.0 software and 1172 and 1139 SNP markers from the Yu82/Shen137 and Yu537A/Shen137 parents, respectively. Total map lengths were 1629.61 cM with an average interval of 1.39 cM for Pop. 1 and 1681.75 cM with an average interval of 1.48 cM for Pop. 2 (Han *et al.* 2014).

QTL analysis

QTL analysis was conducted using composite interval mapping in WinQTLcart 2.5. For the composite interval mapping, model 6 of the Zmapqtl module was employed to identify QTLs and their effects. To identify an accurate threshold for significance of each trait, an empirical threshold was determined by performing 1000 random permutations (Churchill and Doerge 1994). QTL positions were assigned to relevant regions at the points having the highest likelihood odds (LOD) ratio. QTL confidence intervals were calculated by subtracting one LOD unit on each side from the maximum LOD position (Lynch and Walsh 1998).

mQTL analysis

To integrate QTL information for the evaluated seed vigour traits in the two connected RIL populations, the two genetic linkage maps were integrated and consensus QTL were identified by meta-analysis (Chardon *et al.* 2004). Meta-analysis was performed using BioMercator2.1 software (Chardon *et al.* 2004). The Akaike information criterion (AIC) was used to select the QTL model on each chromosome (Hirotugu 1974). The QTL model with the lowest AIC value was considered to be a significant model indicating the number of mQTL. The number of mQTLs best fitting the results for a given linkage group was determined based on a modified AIC (Goffinet and Gerber 2000). mQTL were named using the following nomenclature: 'm' + 'QTL' + 'chromosome number'.

Results

Phenotypic variation

A GP of 100% was obtained for Yu82, Yu537A and Shen137. Other vigour-related traits within the three parental lines exhibited no significant differences under normal treatment conditions (28 ± 1°C; Han *et al.* 2014). For all five traits other than GI in Yu82 versus Shen137, some clear varietal differences ($P < 0.05$) were observed in parental lines Yu82 versus Shen137 and Yu537A versus Shen137 under low-temperature treatment conditions (18±1°C; table 1). GP values under low-temperature treatment conditions decreased by 10 and 20% in Yu82 and Yu537A, respectively, relative to normal treatments. Values of the measured traits between the two sets of populations were normally distributed around the mean under low-temperature treatment conditions (table 2). The range of variability of each studied trait was large among RILs, and the traits differed substantially in response to low-temperature treatments. In addition, h^2 for the four measured traits ranged from 67.53 to 76.21% in the two populations under the low-temperature treatments (table 2).

The correlation coefficients for all traits measured were higher under low-temperature treatment conditions (table 3). GP, GI, SL, SVI and MGT values showed positive significant correlations with one another, and the correlation trends were consistent under low-temperature conditions in both populations. The strongest correlations were observed for GP with SVI and GI.

Analysis of QTL for five measured traits under low-temperature treatment conditions

In the two connected RIL populations under low-temperature conditions, 26 putative QTL for GP, MGT and other seed vigour traits were detected in all maize chromosomes except for chromosome 10, namely nine QTL in Pop. 1 and 17 in Pop. 2 (table 1). Individual QTL explained 5.49–11.58% of the phenotypic variation, with five QTL accounting for more than 10% of the total phenotypic variation.

Under low-temperature conditions, the seven GP-related QTL were located on chromosomes 1, 2, 3, 5, 6 and 7 in the two populations, with two QTL in Pop. 1 and five QTL in Pop. 2 (table 1). Contributions of the QTL to

Table 1. QTLs detected for five traits in two maize RIL populations under low-temperature conditions.

Trait	QTL	Chr.	Position (cM)	Marker interval	LOD	R^2 (%)	*A*
RILs of Yu82 × Shen137							
GP	*qGP1-2*	2	74.69	SYN2544–PZE-102074262	2.98	6.89	−0.03
	qGP1-5	5	173.68	SYN14676–SYN33425	3.66	7.98	−0.02
GI	*qGI1-3*	3	103.93	PZE-103104806–PZE-103110761	3.02	7.80	−0.08
	qGI1-7	7	143.49	SYN34644–PZE-107137037	3.88	11.01	0.16
SL	*qSL1-3*	3	13.56	PZE-110007326–PZE-110007326	2.99	7.58	−0.53
SVI	*qSVI1-5*	5	172.56	SYN14680–SYN14676	3.06	7.70	−0.02
MGT	*qMGT1-2-1*	2	76.04	PZE-102074262–PZE-102077128	4.94	10.59	0.24
	qMGT1-2-2	2	168.20	SYN7209–SYN36607	3.29	7.37	0.19
	qMGT1-3	3	169.32	SYN29941–SYN31522	2.81	5.95	−0.17
RILs of Yu537A × Shen137							
GP	*qGP2-1*	1	36.09	PZE-101052634–PZE-101001107	2.57	6.63	0.03
	qGP2-2	2	77.64	PZE-102116144–PZE-102111891	3.86	9.98	−0.04
	qGP2-3	3	72.49	SYN28063–PZE-103180642	3.11	7.46	−0.04
	qGP2-6	6	139.19	PZE-106005121–PZE-106007551	2.80	6.87	−0.03
	qGP2-7	7	41.49	PZE-107045266–PZE-107032490	3.71	9.06	−0.04
GI	*qlGI2-3*	3	114.87	PZE-103027544–PZE-103024939	2.51	5.49	−0.07
	qlGI2-8	8	46.05	PZE-108021854–PZE-108024244	3.15	7.55	0.08
SL	*qSL2-3*	3	72.49	SYN28063–PZE-103180642	3.32	7.62	−0.45
	qSL2-8	8	100.61	PZE-108096541–PZE-108103951	3.21	6.73	0.34
	qSL2-9-1	9	83.58	PZE-109061997–SYN37647	5.01	10.57	−0.44
	qSL2-9-2	9	91.09	PZE-109055211–SYN34709	2.72	6.06	−0.33
SVI	*qSVI2-3-1*	3	70.95	PZE-103160158–SYN20833	2.6	6.5	−0.02
	qSVI2-3-2	3	39.60	PZE-103139833–SYN23237	3.01	7.22	−0.02
MGT	*qMGT2-2*	2	80.23	SYN13599–PZE-102112161	5.12	10.96	0.32
	qMGT2-4	4	156.95	PZE-104009393–SYN8509	2.55	7.22	−0.13
	qMGT2-9-1	9	91.09	PZE-109055211–SYN34709	3.42	8.01	0.13
	qMGT2-9-2	9	98.16	PZE-109050931–PZE-109047581	4.69	11.58	0.16

GP, germination percentage; GI, germination index; SL, seedling length; SVI, simple vigour index; MGT, mean germination time; *A*, additive effect.

Table 2. Phenotypic performance of five seed vigour-related traits in three parental lines and two RIL populations under low-temperature conditions in maize.

Population	GP	GI	SL	SVI	MGT
Yu82 (P_1)	90.00	3.52	8.00	7.20	6.15
Yu537A (P_2)	80.00	2.84	6.71	5.37	3.00
Shen137 (P_3)	100.00	3.70	8.85	8.85	2.40
P_3 versus P_1[a]	**	*	*	**	**
P_3 versus P_2	**	*	**	**	*
RILs of Yu82 × Shen137					
Mean ± SD	80.00 ± 18.00	2.76 ± 0.72	7.70 ± 1.28	6.16 ± 0.23	4.37 ± 0.69
Range	17.00–100.00	0.74–3.76	4.20–10.70	0.71–10.70	4.15–7.20
Skewness	−0.12	−0.79	−0.25	0.36	−0.72
Kurtosis	0.77	0.45	−0.15	0.10	−0.04
h^2 (%)	76.21	69.86	73.15	65.43	70.58
Confidence interval	64.38–79.54	61.35–75.42	60.33–79.33	59.72–72.18	62.46–79.47
RILs of Yu537A × Shen137					
Mean ± SD	85.92 ± 12.50	3.08 ± 0.23	7.95 ± 1.46	7.08 ± 0.56	2.62 ± 0.02
Range	30.00–100.00	1.78–3.95	4.65–10.84	1.61–10.46	2.09–3.19
Skewness	−0.70	−0.99	−0.05	−0.64	0.12
Kurtosis	0.27	0.62	0.23	0.97	0.87
h^2 (%)	69.44	67.53	72.56	71.41	68.73
Confidence interval	60.89–75.37	58.45–73.75	64.32–78.93	62.63–76.53	59.42–76.50

GP, germination percentage; GI, germination index; SL, seedling length; SVI, simple vigour index; MGT, mean germination time.
[a]Statistical test for differences between two parents significant at $P = 0.05$ (*) and $P = 0.01$ (**) levels of probability.

phenotypic variation ranged from 6.63 to 9.98%. All positive alleles except for qGP2-1 were contributed by Shen137 and contributed to increases in the GP phenotypic variation values.

Four QTL for GI were identified under low-temperature conditions, two in Pop. 1 and two in Pop. 2. These QTL were distributed on chromosomes 3, 7 and 8 and explained

Table 3. Phenotypic correlations among five seed vigour-related traits under low-temperature treatment conditions in two maize populations.

Trait	GP	GI	SL	SVI	MGT
GP		0.88**	0.37**	0.81**	−0.36**
GI	0.89**		0.28**	0.74**	−0.40**
SL	0.57**	0.57**		0.75**	−0.50**
SVI	0.68**	0.69**	0.60**		−0.55**
MGT	−0.35**	−0.34**	−0.37**	0.47**	

Correlation coefficients above and below the diagonal line are for Yu537 × Shen137 and Yu82 × Shen137 RIL, respectively. GP, germination percentage; GI, germination index; SL, seedling length; SVI, simple vigour index; MGT, mean germination time.
**significant at $P = 0.01$.

Table 4. mQTL for five traits in two maize RIL populations under low-temperature conditions.

mQTL	Chr.	Position (cM)	Confidence interval (cM)	Flanking marker	Number of QTL	Trait involved	Integrated QTL
mQTL2	2	77.44	75.22–80.38	PZE-102074262–PZE-102112161	4	GP, MGT	*qGP1-2*, *qMGT1-2-1*, *qGP2-2*, *qMGT2-2*
mQTL3-1	3	72.08	71.54–73.61	SYN28063–PZE-103180642	3	GP, SL, SVI	*qGP2-3*, *qSL2-3*, *qSVI2-3-1*
mQTL3-2	3	109.48	107.89–113.87	PZE-103104806–PZE-103027544	2	GI	*qGI1-3*, *qlGI2-3*
mQTL5	5	173.68	171.64–175.42	SYN14676–SYN33425	2	GP, SVI	*qnGP1-5*, *qSVI1-5*
mQTL9	9	95.86	91.75–98.26	PZE-109050931–SYN34709	3	SL, MGT	*qSL2-9-2*, *qMGT2-9-1*, *qMGT2-9-2*

5.49–11.01% of the phenotypic variation (table 1). Among these QTLs, favourable alleles increasing the trait values at qGI1-3 in Pop. 1 and qGL2-3 in Pop. 2 were derived from Shen137. The QTL qGI1-7 explained 11.01% of the total phenotypic variance in GI.

One QTL in Pop. 1 and four QTL in Pop. 2 for SL were identified on chromosomes 3, 8 and 9 under low-temperature treatment conditions. The contribution rates of these QTL to the total phenotypic variance ranged from 6.06 to 10.57%. Except qSL2-8, all positive alleles contributing towards an increase in SL values were derived from Shen137, with one QTL explaining 10.57% of total phenotypic variance.

Three QTL for SVI were detected under low-temperature treatment conditions in the two populations, one in Pop. 1 and two in Pop. 2. The three alleles were distributed on chromosomes 3 and 5, and contributed to the phenotypic variation for a single QTL of 6.50–7.70% (table 1). All positive alleles were derived from Shen137.

Three QTL in Pop. 1 and four QTL in Pop. 2 were identified on chromosomes 2, 3, 4 and 9 under low-temperature conditions. The contribution rates of these QTL to the total phenotypic variance ranged from 5.95 to 11.58% (table 1). All positive alleles except for qMGT1-3 and qMGT2-4 were derived from Yu82 or Yu537A and contributed towards an increase in MGT values, with three QTL contributing more than 10% of the phenotypic variance.

Through comparison of the QTL identified in the two connected RIL populations, we found that two QTL were identified under control and low-temperature conditions, one for GP and MGT on chromosome 2 between PZE-102074262 and PZE-102112161 and the other for GI on chromosome 3 between PZE-103104806 and PZE-103027544. These QTL showed high consistency across both populations and may merit further study using marker-assisted selection (MAS).

mQTL analysis

The integrated genetic map constructed for the two populations contained 1712 SNP markers; it was 1712.6 cM long with an average of 1.00 cM between markers. We performed a meta-analysis to identify mQTL associated with the observed variation of the five seed vigour traits under low-temperature treatment conditions. Five mQTL were identified from the initial 26 QTL based on the variation in the five traits (table 4). Fourteen of the initial QTL (53.85%) were integrated into the five mQTL regions. The five mQTL were mapped to chromosomes 2, 3, 5 and 9. On average, each mQTL included 2.8 QTL, with a range of 2–4 QTL for 1–3 traits. The initial QTL included in mQTL2 and mQTL3-2 were detected in the two populations under low-temperature treatment conditions. The initial QTL with values of $R^2 > 10\%$ were integrated into two mQTL, mQTL2 and mQTL9, that included 3–4 initial QTL for two traits in one or both populations. The genomic regions associated with these mQTL may be hot spots for important QTL related to seed vigour traits under low-temperature conditions.

Discussion

Assessments of importance and main results in this study for seed vigour under low-temperature stress

Crop yield potential is severely and irreversibly affected by stress damage at any stage of growth (Pirasteh-Anosheh *et al.* 2011; Hamidi *et al.* 2013). Low temperatures at planting and germination cause a slow emergence rate, a reduced emergence percentage, and a reduced growth rate in maize seedlings after emergence. Therefore, rapid uniform field emergence under low-temperature stress is an essential criterion for yield and quality (Pirasteh-Anosheh and Hamidi 2013). Elucidation of the genetic mechanisms underlying seed vigour under low-temperature conditions is therefore important. In the present study, we evaluated five seed vigour traits in two connected RIL populations under low-temperature conditions. A total of 26 QTL were identified. Individual QTL explained 5.49–11.58% of variation in the traits associated with seed vigour with five QTL explaining more than 10% of phenotypic variance of corresponding traits. Fourteen initial QTL were integrated into five mQTL in a meta-analysis, four of the initial QTL integrated into the mQTL had R^2 values greater than 10%. These QTL may provide useful information for MAS to improve seed vigour under low-temperature conditions.

Associations between QTL and candidate maize genes

Chilling damage endangers seed germination and seedling growth. Continuous low temperatures can greatly reduce metabolic activities such as protein synthesis, the cell cycle signal-transduction pathway and the secretion of plant growth-regulating substances, with concomitant damage to nucleic acids, lipids and proteins (Chen *et al.* 2006). During long-term evolution, plants under low-temperature stress have developed the ability to rapidly perceive surrounding signals and enhance resistance to low temperature through the activation of a complex series of signal transduction and specific transcription regulatory factors. To obtain additional information regarding the genetic architecture of seed vigour in maize, we analysed homologous genes associated with seed vigour under low-temperature stress. Sequences of candidate genes from maize, rice, *Arabidopsis* and other crops were downloaded from the National Center for Biotechnology Information, and their homologus in maize inbred line B73 were identified using maize GDB blast with an *E*-value cutoff of 10^{-10} and coverage longer than 60%. ATMG01120 and AT2G29570 were found to be located in mQTL3-2 and mQTL5, respectively. ATMG01120 encodes a subunit of mitochondrial NAD(P)H dehydrogenase which is trans-spliced from three precursors, NAD1A, NAD1B and NAD1C. Additionally, ATMG01120 has a ubiquinone oxidoreductase domain that catalyses the transfer of two electrons from NADH to ubiquinone in a reaction associated with proton translocation across the membrane (Sunderhaus *et al.* 2006). AT2G29570 functions as a sliding clamp for DNA polymerase and is thus a key factor in DNA replication. The protein is also involved in DNA repair, maintenance of heterochromatic regions throughout replication, cell-cycle regulation, and programmed cell death (Meng *et al.* 2007).

Application of QTL for seed vigour to maize breeding

In this study, mQTL2 and mQTL9 (two of the initial QTL with $R^2 > 10\%$) were identified in one or two populations but were involved in different traits. Our results corroborate those of a previous study by Marcelo (2012), who identified QTL for seed vigour traits in the same regions of chromosomes 2 and 9 using a BC_1F_2 population. These results suggest that mQTL2 and mQTL9 are stable major loci under low-temperature conditions in different genetic backgrounds. These mQTL might be used to improve maize seed vigour under low-temperature conditions in future maize breeding programmes.

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References

Chardon F., Virlon B., Moreau L., Falque M., Joets J., Decousset L. *et al.* 2004 Genetic architecture of flowering time in maize as inferred from quantitative trait loci meta-analysis and synteny conservation with rice genome. *Genetics* **168**, 2169–2185.

Chen L., Lou Q. J., Sun Z. X., Xing Y. Z., Yu X. Q., Luo L. J. *et al.* 2006 QTL mapping of low temperature on germination rate of rice. *Rice Sci.* **13**, 93–98.

Chen M. S., Geng Z. Y. and Zhao J. L. 2007 Effect of temperature on germination characters of maize. *J. Shangdong Agric. Univ. (Nat. Sci.)* **38**, 196–202.

Churchill G. A. and Doerge R. W. 1994 Empirical threshold values for quantitative trait mapping. *Genetics* **142**, 285–294.

Frachebound Y., Jompuk C., Ribaut J. M., Stamp P. and Leipner J. 2004 Genetic analysis of cold tolerance of photosynthesis in maize. *Plant Mol. Biol.* **56**, 241–253.

Ganal M. W., Durstewitz G., Polley A., Berard A. and Buckler E. S. 2011 A large maize (*Zea mays* L.) SNP genotyping array: development and germplasm genotyping, and genetic mapping to compare with the B73 reference genome. *PLoS One* **6**, e28334.

Goffinet B. and Gerber S. 2000 Quantitative trait loci: a meta-analysis. *Genetics* **155**, 463–473.

Hamidi R., Pirasteh-Anosheh H. and Izadi M. 2013 Effect of seed halo-priming compared with hydro-priming on wheat germination and growth. *Inter. J. Agron. Plant Product* **4**, 1611–1615.

Han Z. P., Ku L. X., Zhang Z. Z., Zhang J., Guo S. L., Liu H. Y. *et al.* 2014 QTLs for seed vigor-related traits identified in maize seeds terminated under artificial aging conditions. *PLoS One* **9**, e92535.

Hirotugu A. 1974 A new look at the statistical model identification. *IEEE Trans. Auto. Contr.* **19**, 716–723.

Hope H. J., White R. P., Dwyer L. M., Maamari R., Seguin S. and Hamilton R. I. 1992 Low temperature emergence potential of

short season corn hybrids grown under controlled environment and plot conditions. *Can. J. Plant Sci.* **72**, 83–91.

Jompuk C., Fracheboud Y., Stamp P. and Leipner J. 2005 Mapping of quantitative trait loci associated with chilling tolerance in maize (*Zea mays* L.) seedlings grown under field conditions. *J. Exp. Bot.* **56**, 1165–1175.

Lynch M. and Walsh B. 1998 *Genetics and analysis of quantitative traits*. Sinauer Associates, Sunderland, USA.

Marcelo Q. 2012 Cold tolerance studies in maize. Academic dissertation, Michigan State University, Michigan, USA.

Meng P. H., Blanchet S., Raynaud C. and Bergounioux C. 2007 MIPS, the missing link between cell cycle and cell death. 18th International Conference on *Arabidopsis* research. Bejing, China.

Pirasteh-Anosheh H., Sadeghi H. and Emam Y. 2011 Chemical priming with urea and KNO_3 enhances maize hybrids (*Zea mays* L.) seed viability under abiotic stress. *J. Crop. Sci. Biotech.* **14**, 289–295.

Pirasteh-Anosheh H. and Hamidi R. 2013 Does seed chemical priming improves germination and early growth of oil rapeseed? *Inter. J. Agron. Plant Product.* **4**, 805–808.

Presterl T., Ouzunova M., Schmidt W., Möller E. M., Röber F. K., Knaak C. *et al.* 2007 Quantitative trait loci for early plant vigour of maize grown in chilly environments. *Theor. Appl. Genet.* **114**, 1059–1070.

Rodriguez V. M., Butron A., Malvar R. A., Ordas A. and Revilla P. 2008 Quantitative trait loci for cold tolerance in the maize IBM population. *Int. J. Plant. Sci.* **169**, 551–556.

Sunderhaus S., Dudkina N. V., Jänsch L., Klodmann J., Heinemeyer J., Perales M. *et al.* 2006 Carbonic anhydrase subunits form a matrix-exposed domain attached to the membrane arm of mitochondrial complex I in plants. *J. Biol. Chem.* **281**, 6482–6488.

Sun Q., Wang J. H. and Sun B. Q. 2007 Advances on seed vigor physiological and genetic mechanisms. *Agric. Sci. China* **6**, 1060–1066.

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