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Seed Storability of CIMMYT Core Wheat Germplasm Panel and Their Haplotypes in *Lipoxygenase* Locus

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Abstract

Seed storability (SS), also called seed longevity, is a valuable trait for seed banks and providing reliable crop seeds to farmers, which is usually negatively correlated to lipoxygenase (LOX) activity. In this study, the seed storability of 60 accessions of CIMMYT core wheat germplasm panel (CIMCOG) was investigated through artificial aging (AA) test, including three parameters relative germination potential (RGP), relative germination rate (RGR) and relative seedling vigor index (RVI). Significant positive relationships were observed among RGP, RGR and RVI. And the genotypes at three LOX activity related QTLs/genes *QLpx.caas*-4*B*, *QLpx.caas*-1*AL* and *TaLOX-B*1 were also identified with published trait-associated molecular markers. For *QLpx.caas*-4*B*, a total of five alleles were detected at the locus of *Xgwm*251, and one marker-trait association was identified for RVI. Four and two alleles were detected at the loci of *QLpx.caas*-1*AL* and *TaLoxB*1 that were significantly associated with RGP, RGR and RVI, respectively. A total of 9 haplotypes were detected at three lipoxygenase activity related gene loci, and the haplotype of three lipoxygenase loci showed a significant association with RGP, RGR and RVI. The haplotype of $Xgwm251_{-125bp}$ + $Xwmc312_{-247bp}$ + *TaLox-B*1*b* produced seeds with the best storability in the CIMCOG, which could benefit the breeding for wheat with good seed storability.

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Keywords

Wheat, Seed Storability, *Lipoxygenase*, Trait-Marker Association, Haplotype

1. Introduction

Seed storability (SS) or seed longevity is defined as seed viability after dry storage. It's a valuable trait for seed banks and providing reliable crop seeds to farmers. Seed storability is often negatively correlated with the advancement of germination [1]. It is a complex trait influenced by two most important environmental factors: 1) relative humidity, which is related to seed moisture content; 2) temperature, which affects the rate of biochemical processes in seeds [2] [3]. More importantly, seed storability is usually controlled by several genes [4]. Genetic dissection of seed storability has been reported in rice [5] [6] [7], soybean [8] and oilseed rape [9]. Seed storability shows their diversification in different varieties of wheat [10] [11], and genetic studies for storability such as seed longevity [12].

Lipoxygenase activity exerts significant effects on seed storability negatively, and a reduction of lipoxygenase activity is therefore of interest for seed longevity in many crops [13] [14] [15] [16]. In cultivated bread wheat, seeds often obtained much higher lipoxygenase activity [17], owing to the artificial selection for higher flour whiteness for degradation of carotenoids by lipoxygenase [18] [19], while carotenoids can scavenge singlet molecular oxygen and peroxyl radicals to protect plants against oxidative processes, and increase the seed longevity [16] [20].

Lipoxygenase activity of wheat seed is mostly controlled by lipoxygenase (LOX) genes on wheat group 4 and 5 chromosomes [21]. And Hessler *et al.* [22] and Geng *et al.* [23] detected a major QTL with the highest LOD score related to lipoxygenase activity around *Xgwm*251 on 4BS in different hexaploid germplasms. Carrera *et al.* [24] identified a deletion at *Lpx-B*1 locus on 4BS weakening the lipoxygenase activity of durum wheat significantly. Therefore, this locus decided most of the lipoxygenase activity in the cultivated wheat, and two functional markers LOX16 and LOX18 were developed to identify *TaLOX-B*1*a* and *TaLOX-B*1*b*, corresponding to high and low LOX activity, respectively [23]. In the chromosome arm 1AL, another major QTL was also detected, explaining more than 25% of the total phenotypic variation for LOX activity, and the linked marker was *Xwmc*312 [25]. And both SSR sites *Xgwm*251 and *Xwmc*312 were significantly associated with lipoxygenase activity in the germplasm pool collected from four major wheat-growing regions of China [25].

In this study, both seed storability and the genotypes of LOX activity related loci were evaluated using AA-test and identified using molecular markers in CIMCOG, respectively. And the relationship between LOX activity related loci and seed storability was also executed using general linear model (GLM). The

aim of this study is to scan the CIMCOG to find the favor haplotype at three lipoxygenase activity related loci with good seed storability for marker-assisted selection (MAS).

2. Materials and Methods

2.1. Plant Materials

A total of 60 elite accessions from the Core Germplasm set (CIMCOG) provided by the Mexico International Maize and Wheat Improvement Center were planted at Yangma of Sichuan Province in the growing season of 2012-2013. Each accession was harvested in its maturity stage, the seeds of each accession were air-dried in the shade after threshing by hand, and stored in an airtight container after aluminium phosphide (AlP) treatment for protecting grains from insect pests. The pedigrees of the 60 accessions were shown in Zhang *et al.* [11].

2.2. Seed Storability (SS) Measurement

2.2.1. Artificial Aging (AA) Test

AA test was conducted to simulate long-term storage artificially and hence allow for the evaluation of SS. According to Zhang *et al.* [11], 50 uniform seeds were selected for AA tests with 4 replicates for each accession, and these seeds were dispersedly placed in a stainless metal cage sealed inside a required container adding 2 cm of deionized and sterilized water to its bottom. The container was placed in an accelerated aging chambers (LH-80, Zhejiang Top Cloud-Agri Technology CO., LTD) and held at 43˚C ± 0.5˚C & 82% relative humidity for 72 h, and then these treated seeds were air-dried and stored at 4˚C. The blank control without AA treatment was set with 3 replicates.

2.2.2. Germination and Seedling Vigor Test

Four replicates of 50 seeds each for AA tests with three replicates for control were subjected to a standard ISTA germination test [26]. The seed germination potential (GP) and rate (GR) were recorded on the 4^{th} and 8^{th} day, respectively. Apart from the absolute germination (in both non-treated and treated seed lots), a relative germination potential (RGP) and rate (RGR) was determined by dividing the rates obtained after AA treatment by that of the non-treated control.

For the seedling vigor, 10 seedlings for each 50-seed plot were randomly selected from the geminated seedlings without any injury or defect in the 8^{th} day simultaneously, to measure average seedling length (AL). The seedling vigor index (VI) and relative seedling vigor index (RVI) were calculated following the formula described as Abdul-Baki and Anderson [27]: VI = GR × AL, RVI (%) = [(VI of AA treatment)/(VI of control)] × 100%.

2.3. Genotyping of Lox Locus

Genomic DNA was isolated from 2-week-old wheat leaves of each accession by a modified cetyl trimethyl ammonium bromide (CTAB) plant DNA extraction

method [28]. Young leaves were ground to a powder in liquid nitrogen and transferred to 1.5 ml centrifuge tubes. 600 ul hot CTAB buffer (2% CTAB w/v, 20 mM EDTA, 1.4 M NaCl, 1% PVP, 100 mM Tris, pH8.0) was added to the centrifuge tubes. The mixture was placed at 65˚C for 5 min; then 600 ul chloroform/isoamyl alcohol (24:1) added and mixed. After centrifugation (12,000 rpm, 10 min), DNA was precipitated from the supernatant with 0.6 volumes of isopropanol after 12 hours at −20˚C. Following centrifugation, the DNA pellet was dried and resuspended in deionized water. The DNA was used to analyze molecular allelic variations of lipoxygenase activity related loci (*Lox*). The PCR primers used for molecular analysis are shown in **Table 1**. The PCR amplification programs for these molecular markers and the isolation of amplification DNA fragments were referred to Wan *et al.* [29].

2.4. Statistical Analysis

Pearson correlation analysis for phenotypes, Duncan's multiple range test (DMRT) were made in IBM SPSS Statistics Version 22 package (IBM Corp., Chicago, IL). Population distribution of phenotypic data was performed in MS Excel 2003 and SPSS. Associations between molecular markers and phenotypes were tested by general linear model (GLM) in SPSS statistical package.

3. Results

3.1. Seed Storability Related Traits

A total of three indexes RGP, RGR and RVI were calculated for the measurement of SS after artificial aging. The frequency distribution, mean, median, phenotypic standard deviation (S.D.) and coefficient of variance (C.V.) of three SS related traits in CIMCOG set are showed in **Figure 1**. The medians of RGP, RGR, and RVI are more than their means in the population. The C.V. of RVI were more than the other two traits, for that RVI, for that the index of RVI is relevant to both seed germination and seedling growth.

The correlation coefficient among all investigated traits were showed in **Table 2**.

Table 1. Molecular markers used for detecting the allelic variations of *Lox* loci.

Locus	Linked marker	Primer sequence (5'→3')	Fragment size
TaLOX-B1a	LOX16	F: CCATGACCTGATCCTTCCCTT R: GCGCGGATAGGGGTGGT	489bp
TaLOX-B1b	LOX18	F: ACGATGTGAGTTGTGACTTGTGA R: GCGCGGATAGGGGTGC	791bp
QLpx.caas-4B	GWM251	F: CAACTGGTTGCTACACAAGCA R: GGGATGTCTGTTCCATCTTAG	79bp, 101bp, 113bp, 117bp, 125bp
QLpx.caas-1AL	WMC312	F: TGTGCCCGCTGGTGCGAAG R: CCGACGCAGGTGAGCCAAG	219bp, 227bp, 235bp, 247bp

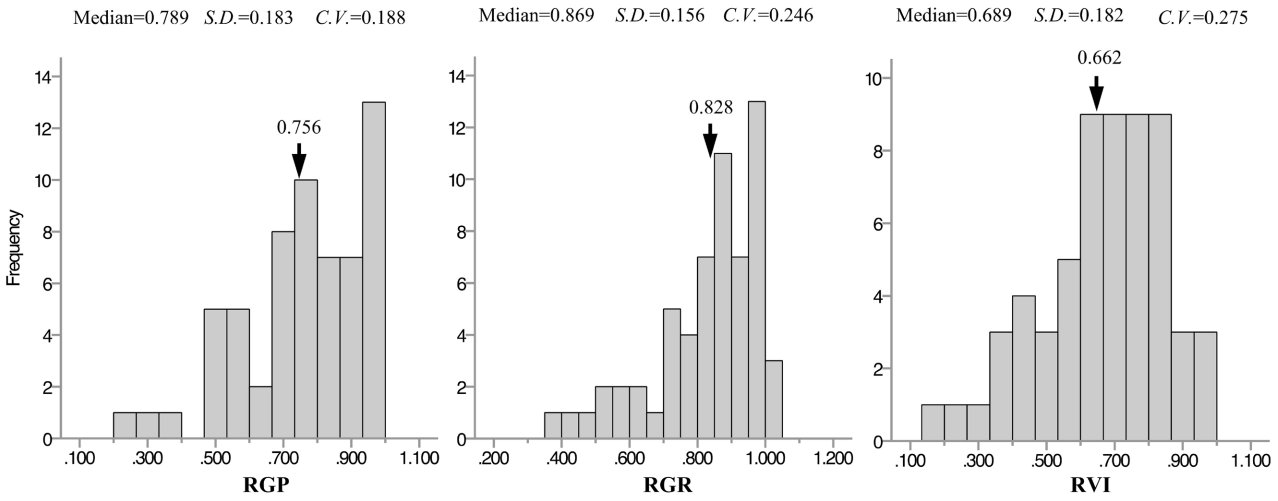

Figure 1. Frequency distribution of seed storability related traits in CIMCOG set. The position pointed by black arrow in X-axis represents phenotypic mean for the population. "*Median*" means the middle value of the population. "*S.D.*" means its phenotypic standard deviation. "*C.V.*" means coefficient of variation.

Table 2. Correlation analysis between SS-related traits[¶].

	GP(A)	RGP	GR(C)	GR(A)	RGR	VI(C)	VI(A)	RVI
GP(C)	0.679**	0.193	0.975**	0.701**	0.394**	0.811**	0.640**	0.370**
GP(A)		**0.845****	0.660**	0.937**	0.843**	0.639**	0.928**	0.824**
RGP			0.197	0.761**	0.865**	0.272*	0.771**	0.843**
GR(C)				0.719**	0.313*	0.814**	0.642**	0.387**
GR(A)					**0.919****	0.588**	0.902**	0.867**
RGR						0.323*	0.811**	0.933**
VI(C)							0.709**	0.278*
VI(A)								**0.853****

[¶](A) means AA treatment, (C) means control without AA treatment.

The GP, GR and VI of the seeds of the accessions after AA treatment were significantly correlated with their original GP, GR and VI without AA treatment. In order to reflect the effects caused by AA treatment, the RGP, RGR and RVI was introduced using relative rate between GA(A) under AA test and GA(C) of control, and the correlation coefficient between relative rate and control of GP, GR and VI was decreased by more than at least 2 fold, comparing with the correlation coefficient between relative rate and AA treatment for GP, GR and VI (Table 2: correlation coefficient with dotted underline), while the relationships between relative rate and GP, GR, VI with AA treatment were increased to 0.845, 0.919 and 0.853 (in Table 2 with bold font). The correlation coefficients among RGP, RGR and RVI were 0.865, 0.843 and 0.933, respectively (Table 2: correlation coefficient with solid underline). Moreover, the significant positive relationships among GP, GR and VI without AA treatment were also observed with

high correlation coefficients in CIMCOG set (Table 2: correlation coefficient with wavy underline), and this situation also happened among GP, GR and VI with AA treatment (Table 2: correlation coefficient with double solid underline).

3.2. Allelic Variation at Lipoxygenase Loci and Phenotypic Effects

Three loci associated to lipoxygenase activity on chromosomes 1A and 4B were genotyped using linked or functional markers. The simple sequence repeats (SSR) sites of *Xgwm*251 and *Xwmc*312 is tight linked to *QLpx.caas*-4*B* and *QLpx.caas*-1*AL* related to lipoxygenase activity, respectively. And LOX16 designed from the *TaLox-B*1*a* amplified 489bp PCR fragment in accessions with higher LOX activities, while the marker LOX18 of 791bp PCR fragment was for *TaLox-B1b* with lower LOX activities. Associations between *QLpx.caas*-4*B*, *QLpx.caas*-1*AL*, *TaLox-B*1 and three SS-related traits were executed using the general linear model (GLM). *QLpx.caas*-4*B* was only significantly associated with RVI at the level of $P = 0.05$ (Table 3). Both *QLpx.caas*-1*AL* and *TaLox-B*1 were significantly associated with all three SS-related traits at the level of $P = 0.001$ (Table 3), explaining the percentage of phenotypic variation from 17.5% (0.175) to 28.3% (0.283) with GLM (Table 3).

A total of 5 alleles were detected at the locus of *Xgwm*215 with 79, 101, 113, 117 and 125bp PCR fragments in the 60 CIMCOG accessions, the numbers of the 5 allels were 17, 29, 5, 3 and 6, respectively (Table 4). The RGR and RVI of the allele of *A*-125*bp* was significantly higher than those of *A*-113*bp* at $P = 0.05$ level (Table 4). At the site of *Xwmc*312, four alleles *A*-219*bp*, *A*-227*bp*, *A*-235*bp* and *A*-247*bp* were detected with the numbers of 4, 7, 17 and 32 in CIMCOG set, respectively. For RGP, the phenotypic mean of *A*-235*bp* and *A*-247*bp* was significantly higher than that of *A*-227*bp*. For RGR, the phenotypic mean of *A*-235*bp* and *A*-247*bp* was significantly higher than that of both *A*-219*bp* and *A*-227*bp*. For RVI, the phenotypic mean of *A*-247*bp* was significantly higher than that of both *A*-219*bp* and *A*-227*bp*. The phenotypic mean of *A*-247*bp* on all three traits was the highest among the 4 alleles (Table 4). In the CIMCOG set, only 6 accessions carried *TaLox-B*1*a* associated to high LOX activity, and the averages of RGP, RGR and RVI of *TaLox-B*1*a* were significantly lower than those of *TaLox-B*1*b*, indicating the significant negative relationship between LOX activity and seed storability.

Table 3. Trait-marker associations between three lipoxygenase loci and SS-related traits in CIMCOG set.

SS-related trait	Source	Sum of Squares	D.F.	Mean Square	F value	*P* value	−Log(*P*)	R^2
RGP	*Xgwm*251	0.239	4	0.060	1.800	0.142	0.848	0.051
	Error	1.823	55	0.033				
	Total	2.062	59					
	*Xwmc*312	0.550	3	0.183	6.789	0.001	3.258	0.227

Continued

	Error	1.512	56	0.027				
	Total	2.062	59					
	*TaLoxB*1	0.460	1	0.460	16.674	0.000	3.861	0.210
	Error	1.601	58	0.028				
	Total	2.062	59					
RGR	*Xgwm*251	0.224	4	0.056	2.516	0.052	1.286	0.093
	Error	1.223	55	0.022				
	Total	1.956	59					
	*Xwmc*312	0.462	3	0.154	8.770	0.000	4.134	0.283
	Error	0.984	56	0.018				
	Total	1.446	59					
	TaLoxB1	0.352	1	0.352	18.632	0.000	4.203	0.230
	Error	1.095	58	0.019				
	Total	1.446	59					
RVI	*Xgwm*251	0.352	4	0.088	3.014	0.026	1.593	0.120
	Error	1.604	55	0.029				
	Total	1.956	59					
	*Xwmc*312	0.571	3	0.190	7.686	0.000	3.622	0.254
	Error	1.386	56	0.025				
	Total	1.956	59					
	*TaLoxB*1	0.370	1	0.370	13.528	0.001	3.287	0.175
	Error	1.586	58	0.027				
	Total	1.956	59					

Table 4. Multiple comparison of seed storability between alleles at three lipoxygenase loci.

QTL/Marker	Allele	No.	RGP	RGR	RVI
*Xgwm*251	*A*-113*bp*	17	0.707a	0.764a	0.585a
	A-117*bp*	29	0.753a	0.821ab	0.651ab
	A-79*bp*	5	0.806a	0.884ab	0.701ab
	A-101*bp*	3	0.728a	0.912ab	0.745ab
	A-125*bp*	6	0.931a	0.966b	0.854b
*Xwmc*312	*A*-219*bp*	4	0.671ab	0.646a	0.462a
	A-227*bp*	7	0.536a	0.656a	0.502a
	A-235*bp*	17	0.743b	0.827b	0.623ab
	A-247*bp*	32	0.831b	0.890b	0.742b
*TaLoxB*1	*a*	6	0.498***	0.599****	0.426***
	b	54	0.790	0.854	0.688

DMRT at $\alpha = 0.05$ level. ***, ****mean significant difference at $P = 0.001$ and 0.0001 levels, respectively.

3.3. Haplotypes at Lipoxygenase Loci and Their Phenotypic Effects

A total of 15 types of allele combination (haplotype) at the loci of *QLpx.caas*-4*B*, *QLpx.caas*-4*B* and *TaLox-B*1 were detected in the CIMCOG set, and 9 out of the 13 haplotypes were distributed in more than 3 accession, as their allele frequencies were not less than 5.0% (Table 6). The –[Log(*P*)] of all trait-haplotype associations were more than 4.0, with the R^2 more than 40.0% in the CIMCOG set, indicating that the three LOX-related loci had additive effects on RGP, RGR and RVI.

The number of accessions carrying each main haplotype varied from 3 to 15, and 15 accessions out of 60 carried *Haplotype-VIII* (117bp + 247bp + b), while *Haplotype-I*, *Haplotype-II* and *Haplotype-III* had the lowest haplotype frequencies (Table 5). Significant and large differences were observed among haplotypes on RGP, RGR and RVI for SS (Table 5). For RGP and RGR, the phenotypic mean of *Haplotype-IX* was significantly higher than the phenotypic mean of the four haplotypes *Haplotype-I*, *-II*, *-III* and *-IV*. For RVI, the phenotypic mean of *Haplotype-IX* was significantly higher than that of *Haplotype-I*, *-II*, *-III*, *-IV*, *-V* and *-VI*, and there was no significant difference between *Haplotype-IX* and *Haplotype-VII*, *-VIII* (Table 6; Figure 2). *Haplotype-IX* produced the seeds with the

Table 5. Trait-marker associations between haplotype of lipoxygenase locus and SS-related traits in CIMCOG set.

SS-related trait	Source	Sum of Squares	D.F.	Mean Square	F value	*P* value	–Log(*P*)	R^2
RGP	Haplotype	0.806	8	0.101	5.459	0.000	4.075	0.407
	Error	0.812	44	0.018				
	Total	1.617	52					
RGR	Haplotype	0.672	8	0.084	7.310	0.000	5.404	0.493
	Error	0.505	44	0.011				
	Total	1.177	52					
RVI	Haplotype	0.879	8	0.110	6.280	0.000	4.685	0.448
	Error	0.769	44	0.017				
	Total	1.648	52					

Table 6. Multiple comparison of seed storability between haplotypes at *Lox* loci.

Haplotype	*Xgwm*251 + *Xwmc*312 + *TaLox-B*1	No.	RGP	RGR	RVI
I	*H*-113*bp* + 227*bp* + *a*	3	0.450a	0.529a	0.353a
II	*H*-117*bp* + 219*bp* + *b*	3	0.710b	0.627a	0.428ab
III	*H*-117*bp* + 227*bp* + *b*	3	0.506a	0.679ab	0.548bc
IV	*H*-113*bp* + 235*bp* + *b*	5	0.704b	0.778bc	0.561bc
V	*H*-117*bp* + 235*bp* + *b*	7	0.772bc	0.834cd	0.646c
VI	*H*-79*bp* + 235*bp* + *b*	4	0.787bc	0.875cd	0.663c
VII	*H*-117*bp* + 247*bp* + *b*	15	0.815bc	0.889cd	0.725cd
VIII	*H*-113*bp* + 247*bp* + *b*	8	0.869bc	0.891cd	0.736cd
IX	*H*-125*bp* + 247*bp* + *b*	5	0.942c	0.974d	0.878d

DMRT at $\alpha = 0.05$ level.

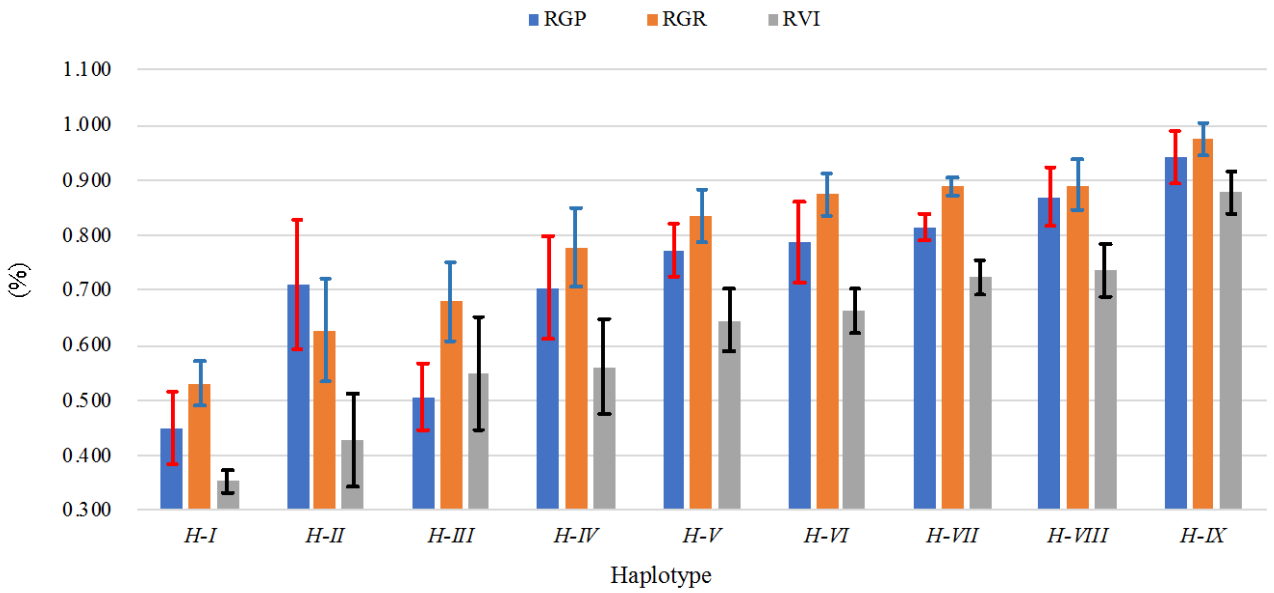

Figure 2. Phenotypic effects of haplotypes at three lipoxygenase loci. Error bars displayed the interval of *Mean* ± *S.E.*

highest RGP, RGR and RVI after AA-treatment (**Table 6**; **Figure 2**), suggesting that the allele combination of *Xgwm*251$_{-125bp}$, *Xwmc*312$_{-247bp}$ and *TaLox-B*1*b* was associated with best seed storability. Plants carried *Haplotype-I* of *Xgwm*251$_{-113bp}$, *Xwmc*312$_{-227bp}$ and *TaLox-B*1*a* generated seed with poorest storability.

4. Discussion

The genomic sites *Xwmc*312 of linked to *QLpx.caas*-1*AL*, *Xgwm*251 linked to *QLpx.caas*-4*B* and *TaLox-B*1 were significantly associated with lipoxygenase activity related genes [23] [24] [25]. With GLM, we also detected significant associations between *Xwmc*312 and *TaLox-B*1 and all three SS-related traits. For *QLpx.caas*-4*B*, the linked SSR marker *Xgwm*251 was only associated with RVI in the CIMCOG set. However, according to Geng *et al.* [25], both *QLpx.caas*-4*B* and *QLpx.caas*-1*AL* were main QTLs explaining > 25.0% of the phenotypic variance of LOX activity on average. Geng *et al.* [23] aligned *TaLox-B*1 locus to the confidence interval of *QLpx.caas*-4*B* in 2012, indicating that *TaLox-B*1 might be the candidate gene of *QLpx.caas*-4*B*. With the release of high-quality assembly of reference sequence of wheat, the *TaLox-B*1 was aligned to the physical interval of 30.0 Mb - 30.1 Mb on chromosome 4BS of Chinese Spring (CS) [30], and *QLpx.caas*-4*B* was on the interval of *Xgwm*149 - *Xwmc*349 [25] with the physical position of 544.6 Mb - 641.0 Mb on chromosome 4BL of CS [30], while the SSR site *Xgwm*251 closely linked to the QTL peak of *QLpx.caas*-4*B* was at the physical location of 567.7 Mb on 4BL of Chinese Spring [30], indicating that they were two different genes. And we thought that the only 71 double haploid lines used for QTL mapping and the lack of high-quality Ref-Seq assembly of CS caused the mis-alignment of *QLpx.caas*-4*B*.

Geng *et al.* [25] analyzed the association between LOX activity and *QLpx.caas*-

1*AL*, *QLpx.caas*-4*B* using their linked markers *Xwmc*312, *Xgwm*251 in 198 Chinese wheat cultivars and lines. The allele of *A*-247*bp* at the site of *Xgwm*312 had significant lower LOX activity than its *A*-235*bp*, and the allele of *A*-247*bp* belonged to the group with lowest LOX activity. At the site of *Xgwm251*, the allele of *A*-125*bp* had lower LOX activity than *A*-117*bp*, and lines carrying *A*-125*bp* have the lowest average LOX activity. And the mean LOX activity of the haplotype *Xgwm*251$_{-125bp}$ + *Xwmc*312$_{-247bp}$ belonged to the DMRT-testing group with lowest LOX activity. The *TaLox-B*1*b* had significant lower mean LOX activity than *TaLox-B*1*a* [23]. Lipoxygenase activity is often negatively related to seed longevity/storability [13] [14] [15] [17] [31] [32]. Hence, these alleles at the three loci with lowest LOX activity in Geng *et al.* [23] [25], such as *Xgwm*251$_{-125bp}$, *Xwmc*312$_{-247bp}$ and *TaLox-B*1*b*, had the highest RGP, RGR and RVI with the best seed storability in our study, and the wheat accessions carrying the haplotype of *Xgwm*251$_{-125bp}$ + *Xwmc*312$_{-247bp}$ + *TaLox-B*1*b* produced seeds with the best storability, comparing with other haplotypes. However, no significant associations between RGP/RGR and *Xgwm*251 were detected by GLM procedure in the panel of CIMMYT core wheat germplasm, mostly due to the small population size of the panel [33] and the existence of other quantitative trait loci except for *Lox* genes [12] [34].

Good seed storability is beneficial to preserving seeds for germplasm banks and providing reliable crop seeds to farmers. Among 5 accessions carrying *Haplotype-IX* (*Xgwm*251$_{-125bp}$ + *Xwmc*312$_{-247bp}$ + *TaLox-B*1*b*), the RGP, RGR and RVI of accessions No. 14, 31, 35 and 57 were more than 0.95, 0.95, and 0.83, and the seed coat color of them were white [11]. These accessions with the lowest LOX activity could cut the greater loss of carotenoids than vitamin E during breadmaking that induced by high LOX activity [18], which could also be used for flour end-quality improvement.

5. Conclusion

Among three reported LOX activity related QTLs/genes, *QLpx.caas*-1*AL* and *TaLOX-B*1 were also significantly associated with three SS-related parameters in CIMMYT core wheat germplasm panel (CIMCOG) with only 60 accessions. A total of 9 haplotypes were detected at three lipoxygenase activity related gene loci, and we found that the haplotype of *Xgwm*251$_{-125bp}$ + *Xwmc*312$_{-247bp}$ + *TaLox-B*1*b* produced seeds with the best storability in the CIMCOG.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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