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ORIGINAL PAPER

QTL in mega-environments: II. Agronomic trait QTL co-localized with seed yield QTL detected in a population derived from a cross of high-yielding adapted × high-yielding exotic soybean lines

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Abstract Seed yield mega-environment-universal and specific QTL (QTL_U and QTL_{SP}, respectively) linked to Satt100, Satt130, Satt162, Satt194, Satt259 Satt277 and Sat_126, have been identified in a population derived from a cross between a Chinese and a Canadian soybean [*Glycine max* (L.) Merrill] elite line. The variation observed in yield could be the consequence of the variation of agronomic traits. Yield-component traits have been reported in the literature, but a better understanding of their impact at the molecular level is still lacking. Therefore, the objectives of this study were to identify traits correlated with yield and to determine if the yield QTL_U and QTL_{SP} were co-localized with QTL_U and QTL_{SP} associated with an agronomic trait. A recombinant inbred line (RIL) population was developed from a cross between a high-yielding adapted Canadian and a high-yielding exotic Chinese soybean elite line. The RIL were evaluated in multiple environments in China and Canada during the period from 2004 to 2006. Four yield $QTL_{U,}$ tagged by markers Satt100, Satt277, Satt162 and Sat_126, were co-localized with a QTL associated with an agronomic trait, behaving as either QTL_U or QTL_{SP} for the agronomic trait. For example, the yield $QTL_{U,}$ tagged by marker Satt100 was associated also with 100 seed weight, pods per plant, pods per node, plant height, R1, R5, R8, oil content and protein content in all Canadian environments, but only with pods per plant, pods per node, plant height, R1, R5, R8 and oil content in two or more Chinese environments. No agronomic traits QTL were co-localized with the yield QTL_U tagged by the marker Satt139 or the yield QTL_{SP} tagged by Satt259, suggesting a physiological basis of the yield in these QTL. The results suggest that a successful introgression of crop productivity alleles from plant introductions into an adapted germplasm could be facilitated by the use of both the QTL_U and QTL_{SP} because each type of QTL contributed either directly or indirectly through yield-component traits to seed yield of RILs.

Introduction

Yield increase could be the consequence of the variation observed in different agronomic traits or due to physiological causes. Part of the variation observed in yield could also be explained by the interaction observed between QTL (Lark et al. 1995). Yield-component traits have been studied through correlations between yield and several agronomic traits to improve the understanding of yield-component

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traits that explained some of the variation observed in yield (Kabelka et al. 2004; Orf et al. 1999b). However, a better understanding of the molecular basis of the relationship between yield-component traits and specific yield quantitative trait loci (QTL) is needed.

Quantitative trait loci have been reported for several agronomic and physiologic traits in soybeans. For example, Tasma and Shoemaker (2003) reported a QTL on linkage group (LG) C2 that was associated with four agronomic traits in two independent populations. QTL analysis has also helped to determine the genomic location of agronomic traits that are co-localized with yield such as maturity, seed size, oil content and others (Kabelka et al. 2004; Orf et al. 1999a, b; Soybase 2008; Tasma and Shoemaker 2003; Yuan et al. 2002). Hyten et al. (2004) grew 131 F6-derived lines from the cross ‘Essex’ and ‘Williams’ in six environments and identified four proteins, six oil and seven seed size QTL, which have been reported previously as traits that are co-localized with yield QTL.

Several major yield QTL were located in the same region as QTL associated with other agronomic traits, such as plant height, lodging, flowering date, maturity, oil or protein content in soybean populations field tested in North American environments (Reinprecht et al. 2006) or both the North and South American environments (Orf et al. 1999b). A total of 61 QTL among 37 measures of six traits, including seed yield was detected by composite interval mapping and single-factor ANOVA in the Sothern germplasm cross Essex × Forrest (Kassem et al. 2006). The data suggested that trait associations with yield were independent of the genetic background used, but dependant on the environment.

Epistatic effects for yield QTL have been reported in several soybean studies (Lark et al. 1995; Orf et al. 1999a, b). Interacting pairs of QTL have been analyzed to determine if either of them was also associated with an agronomic trait (Orf et al. 1999a). The authors reported two epistatic events observed in two different yield QTL, where one of the interacting yield QTL was also associated with several agronomic traits (Orf et al. 1999a).

In a previous study (Palomeque et al. 2009), seven QTL that explained part of the variation observed in seed yield were reported where a population derived from a cross between elite Canadian and Chinese soybean [(*Glycine max* (L.) Merrill] lines were used. The population was evaluated in two mega-environments (Canada and China) where a mega-environment is understood as “a broad, not necessarily contiguous area, occurring in more than one country and frequently transcontinental, defined by similar biotic and abiotic stresses, cropping system requirements, consumer preferences, and, for convenience, by volume of production” (Braun et al. 1996). Five seed yield QTL were found in both mega-environments and were referred to as mega-environment universal QTL ($\mathrm{QTL_U}$). Two QTL were associated with seed yield only at a specific mega-environment ($\mathrm{QTL_{SP}}$), e.g., either China or Canada, respectively. Therefore, the objectives of this study were (1) to determine what agronomic and morphological traits were correlated with seed yield, (2) to determine if seed yield $\mathrm{QTL_U}$ and $\mathrm{QTL_{SP}}$ were co-localized with $\mathrm{QTL_U}$ and $\mathrm{QTL_{SP}}$ associated with an agronomic trait and (3) to determine if QTL associated with yield-component traits behaved as a $\mathrm{QTL_U}$ or $\mathrm{QTL_{SP.}}$

Materials and methods

A complete description of the experimental design, DNA extraction and linkage mapping are presented elsewhere (Palomeque et al. 2009). In brief, a population consisting of 98 $F_{4:7}$ recombinant inbred lines (RIL) developed from the cross OAC Millennium × Heinong #38 was used in this study. OAC Millennium is a high yielding, stable cultivar, adapted to the Canadian mega-environment and Heinong #38 is an elite line adapted to the Chinese one. Both parents had the indeterminate growth habit as well as the progeny. Field trials were planted at six different locations in two mega-environments, Canada and China, as follows. In 2004, three trials were grown, one at Tavistock (43°18′N 80°49′W) and one at Woodstock (43°7′N 80°45′W) both in Ontario, Canada and a third one at Harbin (45°45′N 126°36′E) in Heilongjiang province in China. The parental line Heinong #38 was not evaluated in either Canada or China in 2004, because of problems with seed source. In 2005, three trials were planted in Canada, one at Ottawa (45°24′N 75°42′W), one at Tavistock (43°18′N 80°49′W) and one at Woodstock (43°7′N 80°45′W) in Ontario. In 2006, two trials were planted at Harbin (45°45′N 126°36′E) in Heilongjiang, China at two different sites.

The SSR library available at the University of Guelph, Ontario, Canada, consisted in 450 SSR primer pairs selected from the integrated soybean genetic map (Cregan et al. 1999), which covered approximately equidistantly the 20 soybean genetic linkage groups. Both parental lines were screened with the available primer pairs. One hundred and five of the available 450 SSR were found to be polymorphic between the parents and were used to genotype the entire population. A linkage map was obtained with JoinMap 4® program (van Oijen 2004) where 26 linkage groups were obtained.

Phenotypic scoring

The following agronomic traits were recorded per plot: emergence score taken 3 weeks after planting (on a scale

1–10, where 0 corresponded to no emergence and 10–100% emergence); flowering date (R1, when the first flower is observed), beginning seed stage (R5, which corresponds to the date when a seed of 3 mm long is observed in a pod in the principal stem placed in any of the four superior pods where a completely developed leaf is observed), full maturity date (R8, which corresponds to the plot that shows maturity color in 95% of the pods) (Fehr et al. 1971); lodging score (1 for no lodging to 5 for completely prostrate); plant height; 100 seed weight; oil and protein contents; number of pods per node; number of pods per plant and number of seeds per pod. The last three traits were taken on a sample of five randomly pulled plants from each plot, which was recorded on a plot-mean basis. A detailed protocol on how to take measurements of each trait was provided by the senior author to each group to minimize errors in phenotyping. It was simply a set of instructions on how to plant trial and manage field trials and take notes using standard methods used in North America. Seed yield (kg/ha) and 100 seed weight were measured at 13% moisture in all the environments with the exception of the Harbin trial in 2004. Emergence measurements were used to determine if there was a correlation between emergence and yield. No emergence data were recorded in either environment in China due to a lack of resources in those locations in 2006.

Statistical analysis

The variation in an agronomic trait within a test location was partitioned into the effects of genotype, replications and incomplete blocks within replications using the PROC MIXED procedure from SAS ver. 9.1.3 (SAS Institute Inc. 2003) for a rectangular lattice design (Bowley 1999). Blocks within replications were considered to be random variables. Tests of residuals were evaluated using the PROC UNIVARIATE and PROC PLOT procedure SAS ver. 9.1.3 (SAS Institute Inc. 2003). Agronomic trait means were not averaged over years and locations since significant interactions were observed between genotypes and years and between genotypes and locations (Reinprecht et al. 2006). Variance components attributable to variation among lines (VG) and residual variation (VE) were derived and used to estimate broad sense heritability for seed yield (VG/(VG + VE) (Huynh et al. 2008). PROC CORR and PROC PLOT procedures were performed to determine the linear correlation between emergence and an agronomic trait. Emergence was included as a covariate in the agronomic trait model when the correlation was found to be significant. The type-I error rate (α) was set at 0.05.

Quantitative trait loci were detected by performing a single-factor ANOVA and multiple QTL mapping or MQM (Neto et al. 2007). Interval mapping (IM) was performed with MapQTL5® (van Ooijen 2004) with an LOD score of 2.4 for the linked SSR markers reported by Palomeque et al. (2009) tagging seed yield $\mathrm{QTL_U}$ and $\mathrm{QTL_{SP}}$. The LOD score was calculated by performing a permutation test with MapQTL5® (van Ooijen 2004) with a set of 10,000 iterations. Markers linked to QTL in the IM were used as cofactors in the MQM analysis. Single-factor ANOVA was performed to evaluate unlinked SSR markers reported by Palomeque et al. (2009) that tagged seed yield $\mathrm{QTL_U}$. The association between individual SSR markers and different agronomic traits was determined by using a macro program from SAS ver 9.1.3 (SAS Institute Inc. 2003) obtained from Dr. Elizabeth Lee at the University of Guelph (Guelph, ON, Canada). The type-I error rate (α) was set at 0.01.

Results

Seed yield $\mathrm{QTL_U}$ and $\mathrm{QTL_{SP}}$ also associated with agronomic traits

In a previous study seven QTL were found to be associate with seed yield (Palomeque et al. 2009). Five of the total seven were seed yield $\mathrm{QTL_U}$ and two were seed yield $\mathrm{QTL_{SP}}$. The QTL analysis detected that four of the seed yield $\mathrm{QTL_U}$ which were identified by Satt100, Satt277 (both located on LG C2), Satt162 (LG I) and Sat_126 (LG K) as reported by Palomeque et al. (2009), were also associated with several agronomic traits (Table 1). In particular, the seed yield $\mathrm{QTL_U}$ which were tagged by Satt100 and Satt277 were co-localized with most of the agronomic traits that were evaluated in this study (Table 1). The seed yield $\mathrm{QTL_U}$ tagged by Satt100 was co-localized with $\mathrm{QTL_U}$ associated with seven agronomic and/or seed traits: number of pods per plant, number of pods per node, plant height, R1, R5, R8 and oil content. The seed yield $\mathrm{QTL_U}$ tagged by Satt100 was also linked to $\mathrm{QTL_{SP}}$ associated with 100 seed weight, number of seeds per pod and protein content. The seed yield $\mathrm{QTL_U}$ tagged by Satt277 was co-localized with six $\mathrm{QTL_U}$ associated with: 100 seed weight, number of pods per node, plant height, R1, R5 and R8 each. Satt277 was also linked to two $\mathrm{QTL_{SP}}$ associated with number of pods per plant and oil content each (Table 1). The seed yield $\mathrm{QTL_U}$ tagged by Satt162 was linked to three $\mathrm{QTL_{SP}}$ associated with lodging, 100 seed weight and number of pods per node each. The seed yield $\mathrm{QTL_U}$ tagged by Sat_126 was linked also to three $\mathrm{QTL_{SP}}$ associated with plant height, lodging, and number of pods per plant. The same marker was also linked to a $\mathrm{QTL_U}$ associated with number of pods per node (Table 1). No agronomic traits were detected to be co-localized with the seed yield $\mathrm{QTL_U}$ tagged by Satt139 (located in LG C1) and the $\mathrm{QTL_{SP}}$ tagged by Satt259 (LG O), and Satt194 (LG C1; data not shown). Broad sense heritability has been calculated for all

Table 1 Mega-environment universal and specific agronomic trait QTL identified by the single-factor ANOVA method across different environments in Canada and China from 2004 to 2006

Agronomic trait	Canadian mega-environment			Chinese mega-environment			Type of QTL
	R^2	*P* value	Environment[a]	R^2	*P* value	Environment	
Satt100[b]							
100 seed weight	13	0.0018	W04				$\mathrm{QTL}_{\mathrm{SP}}$
	14	0.0011	OT05				
Pods per plant	21	<0.0001	W04	26	<0.0001	H[1]04	$\mathrm{QTL}_{\mathrm{U}}$
				48	<0.0001	H[1]06	
Pods per node	13	0.0023	T04	27	<0.0001	H[1]06	$\mathrm{QTL}_{\mathrm{U}}$
	31	<0.0001	W04				
Seeds per pode	15	0.0009	T04				$\mathrm{QTL}_{\mathrm{SP}}$
	17	0.0003	W05				
Height	45	<0.0001	T04	42	<0.00010	H[1]04	$\mathrm{QTL}_{\mathrm{U}}$
	45	<0.0001	W04	62	<0.0001	H[1]06	
	54	<0.0001	T05				
	47	<0.0001	W05				
	38	<0.0001	OT05				
R1	54	<0.0001	T04	22	<0.0001	H[1]06	$\mathrm{QTL}_{\mathrm{U}}$
	41	<0.0001	W04	47	<0.0001	H[2]06	
	63	<0.0001	W05				
	55	<0.0001	OT05				
R5	70	<0.0001	T04	54	<0.0001	H[1]04	$\mathrm{QTL}_{\mathrm{U}}$
	7	<0.0001	W04				
	38	<0.0001	T05				
R8	59	<0.0001	T04	44	<0.0001	H[1]04	$\mathrm{QTL}_{\mathrm{U}}$
	53	<0.0001	W04	46	<0.0001	H[2]06	
	50	<0.0001	T05				
	52	<0.0001	W05				
	57	<0.0001	OT05				
Oil content	16	0.0004	T04	18	0.0002	H[2]06	$\mathrm{QTL}_{\mathrm{U}}$
	26	<0.0001	T05				
	20	<0.0001	W05				
Protein content	15	0.0009	T05				$\mathrm{QTL}_{\mathrm{SP}}$
	11	0.0062	W05				
Satt277[b]							
100 seed weight	22	<0.0001	W04	5	0.0032	H[1]06	$\mathrm{QTL}_{\mathrm{U}}$
Pods per plant	15	0.0002	W04	29	<0.0001	H[1]06	$\mathrm{QTL}_{\mathrm{SP}}$
Pods per node	14	0.0004	T04	15	0.0003	H[1]06	$\mathrm{QTL}_{\mathrm{U}}$
	17	<0.0001	W04				
Seeds per pod	11	0.0017	W05				$\mathrm{QTL}_{\mathrm{SP}}$
Height	26	<0.0001	T04	16	0.0002	H[1]04	$\mathrm{QTL}_{\mathrm{U}}$
	23	<0.0001	W04	39	<0.0001	H[1]06	
	24	<0.0001	T05				
	23	<0.0001	W05				
	15	0.0003	OT05				
R1	40	<0.0001	T04	10	0.0038	H[1]06	$\mathrm{QTL}_{\mathrm{U}}$
	32	<0.0001	W04	34	<0.0001	H[2]06	
	39	<0.0001	W05				
	32	<0.0001	OT05				

Table 1 continued

Agronomic trait	Canadian mega-environment			Chinese mega-environment			Type of QTL
	R^2	*P* value	Environment[a]	R^2	*P* value	Environment	
R5	38	<0.0001	T04	31	<0.0001	H[1]04	QTL$_{\text{U}}$
	47	<0.0001	W04				
	16	0.0001	T05				
	42	<0.0001	OT05				
R8	43	<0.0001	T04	20	<0.0001	H[1]04	QTL$_{\text{U}}$
	42	<0.0001	W04	30	<0.0001	H[2]06	
	26	<0.0001	T05				
	30	<0.0001	W05				
	27	<0.0001	OT05				
Oil content	9	0.0055	T05				QTL$_{\text{SP}}$
Sat_126[b]							
100 seed weight				4	0.008	H[1]06	QTL$_{\text{SP}}$
Pods per node				7	0.0088	H[1]06	QTL$_{\text{SP}}$
Lodging	10	0.0041	W05				QTL$_{\text{SP}}$
Oil content	12	0.0042	T04				QTL$_{\text{SP}}$
Sat_126[b]							
Pods per plant				19	<0.0001	H[1]04	QTL$_{\text{SP}}$
				24	<0.0001	H[1]06	
Pods per node	10	0.0086	T04	12	0.0031	H[1]06	QTL$_{\text{U}}$
Height	13	0.0027	T04	11	0.0066	H[1]06	QTL$_{\text{U}}$
	11	0.0064	W04				
	17	0.0003	W05				
	13	0.0021	OT05				
Lodging	19	<0.0001	OT05				QTL$_{\text{SP}}$

[a] (T04), Tavistock in 2004; (W04), Woodstock in 2004; (H(1)04), Harbin location 1 in 2004; (T05), Tavistock in 2005; (W05), Woodstock in 2005; (OT05), Ottawa 2005; (H[1]06) Harbin location 1 in 2006; (H[2]06), Harbin location 2 in 2006

[b] This marker was linked to a mega-environment universal QTL, i.e., QTL$_{\text{U}}$ for seed yield in Palomeque et al. (2009)

traits that were measured at each environment (Table 2) in either Canada or China (Table 2).

Association between agronomic traits and epistatic regions

Three of the seven seed yield QTL reported by Palomeque et al. (2009) interacted with other regions tagged by Satt002 (located on LG D2), Satt162 (LG I), Satt288 (LG G), Satt394 (LG G), Satt528 (LG D) and Satt543 (LGD). The MQM analysis performed for the linked markers (Satt288, Satt394, Satt528 and Satt543) and the single marker analysis performed for the unlinked interacting markers (Satt002, Sat_126) were used to determine the association between any of the 11 agronomic traits analyzed and the interacting regions. No association was found between the interacting markers and the 11 agronomic traits except for Sat_126, which was previously reported as seed yield QTL$_{\text{U}}$. Sat_126 tagged a QTL$_{\text{U}}$ associated with number of pods per node, and three QTL$_{\text{SP}}$ associated with number of pods per plant, plant height and lodging each (Table 1).

Linear correlation between seed yield and agronomic traits

The linear correlation between 11 agronomic traits and seed yield were evaluated in both the Chinese and the Canadian mega-environment (Table 3). Because least square means were calculated per environment and not across environments for each of the agronomic trait evaluated, traits where the analysis of residuals did not meet the analysis assumptions (Bowley 1999) were excluded from the calculations and are shown with the legend “no data” in Table 2.

Seven of the 11 traits evaluated were correlated with seed yield. Reproductive stages (R1, R5 and R8) and plant height were positively correlated with seed yield in most of the environments in both the Chinese and the Canadian mega-environment. R1 was positively correlated with seed yield in six of the eight environments. R5 and R8 were

Table 2 Broad sense heritability for agronomic and seed quality traits at different field environments in Canada and China tested from 2004 to 2006

Trait	Environment							
	Woodstock 2004	Tavistock 2004	Harbin 2004	Woodstock 2005	Tavistock 2005	Ottawa 2005	Harbin1 2006	Harbin2 2006
Height	0.98	0.98	0.96	0.98	0.98	0.99	0.98	
Lodging		0.81	0.97	0.78	0.83	0.82	0.86	
100 seed weight	0.92	0.93	0.91	0.95	0.79	0.95	0.93	
R1	0.92	0.96	0.97	0.96	0.89	0.96	0.86	0.86
R5	0.92	0.81	0.98	0.97	0.96	0.97	0.75	0.98
R8	0.96	0.97	0.97	0.98	0.98	0.98	0.94	0.78
Oil content	0.81	0.86	0.82	0.95	0.88	0.87	0.86	0.70
Protein content	0.90	0.86	0.82	0.87	0.92	0.91	0.89	0.81
Pods per node	0.62	0.52	0.68	0.61	0.80	–[b]	0.52	–
Pods per plant	0.96	0.54	0.89	0.95	0.96	–	–	–
Seeds per pod	0.28	NS[a]	0.44	0.51	0.49	–	0.46	–

[a] No significant variation for the trait

[b] Trait not measured in the environment

positively correlated with seed yield in six environments within the Canadian mega-environment and in one environment in the Chinese one. Plant height was positively correlated with seed yield in five environments, four of which were in the Canadian and one in the Chinese mega-environments (Table 2).

Three traits showed inconsistent correlation with seed yield across environments. One hundred seed weight was positively correlated with seed yield in two environments in the Canadian mega-environment and in one environment in the Chinese one. A negative linear correlation between 100 seed weight and seed yield was observed in one environment in China. The number of pods per node was positively correlated in two environments and negatively correlated in other two within both mega-environments.

Discussion

In a previous study Palomeque et al. (2009) reported seven seed yield QTL detected in a population derived from a cross between a Canadian and a Chinese elite line, which were evaluated in two mega-environments. It was also determined that there were two types of QTL: those that appeared at specific environments within a single mega-environment defined as $\mathrm{QTL}_{\mathrm{SP}}$ and those that appeared in both mega-environments ($\mathrm{QTL}_{\mathrm{U}}$). To determine the co-localization of a QTL associated with an agronomic trait and any of the previously reported seed yield $\mathrm{QTL}_{\mathrm{U}}$ or $\mathrm{QTL}_{\mathrm{SP}}$, 11 agronomic traits were phenotyped and evaluated. Broad sense heritability was for the most part consistent for each trait across different environments and agreed with most reports in the literature for highly inbred RIL populations (e.g., Mansur and Orf 1995; Kabelka et al. 2004; Hyten et al. 2004; Guzman et al. 2007). The QTL analysis detected four seed yield $\mathrm{QTL}_{\mathrm{U}}$ to be co-localized in the same regions as several of the agronomic traits evaluated. Only two seed yield $\mathrm{QTL}_{\mathrm{U}}$ (tagged by Satt100 and Satt277, respectively) were co-localized with traits related to the reproductive period (R1, R5 and R8). Therefore, the variation observed in seed yield could be the result of the variation observed in R8, which is related to seed filling period. These results are in agreement with the previous studies that also reported Satt277 to identified a QTL associated with plant height (Kabelka et al. 2004; Orf et al. 1999b) and seed weight (Orf et al. 1999b). In addition, a QTL that was reported to have a positive association with maturity, plant height, lodging and yield (Specht et al. 2001) and flowering date, seed stage (Tasma and Shoemaker 2003) was mapped at a distance of 4 cM from Satt277 (Kabelka et al. 2004). The consistency of the association between Satt277 and various yield-correlated traits between the current and previous studies indicated that the effects of this genomic region are independent of the environment and genetic background.

Five of the seed yield QTL (three $\mathrm{QTL}_{\mathrm{U}}$ and two $\mathrm{QTL}_{\mathrm{SP}}$) were not co-localized with a QTL associated with a reproductive stage, in particular with maturity. These findings suggest that these five QTL were not maturity QTL that had pleiotropic expression on seed yield. Two seed yield $\mathrm{QTL}_{\mathrm{U}}$ (linked to Sat162 and Sat_126, respectively) were not associated with maturity, but with four different agronomic traits. Thus, seed yield increase could be explained through the variation observed in the number of pods per node, in

Table 3 Correlation analysis between yield and 11 agronomic traits found in a population derived from the cross between OAC Millennium × Heinong #38 tested across different environments in Canada and China from 2004 to 2006

Location	R1	R5	R8	100 seed weight	Plant height	Lodging	Pod per plant	Pod per node	Seed per pod	Oil	Protein
2004[a]											
Tavistock	$r = 0.62$ $P < 0.001$[c]	$r = 0.48$ $P < 0.001$	$r = 0.57$ $P = 0.001$	$r = -0.05$ $P = 0.665$	$r = 0.70$ $P < 0.001$	no data[b]	$r = 0.19$ $P = 0.078$	$r = 0.25$ $P = 0.017$	no data	$r = -0.20$ $P = 0.058$	$r = 0.10$ $P = 0.338$
Woodstock	$r = 0.44$ $P < 0.001$	$r = 0.67$ $P < 0.001$	$r = 0.62$ $P < 0.001$	$r = -0.02$ $P = 0.791$	$r = 0.64$ $P < 0.001$	*[d]	$r = 0.25$ $P = 0.015$	$r = 0.27$ $P = 0.011$	no data	$r = -0.23$ $P = 0.029$	$r = 0.13$ $P = 0.207$
Harbin (1)	no data	$r = -0.03$ $P = 0.787$	$r = -0.20$ $P = 0.054$	$r = -0.24$ $P = 0.026$	$r = 0.03$ $P = 0.774$	no data	$r = -0.08$ $P = 0.408$	$r = -0.05$ $P = 0.629$	$r = -0.08$ $P = 0.429$	$r = 0.03$ $P = 0.777$	$r = -0.10$ $P = 0.331$
2005											
Woodstock	$r = 0.11$ $P = 0.283$	$r = 0.45$ $P < 0.001$	$r = 0.51$ $P < 0.001$	$r = 0.33$ $P < 0.001$	$r = 0.54$ $P < 0.001$	$r = 0.26$ $P = 0.016$	$r = 0.09$ $P = 0.364$	$r = 0.07$ $P = 0.495$	$r = 0.05$ $P = 0.621$	$r = 0.14$ $P = 0.178$	$r = 0.02$ $P = 0.879$
Tavistock	$r = 0.55$ $P < 0.001$	$r = 0.52$ $P < 0.001$	$r = 0.61$ $P < 0.001$	*	$r = 0.62$ $P < 0.001$	no data	$r = 0.16$ $P = 0.121$	$r = -0.21$ $P = 0.047$	$r = -0.22$ $P = 0.037$	$r = -0.31$ $P = 0.003$	$r = 0.02$ $P = 0.228$
Ottawa	$r = 0.32$ $P = 0.002$	$r = 0.29$ $P = 0.005$	$r = 0.463$ $P < 0.001$	$r = 0.36$ $P < 0.001$	$r = 0.15$ $P = 0.146$	$r = -0.07$ $P = 0.494$	no data	no data	no data	$r = 0.39$ $P < 0.001$	$r = -0.27$ $P = 0.011$
2006											
Harbin (1)	$r = 0.37$ $P < 0.001$	*	*	$r = -0.18$ $P = 0.095$	$r = 0.67$ $P < 0.001$	no data	$r = 0.45$ $P < 0.001$	$r = -0.52$ $P < 0.001$	$r = -0.01$ $P = 0.939$	$r = -0.17$ $P = 0.1$	$r = 0.01$ $P = 0.956$
Harbin (2)	$r = 0.53$ $P < 0.001$	$r = 0.56$ $P < 0.001$	$r = 0.70$ $P < 0.001$	$r = 0.51$ $P < 0.001$	no data	no data	no data	no data	no data	$r = -0.40$ $P < 0.001$	$r = 0.09$ $P = 0.407$

[a] Year of testing

[b] *no data* data could not be transformed

[c] P values over 0.05 corresponds to no significant correlation

[d] Correlation not calculated since no significant difference for the trait among lines was observed, according to ANOVA

the number of pods per plant, in height and in lodging. In addition, no association was found between the epistatic regions reported by Palomeque et al. (2009) and maturity. Only the epistatic region tagged by Sat_126 was associated with four agronomic traits other than the ones related to the reproductive stages, in both mega-environments. In the present study, no association between the 11 agronomic traits and the epistatic regions tagged by Satt002, Satt288, Satt394, Satt528 and Satt543, which had exhibited interaction with individual seed yield QTL_U were observed. Therefore, the percentage of the variation in seed yield explained by epistasis might be due to the association of the interacting genomic regions with a physiological process or another trait that was not measured in this study.

Finding exotic germplasm with favorable alleles for yield increase to be used as parents could be a difficult task (Guzman et al. 2007). Thus, the most effective use of exotic lines to introgress high-yielding alleles into the adapted local germplasm could be achieved by the use of both QTL_U and QTL_SP since both contribute either directly or indirectly through trait association to yield in specific adapted environments. More research is needed to confirm both types of QTL in different genetic backgrounds and mega-environments. It may also be of interest to determine if the types of QTL found in this study would change if the RIL population was developed in reciprocal mega-environments, where the roles of each parent changes from an adapted to exotic in the mega-environment where the population is developed. The confirmation of both QTL_U and QTL_SP could provide useful information for using these types of QTL in marker-assisted selection aimed at allele introgression from exotic sources into breeding populations.

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