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Identification of heterotic loci for seven yield and yield-related traits in maize with a set of introgression lines

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Abstract

Dissection of the genetic basis of heterosis facilitates hybrid breeding in crops. In this study, heterotic loci (HL) for seven yield and yield-related traits were identified in a set of maize introgression lines (ILs) under two environments (locations) by a backcross population with one of their parents, Zong 3. Middle parent heterosis of seven yield and yield-related traits was calculated based on the field experiments conducted at two locations. A total of 120 significant loci for six traits were identified by calculating marker-trait coefficients with the software Graphical Genotypes (GGT) 2.0, and 48 loci represent for five traits were commonly identified under two environments. This indicates that it is possible to identify HL with the population derived from ILs. Of the 48 significant loci, 13 were found to be associated with more than 2 different traits, indicating strong genetic correlations among these traits. For yield and most of the yield-related traits, the heterozygosity of the markers at the HL were strongly correlated to the performance of middle parent heterosis, suggesting that the HL identified in this study could be used for heterosis prediction and maker-assisted selection in maize hybrid breeding.

Keywords: introgression lines; middle parent heterosis; heterotic loci; yield and yield-related traits; maize.
Abbreviations: BD-Baoding; ED-ear diameter; EL-ear length; HL-heterotic locus; ILs-introgression lines; KN-kernel number per row; KW-100-kernel weight; MPH-middle parent heterosis; PH-plant height; QTL-quantitative trait loci; RN-row number per ear; WH-Wuhan; YP-yield per plant.

Introduction

The term heterosis was introduced by Shull in 1914 and defined as that the heterozygous offsprings performed better than their homozygous parents with regard to yield and yield related traits (Shull, 1948). Since then, three main hypotheses, dominance (Jones, 1917), overdominance (Hull, 1945) and epistasis (Powers, 1944) have been proposed to explain the phenomenon at the genetic level. With the development of molecular markers and other biological tools, some researchers tried to dissect the genetic basis of heterosis using molecular markers in crops, and dominance (Xiao et al., 1995), overdominance (Stuber et al., 1992), epistasis (Yu et al., 1997) and a combination of these effects (Tang et al., 2010; Hua et al., 2003) have been found contributing to heterosis. Mapping QTL or identify chromosome loci contributing heterosis would be useful in hybrid breeding. For example, Zhang et al. (1994) identified 16 to 30 heterosis related marker loci or positive markers in rice. QTL mapping for heterosis has also been conducted in several crops (Stuber et al., 1992; Xiao et al., 1995; vuylsteke et al., 2000; Luo et al., 2001), and several congruent QTL across three populations were found locating in bins encompassing the centromeres (Schön et al., 2010). QTL associated with heterosis can be used to predict heterosis and provide targets for marker-assisted selection in hybrid breeding. In maize, a model designated TCSM (total contribution of the selected markers) was successfully developed to predict hybrid performance based on the QTL for hybrid performance or heterosis (Vuylsteke et al., 2000). However, up to now, majority of the studies on QTL mapping or trait-marker association analysis for heterosis have been carried out mainly using conventional populations, such as F_2, BC_1 and recombinant inbred lines (RILs). The complex genetic background of these populations would reduce the power of QTL mapping and separate the processes of QTL mapping from breeding practice. Near-isogenic lines (NILs) or introgression lines (ILs) have been employed to map some agronomically important traits (Kaeppler et al., 1993; Eshed and Zamir, 1995; Szalma et al., 2007), and to verify the effects of QTL for heterosis (Pea et al., 2009; Frascaroli et al., 2012). In addition, QTL mapping with NILs or ILs can be integrated into breeding programs. However, none has been addressed for mapping QTL conditioning heterosis for yield and yield-related traits using NILs or ILs to date. In this study, heterosis loci (HL) for seven yield and yield-related traits were firstly identified with a set of ILs in maize, and their possible utility in maize hybrid breeding was also discussed.

Results

Performance of the traits in Zong 3 and F_1 hybrids, and MPH in the ILs

The performance of the yield traits in Zong 3 and the F_1 hybrids, and middle parent heterosis (MPH) in the ILs is given in Table 1. The F_1 hybrids performed better on the yield and yield-related traits at Baoding (BD) than that at Wuhan (WH).

Table 1. Performance of the traits in the parents and F_1 hybrids, and MPH in the ILs.

Traits	HB/Z3 [a]	Z3/HB	Z3	F_1 hybrids		Middle Parent Heterosis (MPH)			
				Mean	Range	Mean	Range	Skew	Kurt
YP(g)	111.3 [b]	165.7*	55.1	55.4	21.5-120.3	18.2	-62.1-156.6	0.8	0.1
	90.5	122.9*	59.9	78.6	40.0-180.5	37.4	-27.0-184.8	1.1	1.1
KW(g)	22.7	29.3	18.6	20.1	14.9-34.8	5.5	-24.5-43.9	0.2	0.3
	21.3	25.9	19.2	22.0	17.9-30.0	9.3	-18.1-58.0	0.9	1.2
EL(cm)	18.8	21.3*	10.2	14.3	11.5-19.0	18.3	-8.4-59.9	0.5	0.1
	15.2	17.6	10.7	13.3	9.1-25.9	17.4	-16.9-75.3	0.6	0.7
ED(cm)	4.3	4.6	3.6	3.7	2.4-4.5	2.4	-30.1-25.7	-0.4	0.0
	3.9	4.2	3.6	3.8	3.0-4.7	5.6	-45.1-41.1	-1.2	3.6
RN	14.2	14.2	13.8	13.8	10.0-16.0	-0.4	-26.8-19.4	-0.6	0.7
	13.9	12.9	14.1	13.8	11.6-16.4	2.5	-16.4-22.9	0.1	0.1
KN	40.6	44.4	25.5	29.6	20.8-42.4	11.7	-32.8-60.6	0.2	-0.1
	31.3	34.7	29.2	25.4	14.5-48.5	5.2	-39.3-103.2	1.3	3.5
PH(cm)	245.8	273.3*	175.4	193.5	156.8-242.5	8.3	-10.7-37.1	0.6	0.0
	208.6	222.4*	183.8	186.7	152.1-252.0	5.2	-14.8-34.8	0.5	0.7

[a] Z3=Zong 3, HB=HB522, ED=ear diameter, EL=ear length, HL=heterotic locus, KN=kernel number per row, KW=100-kernel weight, PH=plant height, RN=row number per ear, YP=yield per plant. [b] values in the first row are investigated in Wuhan, and that in the second rows are from Baoding.
* values in Z3/HB are significant higher than that in HB/Z3 at the level of $P<0.05$.

Between the two reciprocal crosses, the values of all the traits except for the trait of row number (RN) in Zong 3/HB522 were higher than that in HB522/Zong 3, and significant difference ($P<0.05$) was detected between them for yield per plant (YP), ear length (EL) and plant height (PH) at least at one location. Similar reciprocal effects were also detected previously, and QTL mapping for these effects has been conducted in maize (Gonzalo et al., 2007). In general, the values of YP and KW in Zong 3 and the F_1 hybrids at BD were greater than those at WH. In addition, large variations have been observed for YP and PH in the F_1 hybrids. As for MPH, the means of YP, KW (100-kernel weight), ED (ear diameter) and RN at BD were higher than those at WH. In contrast, the means of EL, KN and PH were higher at WH than BD. These traits also varied largely among the ILs especially for the trait of YP, and they all generally fit in a normal distribution except for ED and KN at BD (Table 1). Two-factor ANOVA for the MPH of these traits was conducted, and significant difference was detected among the ILs except for ED and RN, suggesting that the introgressed chromosomal fragments had significant effects on heterosis for most of the traits (Table 2). In addition, significant difference was also detected between the two locations for the traits of YP, EL, KN and PH.

Correlation analysis among the traits

Table 3 gives the correlation coefficients among the MPH of these traits. The MPH of YP was positive and significantly correlated to the MPHs of yield related traits. In particular, the MPH of YP was strongly correlated to the MPH of EL and KN with coefficients ranging from 0.69 to 0.83. Positive, significant correlations were also detected among the MPH of EL, ED, RN, KN and PH. Of them, the strongest correlations were detected between the MPH of EL and KN at both locations (r=0.86). However, correlations between the MPH of KW and other yield-related traits were relatively low or not significant. Particularly, coefficients between the MPH of KW and RN were negative at both locations. Correlations between the MPH of PH and the MPH of RN or KN were also not strong. Significant correlation was not observed between the MPH of PH and the MPH of RN at BD.

Genotyping and identification of heterotic loci (HL)

Genotyping with 215 SSR markers revealed that the number of introgression segment in each IL varied from 2 to 46 with an average of 14. The background recovery rate ranged from 51.0% to 97.9% with an average background recovery rate of 83.0%. For the seven traits, a total of 120 loci were found to be associated with heterosis. Totally 36, 25, and 33 HL for YP, EL and PH were detected, respectively. While only 2 HL for ED and none for RN were identified. Table 4 shows the 48 HL detected at both locations.

Identification heterotic loci for yield per plant

Totally 36 heterotic loci were detected for YP, and they were distributed on all the chromosomes of maize. Of them, 23 were identified at both locations with -lg values ranging from 1.9 to 5.0 at WH and 1.8 to 4.9 at BD, and the heterozygotes at these loci had positive effects (Table 4). Large effects at several heterotic loci might be caused by the reason that some ILs have heterozygotes at more than one significant loci.

Identification heterotic loci for kernel weight

Five and eight HL for KW were detected at WH and BD, respectively. Among them, three loci distributed on chromosome 6, 7 and 10 were identified at both locations. The heterozygotes at these three loci increased the MPH of KW from 14.0% to 32.6% (Table 4).

Identification heterotic loci for ear length, ear diameter and kernel number per ear

A total of 25 loci for EL were detected, and nine of them were commonly identified at both locations. The –lg values ranged from 2.0 to 4.5, and the heterozygotes increased the MPH of EL from 14.4% to 33.8% at both locations (Table 4). For the trait of ED, one locus was found to be associated with MPH at each of the locations, and no common locus was detected. Although six and ten HL for KN were detected at WH and BD, respectively, only two loci on chromosome 1 and 3 were commonly detected at both locations.

Identification heterotic loci for plant height

Totally 33 HL for PH were detected, and 18 and 26 loci were detected at WH and BD, respectively. A total of 11 loci distributed on seven different chromosomes were commonly detected at both locations, and the -lg values ranged from 2.4 to 4.9 at WH and 1.8 to 4.9 at BD. The heterozygotes at these loci increased the MPH of PH from 7.1% to 25.7% (Table 4).

Table 2. ANOVA for the MPH of the seven traits investigated.

Traits	Sources	F value	*P*
YP [a]	G	6.05	0.00
	E	6.08	0.02
	G*E	0.24	0.99
KW	G	2.34	0.00
	E	0.77	0.39
	G*E	0.59	0.93
EL	G	4.60	0.00
	E	10.20	0.00
	G*E	0.65	0.89
ED	G	0.86	0.68
	E	1.29	0.26
	G*E	0.78	0.75
RN	G	1.25	0.24
	E	1.49	0.23
	G*E	1.28	0.21
KN	G	3.21	0.00
	E	15.65	0.00
	G*E	0.61	0.91
PH	G	3.26	0.00
	E	15.65	0.00
	G*E	0.76	0.80

[a] G=genotype, E=environment, see the explanation for the other abbreviations in the legends of Table 1.

Pleiotropism of the heterotic loci

The phenomenon of pleiotropism was found for most of the traits. In general, there were 2, 5 and 6 marker loci simultaneously associated with 4, 3 and 2 traits, respectively (Table 4). For example, *bnlg1124* on chromosome 1 and *bnlg1957* on chromosome 3 were found to be associated with the MPH of YP, EL, KN and PH simultaneously. In addition, 6 marker loci simultaneously controlling the MPH of YP and EL, and 7 marker loci simultaneously related to the MPH of YP and PH were detected. This is coincidence to the fact that the genetic correlations among these traits were very strong.

Correlations between MPH and heterozygosity in the ILs

For each trait, correlation between MPH of the ILs and the heterozygosity at all the marker loci or at HL was analyzed. For all the traits except for RN, positive and significant correlations were identified at least at one location using all the markers data set (Table 5). The MPH of all the traits except for RN was also significantly and strongly correlated to the heterozygosity of the markers at the HL. In comparison to the coefficients at all the marker loci, the correlations at the HL were much stronger for all the traits analyzed. At BD, heterozygosity at the HL (only one was detected) was negatively related to the MPH of ED (r=0.45).

Discussion

Molecular markers can be used to dissect the genetic basis of heterosis, and heterosis-related loci have been identified using various genetic populations including F_2, $F_{2:3}$, RIL and IF_2 (immortal F_2). In comparison to these populations, ILs should have more advantages to conduct genetic studies due to its relatively simple background. In this study, marker-trait associations for middle parent heterosis of seven yield and yield-related traits were firstly determined in a set of maize ILs under two environments. A total of 120 significant heterotic loci were detected by the software GGT2.0, and 48 loci for five traits were commonly identified at the both locations. The locus, *umc2149*, associated with HL for YP in this study was also found to be related to a heterotic QTL for grain yield in maize (Tang et al., 2010). Heterotic metabolite QTL was also successfully identified in 41 ILs in Arabidopsis (Lisec et al., 2009). These results indicate that it is possible to dissect the genetic basis of heterosis with ILs in plants. Genetic correlation analysis in this study revealed that the heterozygosity at HL was strongly correlated to the MPH of the yield traits. Moreover, the heterozygotes at all of the commonly detected HL had positive effects on the MPH. These results indicated that overdominance might be a part of the genetic basis of heterosis in this IL population. Stuber et al. (1992) also reported that strong and positive correlation existed between heterozygosity and grain yield in a maize population, and overdominance was found to play an important role in the genetic basis of heterosis in that population. In this study, the heterozygotes at all of the common HL had higher phenotypic values than their corresponding homozygotes. Correlations between the MPH of the ILs and the heterozygosity at the HL were much stronger than those between the MPH and heterozygosity at all the marker loci. Similar results were also observed in previous studies. For instance, heterozygosity at the heterosis related marker loci was significantly correlated with several attributes of overall phenotypic performance and heterosis in rice (Zhang et al., 1994). In maize, hybrids heterozygous for the markers flanking heterotic QTL showed a higher grain yield than hybrids homozygous for those marker loci (Vuylsteke et al., 2000). Therefore, the HL identified in this study can be potentially used to predict and enhance heterosis in maize hybrid breeding through marker-assisted selection.

Materials and methods

Materials and planting

An IL population including 75 lines was used in this study. The ILs were developed from a cross between Zong 3 and HB522 by Wang et al. (2007). Zong 3, a parent of an elite hybrid (Yuyu22) used in China, was used as recurrent parent, and HB522, a wax inbred, was the donor. In the summer of 2009 in Wuhan, each IL was crossed to the parent of Zong 3, and a total of 70 hybrids were obtained. In the same season, two reciprocal hybrids, Zong3/HB522 and HB522/Zong 3, were also produced. The 70 hybrids, ILs, Zong 3, and the two reciprocal hybrids were planted at two locations, Wuhan (WH, spring growing area in China) and Baoding (BD, summer growing area in China), in a field design of randomized complete blocks with two replicates in 2010. The sowing date at WH was on April 4, and BD was on June 13. Twelve seedlings were kept in each one-row plot with a plant space of 25 cm within each row and 60 cm between adjacent rows, and the field management was the same as the normal local maize field.

Trait measurements

At harvesting stage, plant height (PH, cm) was measured on the middle five competitive plants in each plot, and ears on these plants were harvested for yield and yield-related traits investigation. Six traits including yield per plant (YP, g), row number (RN), kernel number per row (KN), ear length (EL, cm), ear diameter (ED, cm), and 100-kernel weight (KW, g) were measured after the ears were dried by air. The former five traits were investigated on each ear, and two random 300-kernels samples from each plot were counted and weighed. Middle parents heterosis (MPH, %) for the *i*th IL was calculated as MPH*i* (%)= (H*i*- Mp*i*)/ Mp*i**100, in which H*i* was the mean of the values in the hybrid of Zong 3 / IL*i* in two replicates, and Mp*i* was the mean of the average of Zong 3 and IL*i* in two replicates.

Table 3. Correlation analysis for the MPH of the seven traits investigated

Traits	YP[a]	KW	EL	ED	RN	KN
KW	0.21/0.57**					
EL	0.83**/0.69**	0.17/0.32**				
ED	0.85**/0.14	0.24*/0.09	0.66**/0.28*			
RN	0.50**/0.29*	-0.14/-0.10	0.43**/0.34**	0.65**/0.34**		
KN	0.77**/0.83**	0.14/0.37**	0.86**/0.86**	0.53**/0.31**	0.37**/0.39**	
PH	0.68**/0.44**	0.02/0.53**	0.56**/0.56**	0.62**/0.21	0.32**/-0.02	0.48**/0.47**

[a] values on the left side of the sign "/" are from WH, and that on the right from BD. * and ** represent significant at the level of $P<0.05$ and $P<0.01$, respectively.

Table 4. MPH related loci commonly identified at the two locations

Traits	Chromosome	Loci	HN			BD		
			-lg	Effects [a]	*P*	-lg	Effects	*P*
YP	1	bnlg1124	4.1	101.0	0.00	2.5	51.4	0.01
	1	umc1106	2.2	89.6	0.01	2.1	58.0	0.02
	1	umc1184	3.3	60.5	0.00	1.9	29.8	0.02
	1	umc2149	4.3	77.9	0.00	2.4	41.0	0.00
	2	phi083	1.9	51.6	0.01	2.7	44.7	0.01
	2	bnlg1225	2.9	106.3	0.00	3.7	60.2	0.00
	2	umc1946	2.1	68.0	0.01	2.3	42.4	0.01
	3	phi104127	2.3	107.8	0.00	3.7	68.7	0.00
	3	bnlg1957	3.4	92.7	0.01	2.4	40.5	0.04
	3	umc1399	2.7	91.8	0.01	2.5	49.6	0.04
	3	umc2081	3.2	76.7	0.00	3.9	67.2	0.00
	4	phi308090	3.5	106.1	0.00	3.0	83.2	0.00
	4	bnlg2162	2.4	65.8	0.01	3.4	49.5	0.00
	5	umc2198	2.0	63.8	0.01	3.3	48.5	0.00
	5	umc2013	2.0	63.8	0.01	3.2	48.6	0.00
	6	umc1178	1.9	73.5	0.02	2.9	59.7	0.00
	7	umc1642	1.9	57.8	0.01	2.2	46.6	0.01
	7	umc1932	2.8	68.5	0.00	2.4	50.0	0.00
	7	umc2332	2.8	83.3	0.01	2.4	42.0	0.01
	8	umc1724	1.9	53.9	0.01	1.9	36.4	0.01
	9	phi027	3.2	106.2	0.00	1.8	36.7	0.04
	10	umc1337	5.0	87.0	0.00	3.9	51.2	0.00
	10	bnlg1526	2.5	53.1	0.01	4.9	52.9	0.00
KW	6	umc1018	3.8	32.6	0.00	4.9	26.3	0.00
	7	umc1932	2.6	20.3	0.00	2.5	18.0	0.00
	10	umc1337	3.2	18.6	0.00	2.3	14.0	0.01
EL	1	bnlg1124	4.2	28.5	0.00	2.5	21.2	0.01
	1	umc1184	3.2	16.2	0.00	2.2	14.4	0.01
	2	bnlg1225	2.0	26.1	0.01	2.6	26.9	0.00
	3	phi104127	2.5	30.4	0.00	2.8	22.5	0.00
	3	bnlg1957	4.5	33.8	0.00	3.1	24.3	0.00
	3	bnlg1035	3.0	32.7	0.00	3.1	26.5	0.00
	4	bnlg2162	2.6	19.1	0.00	3.7	20.9	0.00
	5	umc2198	2.2	18.5	0.01	3.1	19.0	0.00
	7	umc2332	2.0	17.3	0.04	2.3	17.6	0.01
KN	1	bnlg1124	3.7	37.7	0.00	3.0	31.5	0.00
	3	bnlg1957	3.2	37.6	0.01	2.7	28.9	0.01
PH	1	bnlg1124	3.8	17.8	0.00	3.0	12.0	0.00
	1	umc1106	3.4	25.7	0.00	2.4	14.5	0.01
	1	umc1184	3.1	11.0	0.00	2.2	7.1	0.01
	2	umc1946	2.3	13.7	0.01	3.3	10.5	0.00
	2	umc1736	3.1	15.2	0.00	3.2	10.9	0.00
	3	bnlg1957	2.8	13.5	0.02	2.9	10.9	0.01
	4	bnlg2162	3.3	15.6	0.00	4.5	12.2	0.00
	5	umc2198	2.8	15.2	0.00	4.9	12.9	0.00
	7	umc2332	2.3	16.9	0.01	3.3	11.5	0.00
	8	umc1724	2.5	12.3	0.00	2.8	9.1	0.00
	10	umc1337	2.4	10.8	0.00	2.2	8.0	0.01

[a] Effects are the means of MPH in heterozygotes minus the means of MPH in homozygotes at the HL.

Table 5. Correlations analysis of MPH with heterozygosity at all markers loci and HL

Traits	All the markers	Markers at HL
YP	$0.67^{**}/0.60^{**}$ [a]	$0.74^{**}/0.66^{**}$
KW	$0.23^{*}/0.50^{**}$	$0.61^{**}/0.65^{**}$
EL	$0.59^{**}/0.49^{**}$	$0.70^{**}/0.60^{**}$
ED	0.50^{**}/-0.12	0.52^{**}/-0.45^{**}
RN	0.21/0.06	-/-
KN	$0.55^{**}/0.44^{**}$	$0.64^{**}/0.62^{**}$
PH	$0.52^{**}/0.60^{**}$	$0.66^{**}/0.67^{**}$

[a] values on the left side of the sign "/" are from WH, and that on the right from BD. * and ** represent significant at the level of $P<0.05$ and $P<0.01$, respectively.

Genotyping

A total of 215 SSRs (simple sequence repeats) were employed to genotype the population. Besides the 121 SSR markers used for ILs construction (Wang et al., 2007), another 94 polymorphismic SSRs selected from 422 SSRs (http://maizegdb.org) were used to genotype the whole population.

Data analysis and marker-trait association detection

Two-factor ANOVA (Analysis of variance) was conducted with the analysis tool in Microsoft Excel 2003. Marker-trait associations were calculated with the software GGT 2.0 (http://www.dpw.wau.nl/pv/pub/ggt/). The squared correlation coefficients between marker data and trait values (R^2 values) and the associated probabilities of the correlation values were calculated. As these probabilities were very small, the $-^{10}$LOG (-lg) values were reported, such as a value of $-^{10}$LOG =3 indicated a correlation probability value of 0.001. A false discovery rate (FDR) threshold for the *p*-values of individual association tests was also calculated by GGT (Storey, 2002). In this study, FDR threshold for $-^{10}$LOG (*p*) values of each trait ranged from 1.7 to 2.6. Detected marker-trait associations were then followed by single factor ANOVA analysis to calculate the means of each genotype and the *P* values. For the significant loci clustered on a chromosomal region, only the locus with the least *P* value was selected.

Conclusion

In this study, heterosis loci for seven yield and yield-related traits were firstly identified with a backcrossing population (a set of maize inbred lines crossed with their recurrent parent). A total of 48 heterotic loci for five yield and yield-related traits were commonly identified under two environments, and 13 of them were found to be associated with more than 2 traits. For the five traits, the heterozygosity of the markers at the HL was strongly correlated to the performance of middle parent heterosis, suggesting that the HL identified in this study can be potentially useful for maize hybrid breeding.

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