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ORIGINAL PAPER

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Development, utilization of introgression lines using a synthetic wheat as donor

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Abstract A series of introgression lines (ILs) were generated from repeated backcrossing between the exotic hexaploid wheat genotype Am3 and the common wheat genotype Laizhou953. Am3 was synthesized by crossing *Triticum carthlicum* with *Aegilops tauschii* and was used as the donor parent in this study, and Laizhou953 was used as the recurrent parent. Two hundred and five SSR markers showing polymorphism between the two parents were used to identify the introgressed Am3 chromosome segments in 97 BC_4F_3 ILs. The introgressed segments in each line and the length of the introgressed segments were estimated according to the wheat SSR consensus map. The introgressed segments from Am3 in the 97 lines covers 37.7% of the donor genome. The introgressed segments were most found on 2D, 3B, 6B, and 1D with coverage of 59.8, 59.5, 59.1, and 59% of the chromosomes, respectively. None of the 97 lines tested contained chromosome 4D segments introgressed from Am3. Introgressed segments for each of the chromosomes were mapped using the consensus wheat linkage map. Nine agronomic traits from BC_4F_3 lines were evaluated and the phenotype showed most lines have the tendency to be more similar to the recurrent parent. There were lines showing better agronomic traits than the recurrent parent, which indicated the introgression of favorable alleles from the exotic hexaploid wheat into the elite cultivar Laizhou953. Marker and phenotype data were used to identify quantitative trait loci (QTLs) controlling these nine traits. In total, 38, 33, and 28 putative QTLs were detected for seven of the nine traits in 2003, 2004, and 2005, respectively. Some of these agronomic important QTLs were detected in more than one season.

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Introduction

In crops, the majority of traits, particularly those with agronomic importance such as grain yield, tolerances and resistances to abiotic stresses and grain quality, are quantitatively inherited and controlled by a large number of genes. Interactions between these controlling genes are also common. Understanding the genetic bases of these traits has been a major challenge facing scientists. Over the last decade, the application of molecular markers and genetic linkage maps has allowed the identification of specific regions of the genomes controlling polygenic traits in all of the major crop species (Khavkin and Coe 1997; Thomas 2003; Hanocq et al. 2004; Quarrie et al. 2005).

However, as noted by Eshed and Zamir (1995), considerable advances in the methodologies of mapping quantitative genes have not been matched by a parallel development of suitable population structures for precise quantitative trait localization (QTL) and exact evaluation of the genetic effects. It is still difficult to utilize existing mapping results in marker assisted selection (MAS) as well as in map-based cloning of genes conferring these QTLs. Specifically, functional genomics research of complex phenotypes has to resolve the technical difficulties such as to efficiently identify QTLs with large effects on specific target phenotypes, to efficiently fine-map target QTLs and determine candidate genes of QTLs; and to efficiently determine and verify functions of candidate genes conferring these QTLs.

Eshed and Zamir (1994a) proposed to exploit introgression lines (ILs) which could be generated by

systematic backcrossing and introgressing of marker-defined exotic segments in the background of elite varieties. ILs are obtained by several generations of backcrossing with one of the parents (recurrent parent) starting from the F_1 generation and ending with at least one generation of selfing. These lines have a high percentage of the recurrent parent genome and a low percentage of the donor parent genome. So, the genetic backgrounds of the lines are similar to the recurrent parent. These ILs provide a useful tool to resolve a number of questions. First, they enable the phenotypic analysis of specific QTLs based on a common genetic background in which direct comparison of two lines can be used to evaluate the phenotype conditioned by a single introgressed exotic segment (Tanksley et al. 1996). By so doing, the complicated traits controlled by multiple genes can be dissected into Mendelian factors. Second, ILs facilitate fine mapping of QTLs so as to conduct the map-based cloning of QTLs. This is because that the location of a QTL can be narrowed down to a small genomic interval by evaluating a series of ILs that differ for overlapping regions of the genome (Paterson et al. 1990). The QTL may be further fine-mapped by a secondary segregation population constructed by crossing the concerned IL with the recurrent parent. Fine mapping and map-based cloning of the quantitative loci controlling heading date and grain number in rice and the *fw2.2* locus controlling the fruit size in tomato provide good examples in this aspect (Yamamoto et al. 1998; Yano et al. 2000; Frary et al. 2000; Ashikari et al. 2005). Furthermore, as Zamir (2001) proposed, ILs can be used in capitalizing on the genetic diversity in exotic germplasm and in breeding as well as in gene discovery. ILs are useful for breeding purposes, as they contain a low percentage of exotic germplasm and favorable exotic alleles can thus be easily and rapidly isolated and transferred into elite varieties (Toojinda et al. 1998; Shen et al. 2001; Bouchez et al. 2002; Ishimaru 2003; Kashiwagi and Ishimaru 2004). Finally, these ILs provide a valuable resource for the unravelling of gene function by expression profiling or map-based cloning. This approach has been successfully demonstrated in tomato and rice (Nesbitt and Tanksley 2001; Liu et al. 2003; Fridman et al. 2005).

Several sets of ILs have already been developed for various crops, such as tomato (Eshed and Zamir 1994a, b, 1995; Fulton et al. 1997; Bernacchi et al. 1998; Chetelat and Meglic 2000; Monforte and Tanksley 2000), lettuce (Jeuken and Lindhout 2004), rice (Lin et al. 1998), barley (Matus et al. 2003; Pillen and Zacharias 2003; Korff et al. 2004), soybean (Concibido et al. 2003), and *Brassica oleracea* (Ramsay et al. 1996). However, there is no report on the development of ILs in wheat.

In the present paper, we report the development of a series of ILs for wheat by introgressing exotic wheat segments into common wheat genetic background. Our goal is (1) to establish a set of ILs, which represents part of the exotic genome with donor segments of different sizes, (2) to discover the favorable alleles of the exotic wheat, and (3) to fine map QTLs for some agronomic important traits in the future.

Materials and methods

Plant materials

Am3 was synthesized by crossing *Triticum carthlicum* acc. PS5 ($2n = 28$, AABB) with *Aegilops tauschii* acc. Ae38 ($2n = 14$, DD). It was used as the donor parent to be crossed with a Chinese released wheat cultivar, Laizhou953, and then backcrossed with Laizhou953 for four generations. The backcrossing population was developed (Fig. 1) according to the advanced backcross strategy of Tanksley and Nelson (1996). Fifty BC_1 were obtained by backcrossing F_1 with Laizhou953, and 20 of these were random selected for further backcrossing with Laizhou953. Five seeds randomly selected from each of the BC_2 progeny were grown but only two to three plants were randomly selected for further backcrossing. Finally, 500 BC_4 plants were generated. After two generation of selfing, 97 BC_4F_3 plants were randomly selected for genotyping and phenotyping in the present study.

Molecular characterization

Ninety-seven BC_4F_3 lines were used to detect the presence of introgressed exotic segments. DNAs of these lines were extracted from foliage according to the protocol described by Sharp et al. (1989). A total of 792

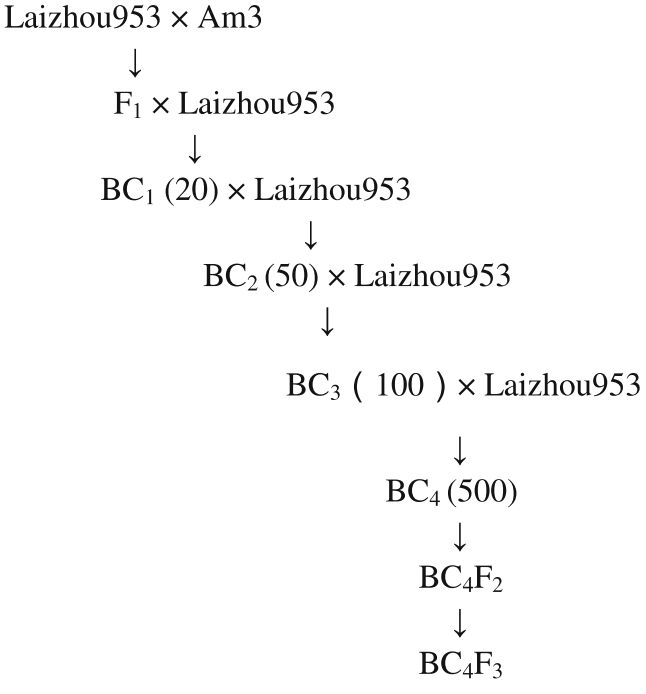


Fig. 1 Development of ILs by introgressing chromosome segments from Am3 into a wheat cultivar Laizhopu953. *Number in brackets* indicated population sizes

SSR markers were screened for polymorphism between the two parents. The primer sequence information and chromosomal location of the amplified loci were primarily taken from the following published sources: Röder et al. (1998), Pestsova et al. (2000), Gao et al. (2004) and http://www.wheat.pw.usda.gov. Two hundred and five polymorphic SSR markers, which consistently detected polymorphism between the two parents and produced minimal stutter bands, were selected for genotyping the 97 ILs. These 205 markers were fairly evenly distributed over the chromosomes.

Polymerase chain reaction amplification was carried out following the method published by Röder et al. (1998). The PCR amplification was performed in 20 μl final volume reactions containing 5 μl template DNA (50 ng), 0.1 μl Taq polymerase (5 U/μl, Promega), 1.5 μl 10×PCR buffer [500 mM KCl, 100 mM Tris–HCl (pH 9.0), 1% Triton X-100], 1.5 μl 25 mM $MgCl_2$, 0.75 μl dNTP (2 mM), and 0.075 μl of the forward and reverse oligonucleotide primers (10 μM). Part of the PCR products were run under standard conditions on 6% polyacylamide gel and visualized by silver staining, the others were detected using automated laser fluorescence (AFL) by ABI PRISM 3700DNA Analyzer. Segment sizes were calculated using the computer program by comparison with internal size standards that had been added to each lane in the loading buffer.

Evaluation of agronomic traits

Evaluation of agronomic traits of the ILs was carried out under field conditions in Beijing in 2003, 2004, and 2005. The materials were planted in the experimental field in Institute of Crops Sciences, Chinese Academy of Agricultural Sciences. The lines were planted in two replications. A single row of 200 cm was used for each of the lines. The spacing between rows was 30 cm and that between plants was 6 cm. Laizhou953 was planted as control in every twenty lines. Nine agronomic traits, including plant height (PH), spike length (SL), spikes per plant (SP), spikelets (SPI), grain number per spike (GNS), thousand grain weight (TGW), grain weight per plant (GWP), days to heading (DH), and days to maturity (DM), were scored. PH was recorded just before harvest. DH and DM were noted in the field. After harvest, SL, SPI, and GNS were determined from five main spikes per line, while SP, TGW, and GWP were determined from five to ten plants. Phenotype differences between the ILs and recurrent parent Laizhou953 were compared by *t*-test. ILs that were less (< Laizhou953) or more than (> Laizhou953) Laizhou953 at the significance level $P < 0.05$ were counted for calculating the ratios (%) of lines less and more than Laizhou953.

Statistical analysis

For the calculation of segment lengths and genome ratios, the half intervals flanking a marker locus were considered to be of the same genotype (Chetelat and Meglic 2000; Korff et al. 2004); in other words, introgressed segments were assumed to extend halfway between the outermost marker for which a given line carried the Am3 allele and the first adjacent marker for which the same line was homozygous for the Laizhou953 allele. For missing marker data, plants were assumed to have the same genotype as that of flanking markers. If flanking markers were not concordant, as would be expected around recombination events, introgressed segments were assumed to extend halfway between the nearest informative markers, as described above. The wheat SSR consensus linkage map (Somers et al. 2004) was used to estimate distances between markers, the length of chromosomes and introgressed segments, and the overall genome size for genome ratio calculations. The markers that were not mapped in the consensus map were not used for the statistical analyses.

Analysis of variance (ANOVA)

Using the package SPSS for Windows, ANOVA-general linear model (GLM) was performed to determine the significances of differences between the genotypes of the lines and between the seasons (environments). Genotype-by-environment (G×E) interactions were also analyzed using ANOVA-GLM (Huang et al. 2004).

One-way ANOVA analysis was used to detect QTLs for nine agronomic traits using the procedure GLM from the SAS software (Pillen and Zacharias 2003). The presence of a QTL near a marker locus was judged to be likely when the significant effect was observed for a single marker/trait combination with $P < 0.01$. The additive effect and the additive percentage were calculated according to the methods of Tanksley et al. (1996). The additive effect was calculated as (AB−AA)/2, the additive percentage of each significant QTL was herein as the additity (AB−AA) divided by the midpoint [(AB + AA)/2] multiplied by 100 = 200 (AB−AA)/(AB + AA), where AA = phenotypic mean for individuals homozygous alleles of Laizhou953 at specified markers, AB = phenotypic means of heterozygous loci.

Results

Polymorphism detection and marker distribution in chromosomes

Ninety-seven of the BC_4F_3 lines were successfully genotyped with SSR markers. In all, 792 wheat SSR markers were used to detect polymorphism between the donor parent Am3 and the recurrent parent Laizhou953. Among them, 610 SSR markers amplified stable products and 205 of them detect polymorphism between the two parents. They accounted for 33.6% of the 610 markers used. Among the 205 polymorphic SSR markers, 166 were mapped in the wheat SSR consensus

linkage map (Somers et al. 2004), with an average of 7.9 markers for each chromosome. Of the remaining markers, 28 were located in different chromosomes but they have not been integrated into the consensus map. A further 11 have not even been located in the wheat chromosomes. The number of markers located in each of the chromosomes was listed in Table 1 and the markers in every chromosome were listed in the supplementary Table 1. Most of the polymorphic markers were detected in homoeologous group 3 with the total number of 35 and least in homoeologous group 4 with the total numbers of 20. Markers on chromosomes 5D, 3B, and 2D were the most while markers on 2B, 4A, 4D, and 6A were the least. Only six polymorphic markers were detected on 4D and three of them have not been mapped in the linkage map. The distance between markers was 15.43 cM in average, but the distribution of the markers in different chromosomes or different chromosome regions were different. Some of the markers were located in the same region with very limited or no recombination events between them. However, distances between some other markers are huge. For example, the distance between markers Xgwm499 and Barc59 on chromosome 5B was 79 cM.

Number, size, and position of introgressed segments

Of the 97 lines analyzed in this study, Am3 segments were not detected in 15 (15.5%) of them. The remaining 82 (84.5%) lines contained 162 homozygous and 166 heterozygous segments. Each of the ILs contained 0–9 homozygous and 0–8 heterozygous introgressed segments, with an average of 1.67 homozygous and 1.71 heterozygous segments (Table 1). There were 16 lines with a single introgressed segment and 17 with two segments. The other ILs have three or more introgression segments. Based on the analysis of the 205 polymorphic markers, 106 Am3 alleles were represented in at least one line with the ratio 51.7% of the polymorphic markers.

According to the wheat consensus map, the size of each of the introgressed segments and the ratio they account for the whole donor genome were estimated (Table 1). The introgressed segment ranged from 1.5 to 62.5 cM, with an averaged size of 15.4 cM in homozygous and 12.3 in heterozygous ILs. The donor genome was represented between 0 and 6% in each ILs with an average of 1.31%. In the genotyped ILs, the total length of the introgressed Am3 genome was 965.5 cM, covering 37.7% of the donor genome. The introgressed segment number of 2D was the most with 48 introgressed segments in 30 lines. While the 6A and 4D chromosomes showing the less introgressed segments with only 2 and 0, respectively. Based on the wheat SSR consensus map, the introgressed segments for each of the chromosomes were summarized in Fig. 2.

Trait performance of BC_4F_3

One hundred and forty BC_4F_3 lines were planted to investigate the phenotypes of nine traits. Most of the lines showed tendency to be more similar to the recurrent

Table 1 Transmission of Am3 segments detected in backcross derivatives and cumulative proportion of donor genome represented by homozygous and heterozygous segments

Chr.	Polymorphic markers	Homozygous segments		Heterozygous segments		Maximum chromosome coverage (%)	
		No. of segments	Average length (cM)	No. of segments	Average length (cM)	Homo	Homo + Hetero
1A	9	4(2)	14.5	(5)		23.0	23.0
1B	9	14	16.1	2	2.0	43.2	43.2
1D	9	6(1)	19.9	7(3)	20.6	47.8	59.0
2A	11	5(4)	21.5	13(6)	18.1	32.9	32.9
2B	5	4	17.8	1	15.0	23.4	23.4
2D	12	19(3)	11.9	21(5)	9.9	55.1	59.8
3A	11	8(1)	15.8	8(4)	16.8	35.7	53.0
3B	14	7	16.1	6	6.9	46.9	59.5
3D	10	7	4.2	9	3.7	19.6	19.6
4A	6	1	5.0	7	16.4	22.1	36.4
4B	8	10	3.8	0	0.0	9.3	9.3
4D	6	0	0.0	0	0.0	0.0	0.0
5A	8	9	14.8	10(1)	24.9	50.9	50.9
5B	7	4	27.0	3(1)	44.0	31.2	31.2
5D	16	7(2)	6.2	10(2)	3.6	27.6	27.6
6A	6	2	6.5	0	0.0	4.2	4.2
6B	7	2	5.8	4	15.6	14.0	59.1
6D	9	5	3.5	10(3)	22.1	35.9	35.9
7A	9	3(2)	13.0	0	0.0	9.9	9.9
7B	11	5	10.0	3	9.5	20.7	20.7
7D	11	1	7.0	12(4)	2.0	5.8	5.8
Unlocated	11	(24)	–	(6)	–	–	–
Total	205	123(15 + 24)	15.4	126(34 + 6)	12.3	31.6	37.7

Number in the bracket refers to the unintegrated and the unlocated segments

parent Laizhou953, but variation exists widely for each trait and the phenotype of each trait showed a continuous distribution (figure not shown). The phenotypes of the nine traits of the two parents, means and distribution ranges of the ILs and the ratio of the lines less or more than the recurrent parent significantly were listed in Table 2. The donor parent Am3 is phenotypically inferior to Laizhou953 for most of the traits examined here, and the means of the ILs for all but two (SPI and GNS) of the nine traits were between those of the two parents. However, transgressive segregants were observed for all traits studied. For example, 10.7% of the BC_4F_3 lines outperformed Laizhou953 with respect to SP, 14.3% of the lines had a higher SL, 24.3% and 26.4% of

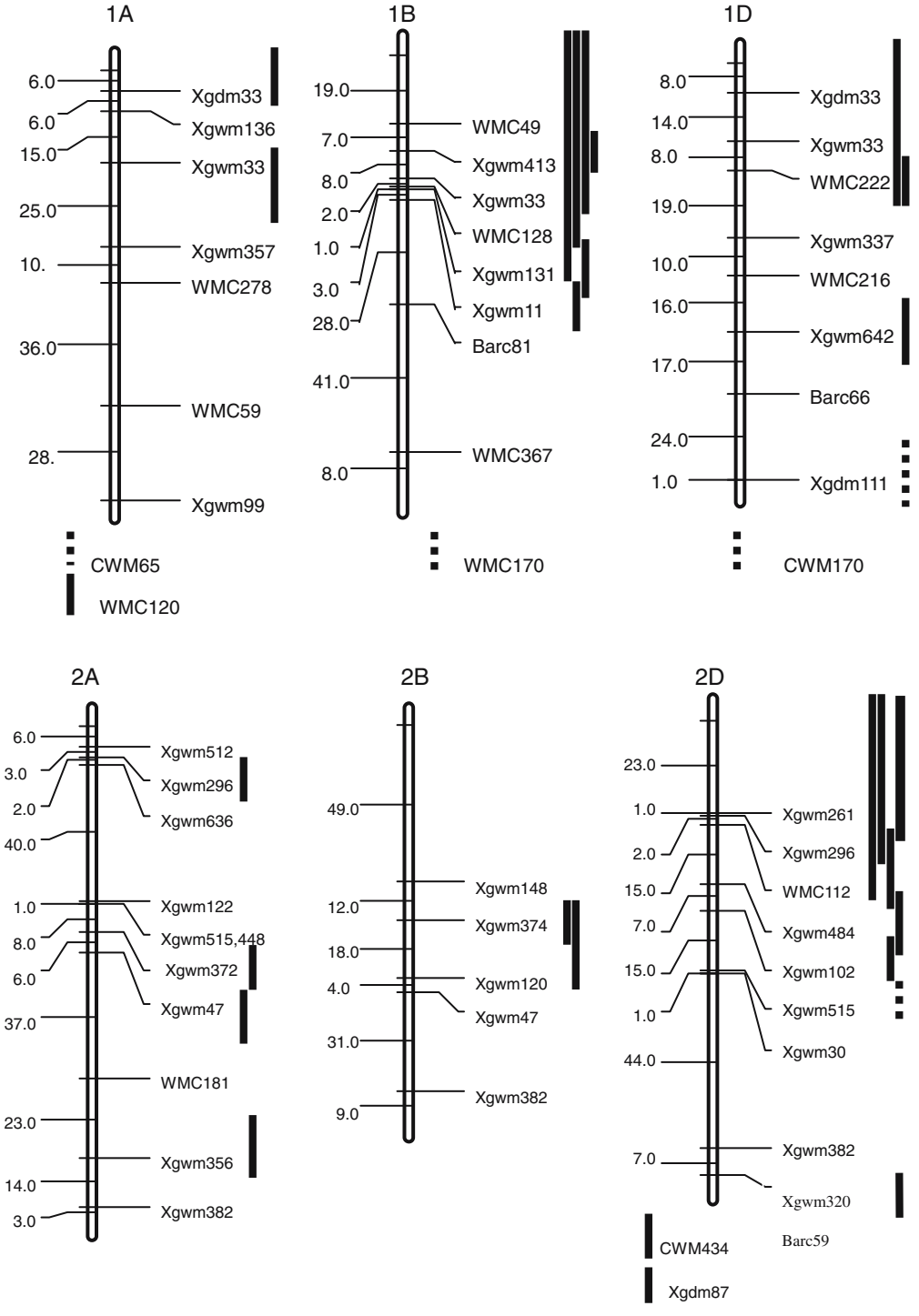
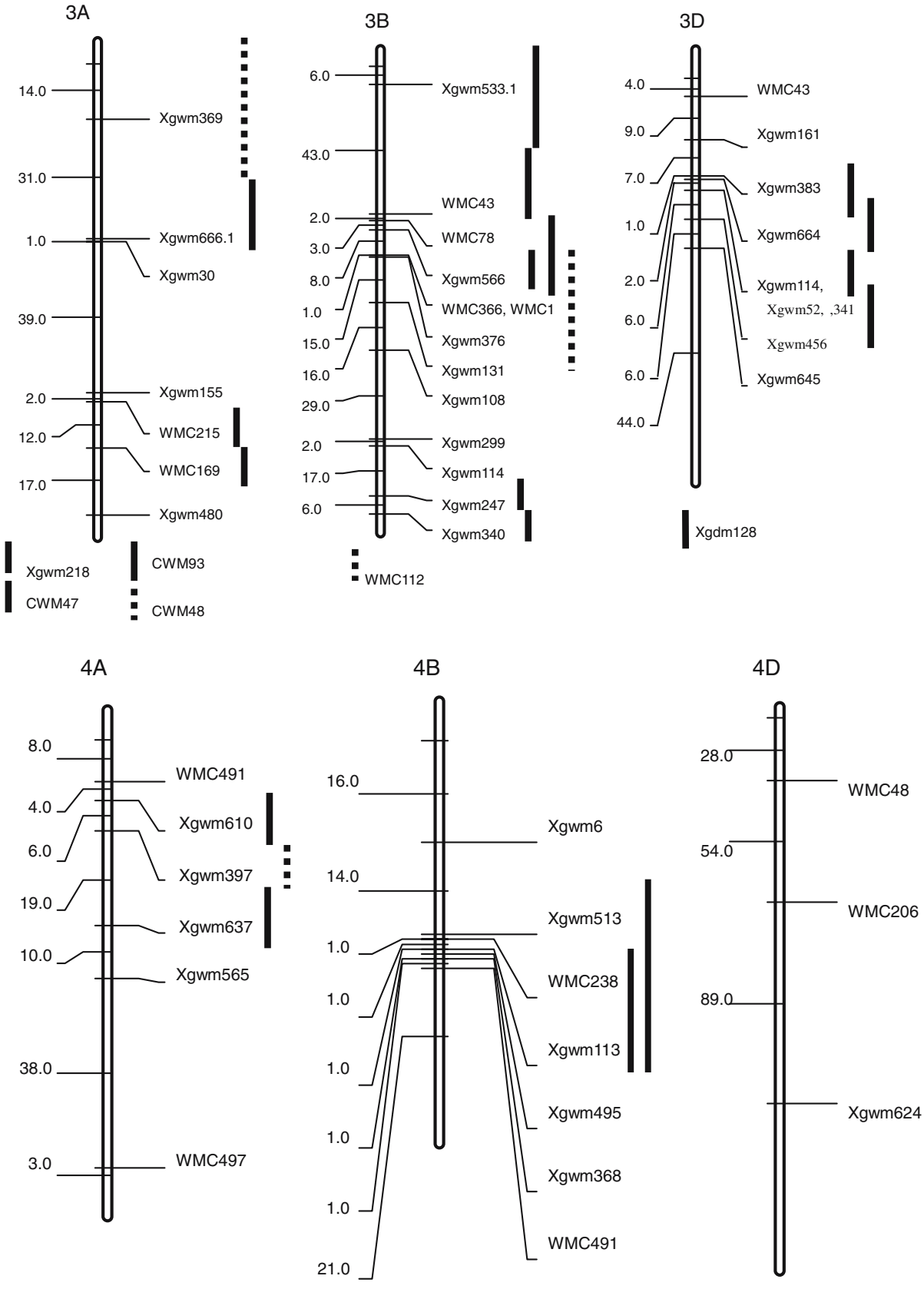


Fig. 2 Map of selected segments introgressed from Am3 into Laizhou953 backcross lines. *Solid bar* represent segments that are homozygous in at least one line, *dot bars* represent segments that have not been fixed (heterozygous). Segments have not been mapped in the consensus map in every chromosome were list below the chromosome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31.0
1.0
Xgwm666.1
Xgwm30
39.0
2.0
Xgwm155
12.0
WMC215
WMC169
17.0
Xgwm480
Xgwm218
CWM47
CWM93
CWM48
3B
6.0
Xgwm533.1
43.0
WMC43
2.0
WMC78
3.0
8.0
Xgwm566
1.0
WMC366, WMC1
15.0
Xgwm376
16.0
Xgwm131
29.0
Xgwm108
2.0
Xgwm299
17.0
Xgwm114
Xgwm247
6.0
Xgwm340
WMC112
3D
4.0
WMC43
9.0
Xgwm161
7.0
Xgwm383
1.0
Xgwm664
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Xgwm565
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3.0
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4B
16.0
Xgwm6
14.0
Xgwm513
1.0
WMC238
1.0
1.0
Xgwm113
1.0
Xgwm495
1.0
Xgwm368
1.0
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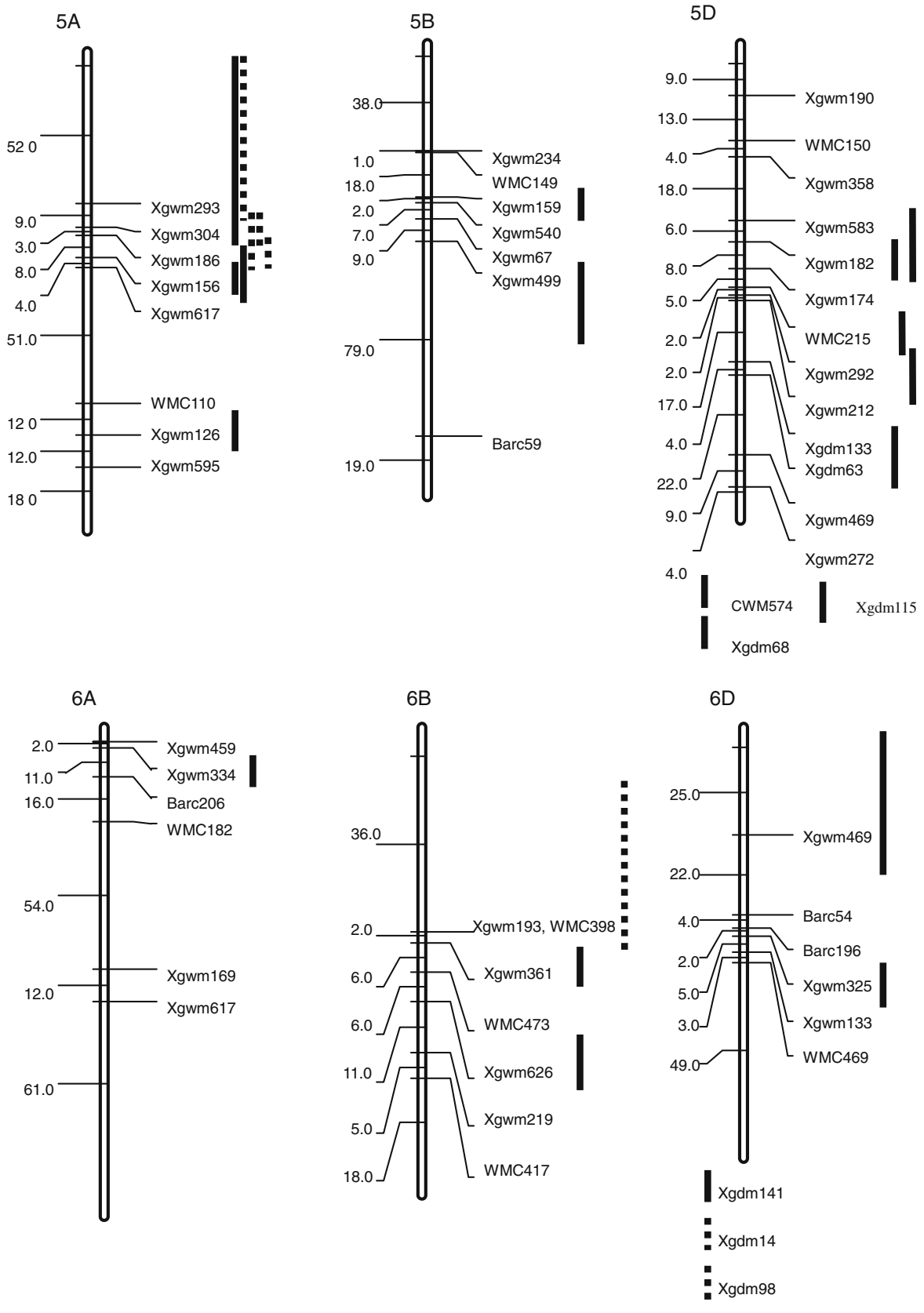
21.0
4D
28.0
WMC48
54.0
WMC206
89.0
Xgwm624

Fig. 2 (Contd.)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Xgwm186
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Xgwm156
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Xgwm617
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WMC110
12 0
Xgwm126
12.0
Xgwm595
18 0
5B
38.0
1.0
Xgwm234
18.0
WMC149
2.0
Xgwm159
7.0
Xgwm540
9.0
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25.0
Xgwm469
22.0
4.0
Barc54
Barc196
2.0
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Fig. 2 (Contd.)

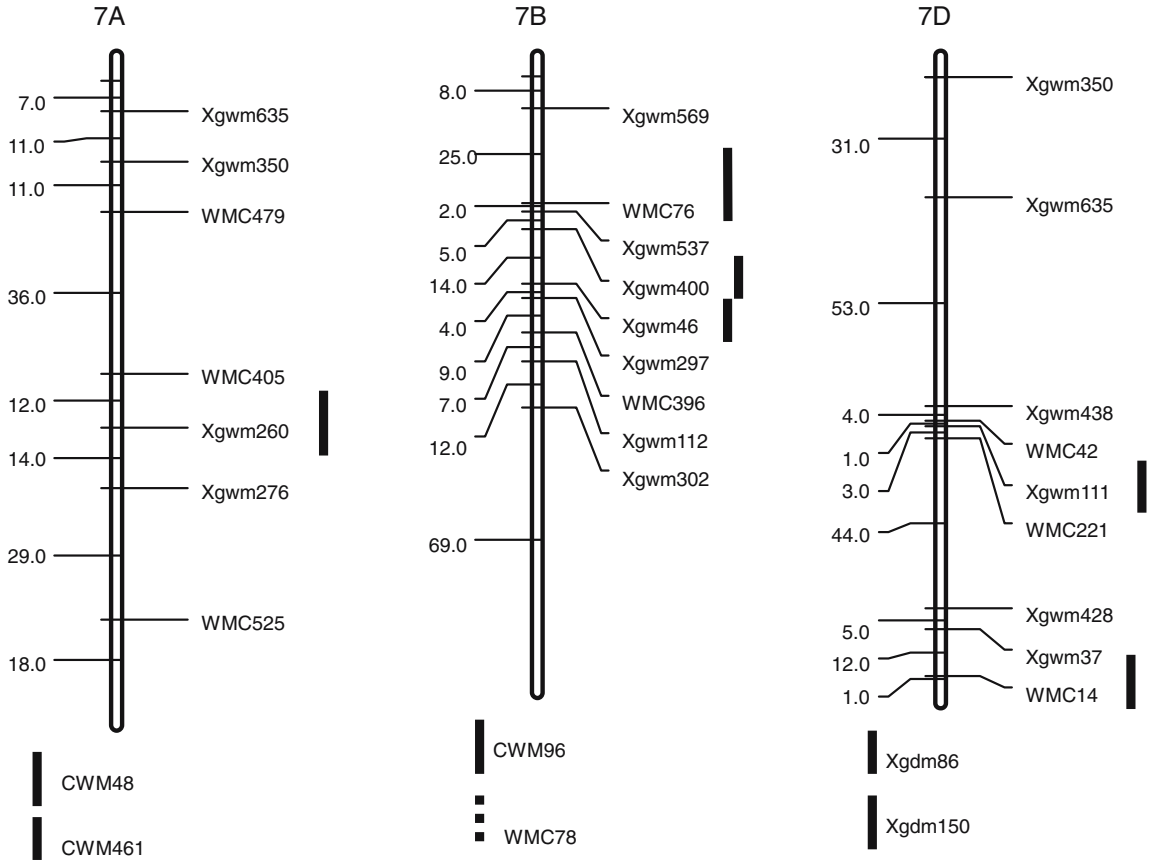

Fig. 2 (Contd.)

the lines had more SPI and GNS, respectively. Fifteen percent and 23.4% of the lines had more TGW and GWP, respectively. Am3 was very late in flowering and maturing; however, 5.0% and 7.1% of BC_4F_3 lines headed and matured earlier than Laizhou953, respectively.

Analysis of variance for genotype, environments and their interactions

The *F*-values of ANOVA for genotypes and environments as well as for their interactions were listed in Table 3. Significant differences between genotypes were found for all nine traits investigated. The *F*-value ranged from 13.45 ($P < 0.05$) for SP to 85.65 ($P < 0.01$) for PH. The environment had a large influence on all nine traits. DH is the most significantly influenced trait ($P < 0.0001$) by environment while SPI, GNS and GWP are the least ($P < 0.05$). Significant G×E interaction was observed for DM ($P < 0.05$), but there were no significant interaction between other genotypes and environment.

Quantitative trait loci detection

One-way ANOVA analysis was used to detect QTLs for the nine agronomic traits. It should be noted that QTL effects simultaneously detected at two or more adjacent marker loci by ANOVA were presumably due to the existence of a single, linked genetic factor located in one introgressed segment which exerts the QTL effects. So, they were looked as one locus in the records. According to the agronomic traits of the 82 ILs in three seasons planted in Beijing, 38, 33, 28 (seven traits) QTL loci were detected in 2003, 2004, and 2005, respectively (Table 4).

Plant height

Three putative QTLs for PH were detected in three seasons, respectively. Two loci [Xgwm664 (3D) and Xgwm113 (4B)] were detected in all three seasons which showed they were stable QTLs. In addition, other QTL located in 2D (Xgwm515), 5A (Xgwm293) and one unlocated locus (Barc1039) were also detected in 2003, 2004, and 2005, respectively. All of the additive effects of the detected loci were positive which showed they can increase PH after introgressed from Am3 into Laizhou953.

Spikes per plant

Three, four, and four putative QTLs for SP were detected in three seasons. One locus, Xgwm113 (4B), was detected in three seasons. Xgwm664 (3D) was detected in two

Table 2 Nine agronomic traits measured from the two parents and the introgression lines

Traits	Parents		Introgression lines		Ratio of lines less and more than Laizhou953 (%)	
	Laizhou953	Am3	Means	Distribution range	< Laizhou953	> Laizhou953
PH(cm)	81.3	139	90.4	69.4–137	13.6	31.4
SP	3.3	4.6	3.8	1.4–7.8	11.4	10.7
SL (cm)	8.7	12.7	9.0	7.2–11.5	9.3	14.3
SPI	19.3	20	20.7	18.1–25.2	3.6	24.3
GNS	39.6	38.0	41.0	33.4–55.2	4.3	26.4
TGW (g)	46.9	41.1	45.2	32.6–60.5	14.3	15.0
GWP (g)	6.1	6.9	6.8	3.2–9.7	11.4	23.4
DH (days)	207	220	215	204–225	5.0	38.6
DM (days)	254	259	257	249–263	7.1	36.4

Significant level $P < 0.05$

Table 3 *F* values of ANOVA-GLM for genotype and environment as well as their interaction in the introgression lines of the cross Laizhou953/Am3

Item	Genotype (G)		Environment (E)		G × E interaction	
	df	*F*	*df*	*F*	*df*	*F*
PH (cm)	96	85.65**	2	30.28**	192	1.32 NS
SP	96	13.45*	2	27.39**	192	1.17 NS
SL (cm)	96	35.90**	2	54.50**	192	2.73 NS
SPI	96	13.85*	2	14.19*	192	0.53 NS
GNS	96	17.40*	2	14.82*	192	0.62 NS
TGW (g)	96	27.05**	1	217.30**	96	7.56 NS
GWP (g)	96	19.10*	1	11.00*	96	9.86 NS
DH	96	37.05**	2	471.70****	192	1.99 NS
DM	96	30.57**	2	102.11**	192	11.50*

NS Not significant
Significant at *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and ****$P < 0.0001$, respectively

seasons (2004 and 2005). The other loci were all detected only in one season. Except Xgwm334 detected in 2004, the additive effects of the other detected loci were all positive which showed they can increase SP after introgressed from Am3 into Laizhou953.

Spike length

Four, three, and three putative QTLs for SL were detected in the three seasons, respectively. Among them, Xgwm320 (2D) was detected in 2003 and 2004, Xgwm113 (4B) was detected in 2004 and 2005. Xgwm304 (5A) and WMC215 (5D) were detected in 2003 and 2005. Additive effect of Xgwm113 was negative which indicated it decrease SL after introgressed into Laizhou953 from Am3. Additive effects of other loci were all positive and they can increase SL after introgressed into Laizhou953.

Spikelets

Four putative QTLs for SPI were detected for each of the three seasons, Two of these, Xgwm159 (5B) and Xgdm68 (5D), were detected in 2004 and 2005. The other loci were all detected in a single season only. Among the loci detected in 2003, there was one locus Xgwm182 showed negative additive effects, the others were positive. Of the four loci detected in 2004, three showed negative additive effects and the other (Xgwm642) positive. All the loci detected in 2005 showed negative effects.

Grain number per spike

Three, four, and four putative QTLs for GNS were detected in the three seasons, respectively. Of these, only Xgdm68 (5D) was detected in two seasons (2004 and 2005). Additive effects of the loci detected in 2003 were all positive. Three of the four loci detected in 2004 showed negative additive effects and only one locus Xgwm642 showed positive additive effect. Additive effects of the loci detected in 2005 were all negative.

Thousand grain weight

Only two seasons of data for TGW were obtained. Five and three putative QTLs for TGW were detected in 2003 and 2004, respectively. Of these, only one, Xgwm159 (5B), was detected in both seasons. Additive effects of the locus were positive in both seasons. The other loci were all detected in a single season. Additive effects of

the remaining loci detected in 2003 were all negative while they were positive of the remaining two loci detected in 2004.

Grain weight per plant

Only two seasons of data for GWP were obtained, with three and two putative QTLs detected, respectively. None of these QTLs were detected in more than one season. The additive effects of the detected loci were all positive.

Days to heading

Nine, six, and five putative QTLs for DH were detected in 2003, 2004, and 2005, respectively. Xgwm642 (1D) was detected in all three seasons. Xgwm159 (5B) and R-15 (unlocated) were detected in 2003 and 2004. The others were all detected in a single season. Additive effects of Xgwm642 were positive. Xgwm159 (5B) and R-15 showed negative additive effects in two seasons.

Days to maturity

Four, four, and five putative QTLs for DM were detected in the three seasons respectively. Xgwm642 (1D) was detected in all three seasons. WMC112 (2D) and Xgdm68 (5D) were detected in 2003 and 2005. Xgwm159 (5B) was detected in 2004 and 2005. Additive effects of Xgwm642 and WMC112 were positive while they were negative for Xgwm159 and Xgdm68.

There were several loci that can affect more than one trait. One of these was Xgwm113, which affected PH, SP, and SL and was detected repeatedly in three or two seasons. Introgression of the locus could increase PH and SP but decrease SL. It was uncertain if the variations were caused by one QTL or by other loci located in the same introgressed segment which can be dissected by selecting a series of ILs containing smaller segment at the locus. Xgwm159 affected SPI, TGW, DH, and DM simultaneously. Xgwm642 was detected to affect DH and DM in all three seasons. The introgressed Am3 Xgwm642 locus seemed to be a major QTL delaying heading and maturity dates. There were other loci that could affect more than one trait such as Xgdm68 which showed negative effect for SPI, GNS, and DM, but positive effect for DH.

Discussion

A set of wheat ILs were developed by backcrossing and SSR genotyping. The phenotypes of these lines were examined in three seasons, which provide a great opportunity for the fine mapping, MAS and gene cloning of agronomic important traits in wheat. Those ILs conferring favorable genes can be used to cross with the donor parent Laizhou953 to construct secondary segregation populations which could be used to further define the markers linked to the traits, to fine map the genes controlling the traits so as to clone the gene by map-based cloning. We can also use the markers to pyramid or transfer useful genes in breeding programs.

Introgression lines have been developed for various crops such as tomato, lettuce, barley and *B. oleracea* and the most outstanding work was done in tomato. During the process of developing ILs, molecular MAS can accelerate the process. In most cases, MAS was conducted from the early backcross generation (Eshed and Zamir 1994a; Ramsay et al. 1996; Howell et al. 1996). In wheat, there is still no report about the development of ILs. In order to develop wheat ILs, we used an artificial synthesized hexaploid wheat as donor parent and an elite wheat cultivar as recurrent parent. In order to decrease the workload of marker detection, we delayed MAS selection until the late backcross generations (BC_4F_3). The results showed that, of the 97 lines identified, there were 82 lines (84.5%) carried donor's segment(s). Donor's segments were not detected from the remaining 15 plants. This could be due to the fact that only 205 markers were used which do not cover the whole genome. This result proved that marker detection at the end of the process of the IL development may be also efficient.

Of the 205 polymorphic markers used, more than 50% of them appeared in the 97 BC_4F_3 ILs. The introgressed segments covered 37.7% of the donor parent. The low introgression ratio of the donor genome may be caused by two reasons. The first one could be that the population we genotyped was small. Only 97 BC_4F_3 plants were random selected and none of them showed the same genotype. This means that if more plants were screened, more distinct ILs could be found. The second reason could be due to the limited number of markers used and their uneven distributions across chromosomes. Only 205 polymorphic markers, with an average of 9.76 per chromosome, were used. In some parts of the chromosomes, the polymorphic markers distributed unevenly. Some markers were clustered in a small region, while no marker was found in some other regions. These could prevent the detections of some introgressed segments. The introgressed donor genome was 1.31% in the ILs, which is lower than the theoretical value after backcrossing for four generations. This may also reflect the fact that the introgressed donor genetic materials were not detected completely. We will complete the construction of whole genome IL by screening more BC_4F_3 plants and by using more molecular markers.

The agronomic traits of the donor parent Am3 were inferior to the recurrent parent Laizhou953. An early study by Frey et al. (1983) in cereals showed that, despite their overall inferior agronomic performance, wild and weedy species are likely to contain genetic factors that can increase the yield of modern varieties. Tanksley et al. (1996) demonstrated that molecular genetic maps can be

Table 4 Putative QTLs detected in three seasons using the ILs

Traits	Markers in 2003	Chr.	Pro.	Additive effect	Additive effect (%)	Markers in 2004	Chr.	Pro.	Additive effect	Additive effect (%)	Markers in 2005	Chr.	Pro.	Additive effect	Additive effect (%)
PH	Xgwm515	2D	0.002	11.3	13.5	Xgwm664	3D	0.003	15.1	18.1	Xgwm664	3D	0	19.4	23.2
	Xgwm664	3D	0.004	10.9	13.0	Xgwm113	4B	0	16.4	19.4	Xgwm113	4B	0	14.4	17.1
	Xgwm113	4B	0.002	10.8	13.0	Xgwm293	5A	0.001	14.9	17.9	Barc1039	?	0.003	13.8	16.4
SP	Xgwm102	2D	0	0.54	10.0	Xgwm664	3D	0	0.96	26.6	Xgwm664	3D	0.001	1.92	20.8
	Xgwm113	4B	0.001	1.18	23.0	Xgwm113	4B	0.65	0.65	18.0	Xgwm113	4B	0.001	0.69	14.7
	Xgwm469	6D	0	0.52	10.0	Xgwm334	6A	0.008	−0.72	18.4	Xgwm293	5A	0.002	1.02	21.7
						CWM639	?	0.01	0.74	21.2	Xgdm115	5D	0.003	0.74	14.8
SL	Xgwm515	2D	0.01	1.23	13.4	Xgwm372	2A	0.007	0.66	7.0	Xgwm113	4B	0.002	−0.35	−3.8
	Xgwm320	2D	0.002	1.21	13.0	Xgwm320	2D	0.1	0.33	3.4	Xgwm304	5A	0.003	0.67	7.3
	Xgwm304	5A	0.004	1.44	15.2	Xgwm113	4B	0.003	−0.37	−4.2	WMC215	5D	0.01	0.67	7.3
	WMC215	5D	0.004	1.27	13.8										
SPI	CWM170	1D	0.01	0.4	2.1	Xgwm642	1D	0.01	1.8	9.3	Xgwm664	3D	0.01	−1.3	−6.7
	Xgwm515	2D	0.004	1.6	8.2	Xgwm383	3D	0.002	−1.7	8.8	Xgwm293	5A	0.001	−0.8	−4.1
	Xgwm182	5D	0.01	−0.5	−2.6	Xgwm159	5B	0.001	−1.1	5.4	Xgwm159	5B	0.01	−1.3	−6.7
	WMC215	5D	0.005	1.5	7.8	Xgdm68	5D	0.001	−1.2	−6.2	Xgdm68	5D	0.01	−1.4	−7.2
GNS	Xgwm186	5A	0.01	5.0	10.8	Xgwm642	1D	0.01	5.8	14.8	Xgwm113	4B	0	−2.6	−6.1
	CWM574	5D	0.01	4.6	10.0	Xgdm33	1D	0.01	−1.3	−3.2	Xgwm293	5A	0.007	−2.8	−6.6
	Xgwm292	5D	0.001	4.3	9.2	CWM434	2D	0.01	−2.1	−2.8	Xgwm159	5B	0.01	−4.4	−10.4
						Xgdm68	5D	0	−1.2	−6.2	Xgdm68	5D	0.001	−2.1	−4.8
TGW	CWM170	1D	0.005	−4.9	−11.8	Xgwm372	2A	0.006	5.4	11.7					
	Xgwm376	3B	0.005	−8.5	−20.0	Xgwm159	5B	0.01	6.3	13.5					
	Xgwm397	4A	0.002	−6.8	−16.1	R−15	?	0.01	4.8	10.5					
	Xgwm159	5B	0.002	6.1	14.5										
	Xgwm111	7D	0.01	−4.6	−11.1										
GWP	Xgwm293	5A	0.002	0.46	4.9	Xgwm664	3D	0.003	1.26	25.9					
	Xgdm115	5D	0	1.39	14.9	Xgdm14	6D	0.06	0.26	5.5					
	Xgwm260	7A	0.007	1.29	13.9										
DH	Xgwm131	1B	0.003	2.4	1.1	Xgwm642	1D	0.003	9.5	4.6	Xgwm413	1B	0.006	2.8	1.3
	Xgdm33	1D	0.006	−0.7	−0.3	Xgwm515	2D	0.003	7.3	3.5	Xgwm642	1D	0.002	3.0	1.4
	Xgwm642	1D	0.003	3.0	1.4	Xgwm126	5A	0.002	6.8	3.3	WMC112	2D	0.003	1.8	0.8
	WMC169	3A	0	3.0	1.4	Xgwm159	5B	0.001	−0.5	−0.2	Xgwm484	2D	0.005	2.0	0.9
	WMC78	3B	0.003	2.1	1.0	Xgdm68	5D	0.004	5.0	2.4	WMC421	?	0.001	2.1	1.0
	Xgwm159	5B	0.001	−2.0	−0.9	R−15	?	0.003	−1.7	−0.8					
	Xgdm115	5D	0.002	−1.3	−0.6										
	R−15	?	0	−2.0	−0.9										
	Barc51	?	0.008	2.8	1.3										
DM	Xgwm642	1D	0.01	3.5	1.4	Xgwm642	1D	0.006	4.3	1.7	Xgwm642	1D	0.003	1.8	0.7
	WMC112	2D	0.01	0.9	0.3	Xgwm383	3D	0.01	−2.0	−0.8	WMC112	2D	0.004	0.9	0.3
	Xgdm63	5D	0.004	5.0	2.0	Xgwm159	5B	0.005	−2.5	−1.0	Xgwm159	5B	0.002	−2.2	−0.9
	Xgdm68	5D	0.01	−1.0	−0.4	Xgdm115	5D	0.01	−0.6	−0.3	Xgdm68	5D	0.002	−2.2	−0.9
											R-15	?	0.002	−2.2	−0.9

used to efficiently exploit the genetic potential of wild species for the improvement of yield and quality in elite processing tomatoes. Using advanced backcross QTL analysis (Tanksley and Nelson 1996), valuable QTL were simultaneously discovered and transferred from wild and unadapted germplasm into elite breeding lines. Xiao et al. (1998) and Moncada et al. (2001) showed that the rice wild QTLs can improve the agronomy traits of cultivars. Gur and Zamir (2004) demonstrated that unused natural variation from wild species of tomato can lift yield barriers. In our study, the agronomic traits of the ILs also showed obvious variation. Although most of the ILs were similar to the recurrent parent, some of them showed variation in one or several traits. For every trait, there are ILs showing better performance than the recurrent parent (Table 2). QTL analysis confirmed that favorable QTL for agronomic traits have been transferred to common wheat Laizhou953 from exotic line Am3 (Table 4). For example, a QTL in the region Xgwm113 of Am3 can increase 0.65–1.18 SP detected in three seasons; a QTL in the region Xgwm159 of Am3 can increase 6.1–6.3 g for TGW in the all detected two seasons. These results suggest that genes introgressed from Am3 can improve agronomic important traits of an elite wheat variety, even though Am3 itself is phenotypically inferior to the cultivated variety. These lines contained the favorable alleles for wheat improvement and can be pyramided or transferred into wheat cultivars to breed better varieties.

There were many studies about QTL detection in wheat (Börner et al. 2002; Hanocq et al. 2004; Huang et al. 2003, 2004; Quarrie et al. 2005). In some of them, SSR linkage maps were also used. Some of the markers used in our study were the same as those used by others. Thus we can compare their results with ours directly. The QTL detected near Xgwm113 for PH in our study was near the region of Xgwm149 and Xgwm1167a (detected by Huang et al. 2003, 2004) and Xgwm165.1 (detected by Quarrie et al. 2005), respectively. Considering that the *Rht-B1* locus was in the same region, the locus might be *Rht-B1*. This QTL also affected SP in our study, which was coincident with the result of Quarrie et al. (2005). Another QTL detected by Xgwm293 in 2004 for PH in our study was near Xgwm304 detected by Huang et al. (2004). The QTL detected by Xgwm664 in 2004 and 2005 for SP in our study was near the marker range Xbarc042–Xgwm383 detected by Quarrie et al. (2005). The QTL detected by Xgwm292 for GNS in 2003 in our study was near the marker range Xgwm212 which was also detected by Quarrie et al. (2005). The probable QTL near Xgwm484 for DH detected in our study in 2005 was also detected by Huang et al. (2003) and Hanocq et al. (2004). It is of note that the *Ppd-D1* gene was also located in the same region (Hanocq et al. 2004). Another locus for DH, Xgwm515 detected in 2004, was also located in this region. Several other QTLs for DH detected in our study seemed also co-locate with those detected by others. For example, WMC169 (detected in 2003) was located near the QTL detected by Xgwm751 (Huang et al. 2004), Xgwm126 (detected in 2004) and WMC 112 (detected in 2005) were located near the QTL detected by Xgwm271b and Xgwm261 detected by Hanocq et al. (2004). The QTL detected by Xgwm642 in 2004 for GNS was located near the region of Xgwm1012 detected by Huang et al. (2004). The QTL detected by Xgwm159 in 2003 and 2004 for TGW was located near the QTL detected by Xgwm544 detected by Huang et al. (2003), and that Xgwm372 (detected in 2004) was the same as detected by Huang et al. (2004). Xgwm376 and Xgwm111 (detected in 2003) were located near the regions of Xgwm685 and Xgwm1220 detected by Huang et al. (2004). Results in our own lab using wheat SSR linkage map to detect QTLs support our results in this study. For example, Song et al. (personal communication, 2005) detected one QTL for DH located on chromosome 2D in the region of WMC144-Xgwm157. This locus was located near the QTL locus detected by Xgwm515 in 2004 in this study. Another locus detected in 5B in the region of Xgwm371–Xgwm335 for DH was located near Xgwm159 which was detected in our study in 2003 and 2004. This locus was located near the WMC73 locus affecting flowering time detected by Toth et al. (2003), and the detected locus was probably the *Eps* gene. There were other detected QTLs which were the same or located in similar regions detected by Song et al. These included Xgwm304 detected in 2003 and 2005 for SL; and Xgwm292 detected in 2003 for GNS; two other QTLs for TGW detected in 2003, Xgwm376 (3B) and Xgwm397 (4A) which located in the same region of Xgwm285 (3B) and Xgwm610 (4A) as detected by Song et al. However, because the confidential regions commonly span more than 10 cM (Alpert and Tanksley 1996). Thus it was difficult to know if the detected QTL was a major QTL with larger effect or several genes with smaller effects were contained. It was also difficult to dissect QTL into Mendelian factors. The ILs developed in this study containing QTL laid a foundation to test the veracity of the putative QTLs and fine mapping of the detected QTLs.

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