Distribution in genome of Quantitative trait loci (QTL) for yield and yield-related traits in common wheat (Triticum aestivum L.)

L.Y. Zhang¹, D.C. Liu¹, X.L. Guo², W.L. Yang¹, J.Z. Sun¹,
Daowen Wang¹, Aimin Zhang¹*

1. The State Key Laboratory of Plant Cell and Chromosome Engineering, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, P.R. China

2. Biological College, China Agricultural University, Beijing 100193, P.R. China

* Correspondent author:
Aimin Zhang, Ph.D.

Phone: +86-10-64852926

amzhang@genetics.ac.cn

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Abstract: A major objective of quantitative trait loci (QTL) studies is to find genes/markers that can be used in breeding programs via marker assisted selection (MAS). From an extensive review, we surveyed the distribution of QTL for yield and yield-related traits on wheat genome. In order to identify the important regions involving in these traits, QTL meta-analysis was performed. As a result, 55 MQTL were identified for these trait, of which 12 significant MQTL were located wheat chromosomes 1A, 1B, 2A, 2D, 3B, 4A, 4B, 4D and 5A. Our study showed the genetic control of yield and its components also involved the important genes such as the Rht and Vrn. Furthermore, several significant MQTL were found in the orthologous region corresponding to some important rice genes underlying QTL for yield related traits. Those results demonstrated that QTL meta-analysis was a potential tool for refining QTL position and could improve the MAS efficiency for wheat grain yield improvement in breeding program.

Keywords: Common wheat; Quantitative Trait Loci (QTL); Yield; Yield-related traits; Meta-analysis
**Introduction**

Bread wheat (*Triticum aestivum* L.) is an allohexaploid species with its extremely huge genome (2n = 6x = 42, approx. 16,000 Mbp). As one of the three most important economic cereals, it is widely cultivated around the world, thus development of high yield cultivar with good end-use quality is paramount in wheat breeding. It is well known that grain yield is manifested via a complex relationship among the yield component traits such as 1000-grains weight (TGW), grains per spike (GPS), grain weight per spike (GWS), and fertile tiller number per plant etc. Genetically, wheat yield or yield components are controlled by numerous genes with additive, additive × additive (epistasis) effects and genotype by environment interactions. Therefore grain yield is perhaps the most commonly studied but poorly understood trait related to agronomic performance of wheat. In addition, plant height (PHT) also plays an important role for grain yield. The height-reducing alleles influence grain yield in wheat by reducing the internal competition for assimilate supply between the developing ear and the stem during the period of stem elongation prior to flowering.

Due to polygenic nature, grain yield and its related traits are usually shows a low heritability. Therefore, it is of utmost interest to obtain more information about QTL (Quantitative Trait Loci) governing those traits. In the past decade, with the availability of high-density linkage maps and the development of QTL methodologies, significant advances have been made in the field of genetic dissection of yield and yield related traits in bread wheat, thus, this greatly increases our knowledge of factors related to yield improvement. However, QTL mapping experiments yield various results due to the use of different genotypes, environments and sampling variation, it would be necessary to know whether QTL identified for a given trait in one population correspond to those detected in other populations in application.

In order to verify the presume that some QTL detected in independent experiments and located in a same region of a chromosome is likely to be in fact several estimations of the position of one single QTL, Goffinet and Gerber (2000) proposed QTL meta-analysis to combine results from independent published QTL studies. This method allows to indicate the most likely number of ‘real’ QTL underlying a pool of QTL of independent experiments, and to provide consensus positions for these QTL, and therefore facilitates the identification of relevant positional candidate
genes. Until now, Meta-analysis combining up to hundreds of QTL from different populations has been successfully used in rice (Ballini et al. 2008; Norton et al. 2008), maize (Chardon et al. 2004; Wang et al. 2006), cotton (Rong et al. 2007), Brassica napus (Shi et al. 2009), and apricot (Marandel et al. 2009). In bread wheat Meta-QTL analysis resulted in an increased precision in QTL position estimation for ear emergence (Hanocq et al. 2007; Griffiths et al. 2009; Löffler et al. 2009) and for resistance against Fusarium head blight (Hanocq et al. 2007; Haberle et al. 2009; Löffler et al. 2009).

In this paper, for the first time QTL meta-analysis for yield and its related traits in hexaploid wheat was performed with the objectives (1) to review the QTL mapping for yield and yield-related traits during the past decade; (2) to investigate their distribution on the wheat genome; (3) to identify stable QTL and to determine reliable markers that can be implemented in the case of marker-assisted selection (MAS) programs, through meta-analysis; (4) to discuss pleiotropic or linkage effects for the major QTL clusters.

**MATERIALS AND METHODS**

**Bibliographic collection of QTL mapping:**

About sixty published studies were found to present QTL for yield, yield component and related traits: yield (YLD), thousand-grain weight (TGW), grains number per spike (GPS), grain weight per spike (GWS), spikelet per spike (SPS) and plant height (PHT). Only 37 provided sufficient information on mapping and QTL characteristics to carry out map projections and QTL meta-analysis. For each QTL study, we reported in Appendix I the names of the parental lines used and the size and type of mapping populations.

**Map projection**

The projection of original genetic maps onto a reference map is a means of comparing the QTL detected using different populations. In order to obtain reliable projection of QTL, we therefore integrated two highly saturated wheat maps as the reference map: the most recent Somers’ consensus SSR map (Somers et al. 2004) and the wheat composite 2004 map serving as template, comprising 1,235 and 4,506 markers, respectively (http://wheat.pw.usda.gov). All calculations for creation of the reference map were performed with the Biomercator software (ARCADE et al.
2004) applying a weighted least square strategy for marker ordering and determining their position on the consensus map.

QTL projection and Meta-analysis
QTL were projected onto the reference map using the BioMercator software. First, the initial QTL and reference maps were linked through their common markers, which were then used to assess a homothetic function. This function enables computation of the most likely position and the confidence interval (CI) of the projected QTL on the reference map. To address possible heterogeneity in definition of CI across studies, whenever possible, initial QTL CI values were replaced by a 95% CI, estimated using the approach described by Darvasi and Soller (1997): 
\[CI = \frac{530}{N\times R^2}\]
where N is the size of the population and \(R^2\) the proportion of variance explained by the QTL. This approach enabled the calculation of a CI when one was not published, and to assess the CI using the same method for each QTL and study.

In the case of Meta-QTL analysis, these consensus QTL obtained from the meta-analysis were referred to as meta-QTL (MQTL). For n individual QTL the BioMercator software tests the most likely assumption between 1, 2, 3, 4 and n underlying QTL. Decision rules are based on an Akaike-type criterion (AIC) and the one with the lowest AIC value was considered the best fit. When the n-model was the most likely model, the meta-analysis was performed again, but on subsets of the QTL. These subsets were considered on the basis of the “progressive” clustering of individual QTL from the 4-model to the 1-model.

Review of yield and yield related QTL mapping in Literatures
On the whole, fifty-nine publications were collected which present QTL mapping for grain yield and major agronomic yield-related traits in wheat (Appendix I). A total of 541 QTL were reported for YLD, GWS, GPS, SPS, TGW and PHT, which unevenly distributed on the whole genome. The mostly reported QTL were for grain yield (33%); followed by TGW (21%) and PHT (16%). Regarding QTL distribution on the wheat three genomes, the most QTL (41%) were mapped on genome A, while almost the same QTL on genome B and D (~30%). Except for the most QTL for plant height on genome B, QTL for all traits were the most common on genome A (Figure 1).

Though QTL were reported on all seven homologue groups, significant difference was observed.
QTL on homologue group 2 were the most abundant representing about 21%, and following by group 4 and 3 representing 18% and 16% respectively. The least QTL were identified on the homologue group 6, accounting for 8.7% only. When considering QTL for individual trait, homologue group 2 harbored the most amounts of QTL for GPS, GWS, TGW and SPS. Not surprising, the most PHT QTL were identified on homologue group 4 owing to possessing two Rht genes on this group. Moreover, QTL for grain yield and SPS on group 4 also were most amounts. Regarding each chromosome, QTL for all six traits were the most amounts on chromosome 5A with the number of 43, followed by those on chromosome 3B and 2D with the number of 41. The least common (10) was found on chromosome 6B (Figure 2).

Table 1, Figure 1 and Figure 2

Grain yield (YLD)

Grain yield is the most commonly agronomic trait studied in QTL analysis. One hundred seventy-eight QTL controlling grain yield were identified in 23 literatures. Those QTL were unrandomly distributed around the genome, the most amount of QTL for grain yield was reported on chromosome 4AL (17), and followed by 3B and 2B, accounting respectively for 15 and 14 QTL (Table 1).

Several yield QTL mapping have performed in ITMI population (W7984×Opata85), and three significance regions on chromosome 2DS, 4AL and 4DL were identified (Ayala et al. 2002; Borner 2002; Kulwal et al. 2003; Kumar et al. 2007). Börner et al. (2002) identified QTL controlling GPS, GWS, PHT, ear length, ear emergence time, and waxiness on 4AL in the ITMI population. According to Kumar’ study (2007), a solitary QTL on 4AL was detected in both the populations (PopWL711 x PH132) and ITMI. A QTL consistently detected for several traits (including yield) on 2DS over environments (Ayala et al. 2002). In other studies, similarly using ITMI population, this region on 2DS was also found associated with growth traits (Kulwal et al. 2003), quality traits (grain protein content and pre-harvest sprouting tolerance (Kulwal et al. 2005), and 11 of the 20 agronomic traits (Borner et al. 2002). The major QTL discovered on chromosome arm 2DS were considered to be most probably caused by pleiotropy of Ppd-D1 (photoperiod-response gene), known to affect yield (Borner et al. 1993; Foulkes et al. 2004).

Advanced backcross (AB) QTL analysis has been successfully applied in detecting and
transferring yield QTL from unadapted germplasm into elite breeding lines for common wheat (Huang et al. 2003, 2004; Narasimhamoorthy et al. 2006). About ten QTL were detected for total yield on chromosomes 1A, 1B, 2A, 2B, 2D, 3B, 3D, 4D, 5A, 5B, 6B and 6D (Huang et al. 2003, 2004). Because the two synthetic wheat lines might have very different genetic backgrounds, only one QTL of them was potentially orthologous between the two synthetic wheat lines. Narasimhamoorthy et al. (2006) also used AB-QTL method to identify two putative QTL for yield on 2DS and 7DL, of which, the QTL on 2DS was co-located with that reported by Huang et al. (2003). These studies confirmed that AB-QTL analysis provided a possibility to use wild, unadapted relatives of crops for the improvement of cultivated varieties.

As a whole, five studies detected QTL for grain yield on long arm of chromosome 4A (Groos et al. 2003; Kuchel et al. 2007a,b; McCartney et al. 2005; Zhang et al. 2009a). Similarly, several significant regions were found to be associated with yield on chromosome 3BS (Ayala et al. 2002; Huang et al. 2003; Maccaferri et al. 2008; Marza et al. 2006).

1000-grains weight (TGW)

Among the yield components, TGW was the most heritability due to least effect of environment. In our survey, a total of 36 literatures reported 116 QTL controlling this trait, and unevenly distributed on the whole genome. Chromosome 3B harbored the most TGW QTL (11).

Significant QTL governing kernel weight were observed on chromosomes 1DS, 2DL and 6BL (Ammiraju et al. 2001), 1A, 1B, 3B and 7A in population NY18×Clark’s Cream (Campbell et al. 2001), 6BL in population Chinese Spring×SQ1 (Quarrie et al. 2006), 2B, 5B and 7A for all environments in Renan x Récital population (Groos et al. 2003), of which the QTL on chromosome 2B co-located with a QTL for heading date. It is possible that this QTL for TGW resulted from an indirect effect of earliness, from Récital, because a gene for response to photoperiod was identified on chromosome 2B (Ppd-B1, Welsh et al. 1973). Five out of the seven QTL for TGW on chromosome 2BL and 2DL were observed to be associated with other kernel traits in RIL from PH132×WL711 (Dholakia et al. 2003). By using AB-QTL method, Huang et al (2003) reported that a significant QTL on chromosome 7B increased TGW by 11.7% . In the population ITMI (W7984×Opata85), QTL for TGW were
mapped on 3AS, 5AL and 6BS (Borner et al. 2002; Breseghello et al. 2007). As reported by Hai et al. (2008), two QTL for TGW were detected on chromosomes 2B and 7B across all four environments in CA9613 x H1488 population. The QTL for TGW was mapped in the same region as GPS on 2B seemed to correspond to the QTL for TGW described by Groos et al. (2003), while the QTL on chromosome 7BS was closely linked to the marker xgwm400 (Hai et al. 2008) same as described before by Borner et al. (2002). Correspondingly, Quarrie et al. (2007) found a QTL significantly associated with GPS and TGW corresponding to that identified by Hai (2008) on chromosome 7B.

Globally, several QTL for TGW were reported on four different mapping populations (Ayala et al. 2002; Dholakia et al. 2003; Groos et al. 2003; Huang et al. 2006) at the short arm of chromosome 2D. On the same chromosome a major QTL for TGW was coincident with QTL for yield, GPS, Days to heading and Grain filling time (Cuthbert et al. 2008). Moreover, other studies identified QTL controlling to TGW on chromosome 3BS (Borner et al. 2002; Cuthbert et al. 2008; Elouafi and Nachit, 2004; Wang et al. 2009a). Of which QTL reported by Cuthbert et al. (2008) was co-located with other QTL for yield, GWS, GPS, Harvest index and Days to maturity in the pericentromeric region of chromosome 3B.

Other yield-related traits

Except for TGW, relatively litter results has been reported for other yield-related traits in wheat, such as GPS, GWS, and SPS etc. Of which GPS is one of the most important yield components and directly determines the grain weight per spike (GWS). On the whole, 68 GPS QTL, 47 GWS QTL and 47 SPS QTL were identified respectively according our investigation. For GPS QTL, the most common (7) was detected on chromosomes 2D and 7A. Both QTL for GWS (8) and SPS QTL (7) were the most amounts on chromosome 5A.

A significant QTL controlling GPS, GWS, spike length, ear emergence time, height, and waxiness was identified on 4A in the ITMI population (Börner et al. 2002). Three QTL for GWS were detected on 1A, 2B and 2D in all four environments (Hai et al. 2008). Similar QTL have been reported by several authors (Borner et al. 2002; Kumar et al. 2006; Quarrie et al. 2005; Verma et al. 2005). Moreover, QTL on 5DL is corresponding to a QTL associated with GPS and TGW (Quarrie
et al. 2005), which is coincided with those in Somers’ map (2004) and in mapping population of CA9613 x H1488 (Hai et al, 2008). Further, at the distal end of chromosome 7AL, QTL associated with GPS have been reported by Quarrie et al. (2005). More recently, four clusters involving YLD, TGW, SPS, GPS and PHT were identified on chromosome 7A, based on the field trials for 24 site x treatment x year combinations (Quarrie et al. 2007).

All in all, a QTL cluster was detected on chromosome 2AL for yield-related traits in three different studies (GWS, Borner et al. 2002; GWS, GPS, SPS and Yield, Peng et al. 2003; GWS, Verma et al. 2003). Furthermore, chromosome 5AL harbored several QTL controlling YLD, TGW, GWS and SPS (Kato et al. 2000; Ma et al. 2007; Kumar et al. 2007).

Plant Height

Plant height has a very important effect on grain yield, which is known to be determined by many genes. In our survey, a total of 85 QTL controlling plant height on 19 of the 21 wheat chromosomes were reported in 30 literatures, except 6B and 6D. It was not surprising that the most common were detected on chromosome 4B (10) and 4D (8), because two GA-insensitive semi-dwarfing genes Rht-B1b and Rht-D1b are located on the two chromosomes. In eight different mapping populations, a major QTL cluster associated with plant height was mapped on chromosome 4BS (Borner et al. 2002; Hai et al. 2008; Huang et al. 2004; Liu et al. 2002; Maccaferri et al. 2008; Mathews et al. 2008; McCartney et al. 2005; Zhang et al.). Similarly, seven out of eight QTL for PHT were grouped on chromosome 4DS (Ellis et al. 2002; Chu et al. 2008; Draeger et al. 2007; Huang et al. 2006; Huang et al. 2003; McCartney et al. 2005; Verma et al. 2005; Wang et al. 2009a). Other two regions for PHT were also observed on chromosome 4B. Three researches reported QTL at the distal region of 4BS ((Liao et al. 2008; Marza et al. 2006; Sourdille et al. 2003). Other QTL for PHT was detested at the long arm on chromosome 4B (Huang et al. 2003, 2006; Verma et al. 2005). In addition, using 194 RILs from cross between the two French varieties, Renan and Récial (Gervais et al. 2003), a QTL for PHT was mapped on chromosome 4AL, which was mapped in the parallel region with other studies (Araki et al. 1999; Borner et al. 2002). QTL for plant height on chromosome 5A was located in the vicinity of Vrn-A1 (Chu et al. 2008). Kato et al. (1999) reported the Vrn-A1 locus to have a height reducing effect, which suggests that Vrn-A1 may be a candidate gene for these QTL.
QTL Meta-analysis

Selected chromosomes for meta-analysis

In order to survey the significant chromosome regions involving in wheat yield traits, the fifteen chromosomes harboring more QTL (>20) therefore were selected to perform meta-QTL analysis, except for chromosomes 3D, 5B, 5D, 6B, 6D and 7B (Table 2). Among fifty-nine QTL studies, only 37 were used to map projection and meta-analysis for lack of sufficient information of QTL characteristics and genetic map data, especially the latter frequently was resulted from using rare molecular markers in the reference map, such as AFLP, RAPD, STS, etc. For the 37 studies used, the 15 wheat chromosome harbored 320 QTL for yield and its related traits, the number of QTL per chromosome ranged from 7 (3A) to 43 (5A), and the number of QTL per trait ranged from 27 for SPS to 83 for grain yield. QTL projected in this study were presented in Table 2.

Map population and QTL heritability

Based on our investigation, for the thirty-three QTL studies twenty-six mapping populations were subjected to the meta-analysis, with the size ranging from 79 to 249, at the mean value of 132. Among these populations, the ITMI population was used in six studies (Ayala et al. 2002; Borner et al. 2002; Kulwal et al. 2003, 2005; Kumar et al. 2007; Li et al. 2008), and the other three populations in six studies (Huang et al. 2003; Li et al. 2007; Liao et al. 2008; Roder et al. 2008; Sun et al. 2009; Wang et al. 2008). The type of populations included 14 RIL (Recombination self-cross lines), 10 DH (Double Haploid lines) and 3 BC (Back Cross lines). The number of individual QTL per population ranged from 2 (Breseghello et al. 2005; Drager et al. 2007; Elouafi and Nachit 2004; Groos et al. 2003; Kulwal et al. 2003; Roder et al. 2008) to 33 (Huang et al. 2004).

Because of their complex quantitative fashion, wheat yield and its related traits generally display a low heritability. For wheat yield, TGW and GPS, above 80% of QTL explained less than 20% of phenotypic variation, while approximate 70% of QTL for GWS, SPS and PHT. In the case of 83 YLD QTL, on average they explained yield variation of 14.7%, ranging from 3.7% to 47.4%. However, SPS shows slightly higher heritability, the average variation explained by QTL was about 20%, ranging from 4.4% to 67.6%.
Preliminary within meta-analysis and map projection

As meta-analysis requires independent QTL, preliminary within meta-analysis were performed on the populations ITMI (on chromosomes 1A, 1B, 2A, 2B, 2D, 3B, 4A, 4B, 4D, 5A, 6A, 7A), AM3 x Lianzhou953 (1A, 4A, 4B), Prinz x M6 (1A, 1B, 2A, 2B, 2D, 3B, 4B, 4D, 7A, 7D) and Chuan35050 x Shannong483(1D, 2A, 2D, 3B, 6A, 7D). The preliminary meta-analysis reduced the total number of QTL from 351 to 320 which potentially could have been projected.

In order to obtain reliable projection of QTL, two highly saturated wheat maps were integrated as the reference map. The wheat composite-2004 map (4,506 markers; http://wheat.pw.usda.gov) was served as template on which the most recent Somers’ consensus SSR map (1,235 markers; Somer et al. 2004) was projected. As a result two hundred nineteen markers were discarded because of resolution of inversion. The mean of markers was 205 for the fifteen chromosomes studied, the most number of molecular markers (279) was on chromosome 1B while the lower one on chromosome 4B (129) and 4D (131), respectively.

Meta-QTL analysis

A total of 257 QTL from 37 studies (26 populations) were projected on the consensus map. The reduction from 320 to 257 QTL was caused by preliminary meta-analyses and by less than two common markers between chromosomes of the initial studies and pre-consensus map. Meta-QTL analysis resulted in 55 MQTL comprising 233 initial QTL and 24 remaining individual QTL. The number of clustered initial QTL ranged from 2 to 11, involving different traits from 1 to 6. On the fifteen chromosomes studied, the number of MQTL ranged from 2 to 7, of which the most MQTL (7) was identified on chromosome 2D, while the low number of MQTL (2) on chromosome 1B, 1D and 4B, respectively. Twelve significant MQTL with the number of initial studies being more than three, were identified on chromosomes 1B, 2A, 2D, 3B, 4A and 5A (Appendix II).

On chromosome 1B, ten initial QTL were aggregated to two MQTL, Both MQTL (MQTL4 and 5), respectively positioned at 60.8 cM and 70 cM, and comprised five initial QTL from four individual studies. MQTL4 was related with five yield and yield-related traits, including YLD, TGW, GPS, GWS and PHT. While MQTL5 involved in four different traits (YLD, GPS, PHT and Tiller Number), including two initial QTL for grain yield (Maccaferri et al. 2008; Quarrie et al. 2006).
Twenty QTL were projected on chromosome 2A and were clustered in three MQTL (MQTL8-10). Of which MQTL8 and MQTL9 were significant due to involving 4 and 5 individual studies, respectively. MQTL 8 was located at 19.1 cM with a narrow CI of 0.96 cM. It comprised 7 initial QTL and was associated with six traits from four individual researches. MQTL9 was positioned at 53.4 cM with a CI of 3.0 cM and comprised seven QTL which originated from both European and Asian populations. Among the seven initial QTL, two were responsible for grain yield and three for GPS.

On chromosome 2D twenty eight QTL were clustered to seven MQTL (14-20), of which two significant MQTL14 and 16 were located on 17.6 cM and 30.2 cM. MQTL14 comprised five initial QTL from four map population, involving four yield and yield-related traits. However, MQTL16 included seven initial QTL originating from six different studies, of which two initial QTL were for GWS.

Twenty nine initial QTL formed six MQTL (24-29) on wheat chromosome 3B, of which two significant MQTL24 and 26 were identified. With a CI of 0.91 cM, MQTL24 was positioned on 11.4 cM at the distal region of short arm, and comprised seven initial QTL, of which two initial QTL were for yield, three QTL for TGW and two for PHT. At the pericentromeric region of chromosome 3B, another significant MQTL26 was located on 45.8 cM with a CI of 2.0 cM, including seven initial QTL regarding yield, GWS, GPS and TGW from four individual population.

Nineteen QTL on chromosome 4A were clustered to three MQTL (30-32). MQTL30 was positioned at the 57 cM and included 8 initial QTL from three individual trials, of which five initial QTL were for yield. Significant MQTL32 was located at the position of 97 cM, including 11 initial QTL from four different studies.

For forty-five initial QTL on chromosome 5A six MQTL (MQTL38-43) were found, of which MQTL39, 40 and 42 were significant MQTL comprising nine, eleven and eleven initial QTL with the positions at 33.3, 50.8 and 82.4 cM, respectively. With a CI of 3.0, MQTL39 consisted of nine QTL from five different map populations, including four initial QTL for yield. The eleven initial QTL comprising in MQTL40 originated from five Asian, European or American parents, and was related with five wheat yield and yield-traits, including yield, SPS, GWS, PHT and Tilling number/m\(^2\). At the long arm on chromosome 5A MQTL42 was responsible for six different traits,
including YLD, TGW, GWS, GPS, SPS and PHT.

**Discussion**

QTL data compilation showed that all chromosome groups were involved in the genetic control of yield and yield-related traits in bread wheat. We used QTL data from 37 studies to identify consensus regions that are linked to these traits on the fifteen wheat chromosomes. The meta-analysis methodology proposed by Goffinet and Gerber (2000) was applied to QTL studies. It resulted in the detection of some meta-QTL, and showed that this method was a very powerful tool which could refine QTL position and accuracy. Chromosome 2A, 2D and 5A were key chromosomes for yield control, while chromosomes 1B, 3B and group 4 had a secondary but consistent incidence.

In common wheat, qualitatively inherited genes are often located in the gene-rich regions with hot spots of recombination (Gill et al. 1996; Faris et al. 2000; Sandhu et al. 2001). Like single genes, QTL controlling yield and yield-related traits generally mapped in the same genomic regions forming clusters. We discussed below these QTL clusters and meta-analysis results from the respects of linkage effects, pleiotropic and comparative genomic.

**Chromosome 1A and 1B**

According to fifty-nine studies, a QTL cluster for seven yield and yield-related traits were discovered on chromosome 1AL (Cuthbert et al. 2008; Hai et al. 2008; Liao et al. 2008; Maccaferri et al. 2008; Wang et al. 2008a; Wang et al. 2009a). Similarly, on chromosome 1BL a major QTL cluster included six yield and yield-related traits: YLD (Huang et al. 2003; Maccaferri et al. 2008), GWS and GPS (Verma et al. 2005), YLD, SPS and GPS (Peng et al. 2003) and TGW (Wang et al. 2009a; Wang et al. 2009b). The results of meta-analysis revealed MQTL2 and two significant MQTL4-5 on the corresponding region on chromosome 1AL (73 cM) and 1BL (61 cM and 70 cM), respectively. Based on our reference map, the genes Glu-A1 (68 cM on 1AL) and Glu-1B (66 cM on 1BL) for high-molecular-weight glutenin were located in the vicinity of these MQTL, and suggesting Glu-1A and Glu-1B as the possible candidate genes for these QTL clusters.
Regarding wheat group 2, two important genomic regions were observed on chromosome 2AS and 2DS. A major QTL clusters was located on chromosome 2AS, involving in eight yield and yield-related traits (Huang et al. 2003, 2004; Kunert et al. 2007; Li et al. 2007; McCartney et al. 2005; Sun et al. 2009; Yao et al. 2009). Consequently, two significant MQTL8 and 9 corresponding to this region were identified at the 19 cM and 54 cM on chromosome 2AS, respectively. MQTL9 included 3 initial QTL for GPS, and suggesting this MQTL had an important effect on grains per spike. Among four MQTL (14-17) on chromosome 2DS, two significant MQTL14 and 16 were located at the position of 17 cM and 30 cM. It is noted that MQTL15 (25 cM) was located on the position coincided with the gene Rht8 on chromosome 2DS, adding to the evidence that genes in this chromosome group influence wheat kernel growth. Correspondingly on rice chromosome 7 (the orthologous region to the short arm of wheat group 2), the Ghd7 gene underlying QTL for plant height, heading day and number of grains per panicle, was cloned (Xue et al. 2008). It is likely that the information of the Ghd7 gene makes the MQTL on chromosome 2A and 2DS be better understood.

Chromosome 3B

As reported by Cuthbert et al. (2008), a QTL for several traits (YLD, TGW, GWS, GPS, Harvest Index, Spike/M2 and Maturity) was mapped in the vicinity of centromere on chromosome 3B. As a whole, nine QTL responsible for yield and yield-related traits were congregated in this region based on 9 different studies, of which QTL for grain yield and TGW were respectively reported by four studies (Borner et al. 2002; Cuthbert et al. 2008; Elouafi and Nachit, 2004; Groos et al. 2003; Huang et al. 2004; Li et al. 2007; Marza et al. 2006; Wang et al. 2009a; Zhou et al. 2006). QTL meta-analysis for this region resulted in a significant MQTL26 at the position of 46 cM on chromosome 3B, and included three initial QTL for YLD and two for TGW. This suggested that MQTL26 is possible to play an important role in wheat grain yield.

Another significant MQTL24 was located at the position of 11.4 cM on chromosome 3BS. In the orthologous region on rice chromosome 1S, a genes (Gn1a) underlying QTL for number of grains per panicle was cloned at the distal region in rice (Ashikari et al. 2005), this gene encodes cytokinin oxidase/dehydrogenase (OsCKX2). Through the homologous cloning method, a gene
(TaCKX2B) on wheat chromosome 3BS was obtained and proved to be able to up-regulate CKX2 activity in bread wheat (Zhong et al. data unpublished). The question if TaCKX2B is the candidate gene for MQTL24 needs further validate. This shows comparative analysis could provide useful information for identifying some genes underlying QTL with large effect.

**Group 4**

In rice, the GS3 locus in the pericentromeric region of chromosome 3 has been identified as a major QTL for both grain weight and grain length (Aluko et al. 2004; Fan et al. 2006; Huang et al. 1997; Redona and Mackill, 1998; Tan et al. 2000; Thomson et al. 2003; Xing et al. 2001; Yu et al. 1997), and was collocated (Fan et al. 2006). Using the sequence information of the GS3 gene, some primers were designed nearby or within the genomic region of GS3 and resulted in identifying one significant marker GW3-1 for TGW on wheat chromosome 4AL (rice chromosome 3 is orthologous to wheat group 4), explaining 19.0% of the variance with a LOD=7.87 in ITMI population (Li et al. 2008). As expected, a large cluster was formed on wheat chromosome 4AL, consisting of QTL for eight yield and yield-related traits. Through meta-analysis, MQTL30 was identified at the position of 57 cM, involving in five initial QTL for grain yield (Araki et al. 1999; Borner et al. 2002; Hai et al. 2008; Huang et al. 2004; Kuchel et al. 2007b; Kumar et al. 2007; McCartney et al. 2005; Wang et al. 2008b; Wang et al. 2009a; Zhang et al. 2009c).

Generally, the genetic control of yield and its components involves the important genes such as Rth and Vrn. Two major QTL clusters were respectively detected on chromosome 4BS and 4DS because of the presence of Rht-1B and Rht-1D genes. Pleiotropy is most likely to explain for the QTL clusters. Regarding chromosome 4B, MQTL34 located on the position (59 cM) coincided with Rht-B1b. Besides major QTL for plant height and lodging resistance, this region still consisted of QTL controlling productivity as well as genes (or QTL) resistance to diseases (Pm, Lr and DON) (Borner et al. 2002; Cuthbert et al. 2008; Groos et al. 2003; Hai et al. 2008; Huang et al. 2003; Liu et al. 2005; Maccaferri et al. 2008; Mathews et al. 2008; McCartney et al. 2005; Quarrie et al. 2005; Zhang et al. 2008a). Likewise, MQTL44 was located in the position (36 cM) of Rht-D1b on chromosome 4DS, which consisted of QTL for PHT and other QTL for yield and yield components, such as YLD, TGW, GPS, GWS, SPS, Test Weight, Tiller Number / m², and Lodging (Chu et al. 2008; Draeger et al. 2007; Huang et al. 2003, 2006; McCartney et al. 2005;

Chromosome 5A
Other pleiotropic effect for grain yield and its related traits was observed on chromosome 5A, which is known to carry a number of genes affecting adaptability and productivity, such as Vrn-A1 and q. Snape et al. (1985) reported pleiotropic effects of Vrn-A1 and q on grain yield and some yield components. According to the result of meta-analysis, MQTL41 consisting numerous QTL for yield and yield-related traits was located on chromosome 5AL in the proximity of Vrn-A1 and q loci. Based on literature review, this region also included QTL for Tiller Number, Compactness, Spike Length and Heading Day (Chu et al. 2008; Cuthbert et al. 2008; Groos et al. 2003; Huang et al. 2006; Kato et al. 1999, 2000; Kumar et al. 2007; Ma et al. 2007; Mathews et al. 2008; Quarrie et al. 2005).

Conclusion
In our research, the fifteen important chromosomes involving in yield and its related traits were found through literature review. Using meta-analysis, 55 MQTL were identified for these traits, of which 12 significant MQTL were located chromosomes 1A, 1B, 2A, 2D, 3B, 4A, 4B, 4D and 5A. Our investigation showed the genetic control of yield and its components frequently involved the important genes such as the Rht and Vrn. Furthermore, several significant MQTL were located in the orthologous region corresponding to some important rice genes underlying QTL for yield related traits. Our results demonstrated that QTL meta-analysis was a potential tool for refining QTL position. However, genes regulating other traits (productivity and plant growth and development, diseases resistance etc.) also play important roles in yield traits, QTL information for these traits should be included in meta QTL-analysis. This will make MQTL for yield and its components more accurately identify, and so could improve the MAS efficiency for wheat grain yield in breeding program.

Acknowledgement
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References:
High-density mapping and comparative analysis of agronomically important traits on wheat chromosome 3A. Genomics 88(1): 74-87.


Huang N, Parco A, Mew T, Magpantay G, McCouch S, Guiderdoni E, Xu JC, Subudhi P, Angeles ER,


Zhang GR, Mergoum M, Kianian S, Meyer DW, Simsek S, Singh PK (2009a) Genetic Relationship and


Figure Legends

Figure 1 QTL distribution on the wheat A, B and D genomes for six yield and yield-related traits. YLD-grain yield, TGW-1000-grain weight, GPS-grain per spike, GWS-grain weight per spike, SPS-spikelet per spike, PHT-plant height.

Figure 2 Distribution of QTL for yield and yield-related traits on the wheat seven homologous genomes.
Table 1 QTLs distribution on the whole wheat genome for six yield and yield-related traits: Yield (YLD), 1000-grains weight (TGW), grains per spike (GPS), grains weight per spike (GWS), spikelet per spike (SPS), plant height (PHT).

<table>
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<th>TGW</th>
<th>GPS</th>
<th>GWS</th>
<th>SPS</th>
<th>PHT</th>
<th>Total</th>
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<td>4</td>
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<td>22</td>
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<tr>
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Table 2 Overview of projected QTL and identified MQTL in meta-analysis, numbers in front of bracket indicate projectable QTL and in the bracket indicate number of MQTL, respectively. "-" indicate meta-analysis was not performed on these chromosomes.

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Total: 178 116 68 47 47 85 541
Figure 1  QTL distribution on the wheat A, B and D genomes for six yield and yield-related traits. YLD-grain yield, TGW- 1000-grain weight, GPS-grain per spike, GWS-grain weight per spike, SPS-spikelet per spike, PHT-plant height.
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