*Pak. J. Agri. Sci., Vol. 55(1), 33-45; 2017*
*ISSN (Print) 0552-9034, ISSN (Online) 2076-0906*
*DOI: 10.21162/PAKJAS/18.4488*
http://www.pakjas.com.pk

# QTL MAPPING FOR EARLY VIGOR RELATED TRAITS IN AN ELITE WHEAT-BREEDING PARENT CHUANMAI 42 DERIVED FROM SYNTHETIC HEXAPLOID WHEAT

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Seedling growth is one essential component of reliable crop establishment, and greater early vigor is often associated with greater drought tolerance, biomass and grain yield. Chuanmai 42 derived from synthetic hexaploid wheat has been widely used as an elite wheat-breeding parent in wheat breeding program of Southwest China. In this study, 127 recombinant inbred lines (RILs) developed from Chuanmai 42 were used to dissect the molecular basis of its great early vigor by QTL mapping, and seven early vigor related traits including number of all expanded leaves, total leaf area, shoot fresh weight, shoot dry weight, number of the main roots, root dry weight and relative growth rate were evaluated for this RILs after 21-day and 28-day growth under a modified Hoagland nutrient solution, respectively. Based on a linkage map containing 148 SSR and 644 DArT makers, a total of 40 QTLs for these traits were detected on 14 chromosomes. Among the 25 QTLs with the phenotypic variance explained more than 10%, 17 QTLs enhanced the related traits through Chuanmai 42 alleles. A total of 4 genomic regions with QTL clusters were detected on chromosomes 5A, 6A, 6B and 7A, respectively. Among them, the genomic regions with QTL clusters on 6B and 7A from Chuanmai 42 enhanced early vigor of seedling, and the other two were from Chuannong 16. Moreover, QTL cluster in *Xgwm154-Wpt7846* of chromosome 6B was the important genomic region with the strongest phenotypic effects that were also strengthened during elongation of the growth period. The findings of this study are relevant to the molecular improvement of early vigor when using Chuanmai 42 as a breeding parent.
**Keywords**: Wheat, Chuanmai 42, early vigor, QTL, DArT markers.

## INTRODUCTION

Seedling growth, described as early vigor, is one essential component of reliable crop establishment and has been reported in many crop species (Lopez-Castaneda *et al.*, 1995 and 1996). Modern wheat varieties exhibit genetic variation in early vigor (Rebetzke and Richards, 1999; Richards and Lukacs, 2002; Maydup *et al.*, 2012). Greater vigor cultivars shade the soil surface faster, thereby reducing evaporative losses from the soil and enhancing the population water-use efficiency (Gregory *et al.*, 2000). It is recognized as a particularly important characteristic for increasing yield potential in dry environments (Siddique *et al.*, 1990; Richards, 2000; Botwright *et al.*, 2002; Richards and Lukacs, 2002). Moreover, rapid early development of leaf area and root system are also associated with increased nitrogen use efficiency (Liao *et al.*, 2004), rates of light interception (Maydup *et al.*, 2012), and weed competitiveness (Coleman *et al.*, 2001; Lemerle *et al.*, 2001). Selection for great early vigor wheat germplasm is favorable to yield improvement under the challenges of agricultural adaptation to global climate change and improving efficiency of inputs.

Due to decades of repeated using of founder parents in breeding, the genetic base of modern bread wheat *Triticum aestivum L.* (2n=6x=42, AABBDD) is rather narrow in recent decades. However, its wild relatives constitute a potential rich source of genetic variation. Bultynck *et al.* (2004) and ter Steege *et al.* (2005) found that the common wheat D genome progenitor *Aegilops tauschii* Coss (2n=2x=14, DD). showed a very rapid leaf expansion rate at the seedling stage. With the help of molecular markers and marker-based genetic maps, genetic dissection for early vigor related traits has been reported in several germplasm under different growing conditions, and QTLs for early vigor related traits were distributed through almost whole genome of wheat (ter Steege *et al.*, 2005; An *et al.*, 2006; Sanguineti *et al.*, 2007; Landjeva *et al.*, 2008 and 2010; Ibrahim *et al.*, 2010 and 2012; Guo *et al.*, 2012; Ren *et al.*, 2012a, b).

'Chuanmai 42' derived from synthetic hexaploid wheat (SHW, 2n=6x=42, AABBDD) carried elite genes from tetraploid wheat *Triticum turgidum* L. (2n=4x=28, AABB)

and *Ae. tauschii*, and has been widely used in wheat breeding program in Southwest China, for its high grain yield potential under multiple growth conditions (Yang *et al.*, 2009; Li *et al.*, 2011, 2014; Tang *et al.*, 2011; Wan *et al.*, 2015). Chuanmai 42 often showed greater early vigor and grain yield in the field. Moreover, a higher rate of aboveground dry matter accumulation, especially in the early growth stages, was observed in the Chuanmai 42-derived cultivars and positively significantly related with grain yield and grain number per $m^2$ (Tang *et al.*, 2015). However, the genetic basis of Chuanmai 42's greater early vigor has not been known yet. And the study was carried out on a RIL population derived from Chuanmai 42 to understand its molecular characterization by quantitative trait locus (QTL) mapping with SSR and DArT makers, with the aim of marker-assisted selection for greater early vigor in the breeding program using Chuanmai 42.

## MATERIALS AND METHODS

***Plant materials*:** One hundred and twenty-seven F8 RILs from the Chuanmai 42 x Chuannong 16 cross and their parents were used for QTL mapping in this study. Chuanmai 42 was selected from Syn769/SW3243//Chuan 6415 and released in 2004 by Sichuan Academy of Agricultural Sciences (SAAS; Chengdu, China). Syn769 (AABBDD) was synthesized from Decoy 1 (AABB) / *Ae. tauschii 188* (DD) and kindly provided by the International Maize and Wheat Improvement Center (CIMMYT; Mexico City, Mexico) (Mujeeb-Kazi *et al.*, 1996). Chuannong 16 (Chuanyu 12 / 87-427) was bred in 2002 by Sichuan Agricultural University (SIAU; Chengdu, China).

***Growth condition, experimental design and trait evaluation*:** 127 RILs and their parents were planted under a hydroponic condition of modified Hoagland nutrient solution (Wan *et al.*, 2007) and performed in randomized complete block design with three replicates. Each replicate contained two groups: one was used for trait evaluation in 21-day growth period; the other one was for 28-day growth period.

Uniform seeds selected with an average kernel weight of each RIL and parent were surface sterilized and germinated at 20-22°C in the dark. Then the germinated seeds were transferred to 1-fold nutrient solution in several black plastic incubators (60cm L x 50cm W x 20cm H). Six manual air vent valve were equipped at internal bottom of each plastic incubator. And a black nylon cloth mesh sandwiched by double black foam boards was made as a floating plate that contained 30 points (holes) (Fig. 1). One point with 2 placed seedlings represented a RIL/parental line, occupying 1 liter (L) of nutrient solution and the horizontal and vertical distances between adjacent points was 10 cm (Fig. 1).

The growth conditions of culture room were as follows: 12-hour artificial light using two/three 45 watt (W) daylight lamps with a luminous flux of 70 lumens per watt (Fig. 1), day/night temperatures of 22°C/18°C, air ventilation rate of 1-hour, twice daily first and then five times per day after 14-day growth. 1-fold modified Hoagland nutrient solution was renewed weekly. The composition of the 1-fold modified Hoagland nutrient solution was 1.5 mM $Ca(NO_3)_2$, 1.0 mM $KNO_3$, 0.25 mM $KH_2PO_4$, 0.5 mM $MgSO_4$, 0.1 mM KCl, 100 μM Fe-EDTA, 3 μM $H_3BO_3$, 1.0 μM $MnSO_4$, 0.5 μM $CuSO_4$, 1.0 μM $ZnSO_4$, 0.05 μM $(NH_4)_6Mo_7O_{24}$ (Wan *et al.*, 2007). Seedlings within one complete replicate were placed in the same height and rotated at least two times per week to minimize the environmental effects.

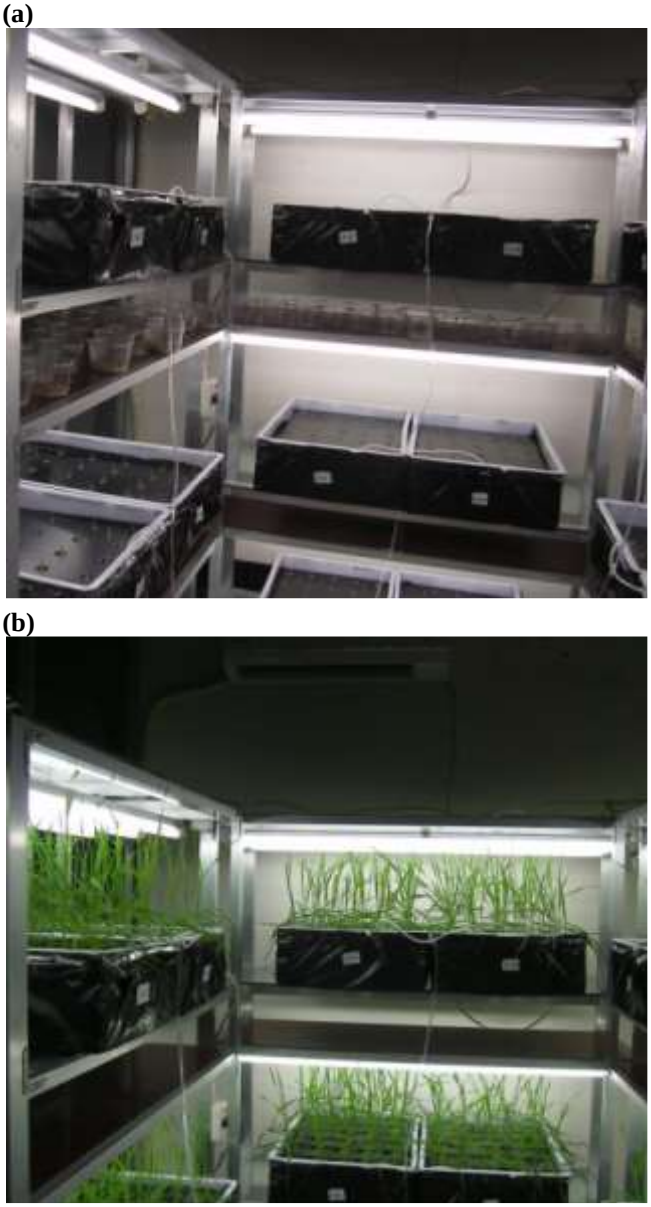


**Figure 1. Seedlings growing in modified Hoagland nutrient solution after (a) 7 days and (b) 21 days.**

For trait evaluation, number of all expanded leaves (LN), shoot fresh weight (SFW) and main root number (RN) were recorded at last. Length (L) and width (W) of each expanded leaf was measured for every seedling to obtain total measured leaf area (TLA). Each leaf area of a single seedling was calculated as L x W x 0.9 (ter Steege *et al*., 2005). Finally, the shoot and root were dried separately to a constant weight measured as shoot dry weight (SDW) and root dry weight (RDW) at 65°C after 10-minute exposure to 120°C, respectively. The measurement for all phenotypic data was accomplished within 12 hours. Relative growth rate (RGR) was measured based on the total dry weight (TDW) on days 0, 21 and 28, where TDW=SDW+RDW. $RGR_{21d}$ and $RGR_{28d}$ were calculated as the following formula: $RGR_{21/28}$=[Ln ($TDW_{21/28}$)-Ln ($TDW_0$)]/($t_{21/28}$-$t_0$). $TDW_0$ was represented by the dry weight per kernel.

***Statistical analysis and QTL mapping*:** Pearson correlation analysis and nonparametric tests for all phenotypes were made in SPSS statistical package (SPSS Inc., Chicago, IL). *t*-test for parental values was performed in MS Excel 2003.

A framework genetic map with 148 SSR and 644 Diversity Arrays Technology (DArT) markers was generated using the method of Xue *et al*. (2008). This map covered over 4,236 cM of wheat genome with an average distance of 5.3 cM between adjacent markers (Li, 2014). For the SSR markers, DNA was isolated from fresh seedling leaves according to the cetyl-trimethyl-ammonium bromide (CTAB) protocol (Saghai-Maroof *et al.*, 1984), and the tailed primer method was applied for the amplification of SSRs (Xue *et al.*, 2008). For the DArT marker, genome DNA was isolated using Plant DNAzol® Reagent by Invitrogen, and the genotypes of each DNA sample were obtained following the procedures of Akbari *et al.* (2006) at Triticarte Pty. ltd.

QTL detection was performed using Mapmaker/QTL Version 1.9 through simple interval mapping (SIM) and composite interval mapping (CIM) as described by Jia *et al.* (2013). The LOD score for declaring a potential QTL was 2.0 in SIM and 1.5 higher than that of the fixed QTL in CIM, while the threshold value for confirming a most likely QTL was 2.5 in both SIM and CIM. QTLs with overlapping confidence intervals were given the same name for each trait.

## RESULTS

***Phenotypic analysis*:** All phenotypic values of Chuanmai 42 were higher than Chuannong 16 except RDW, and significance was showed in TLA, SFW, RN and $RGR_{21d}$ (Table 1). Significant variations of investigated traits were also observed in the population, with their values spanning much larger ranges than those defined by the parental values (Table 1). The absolute values of Kurtosis and Skewness for all traits were less than 1.00, suggesting their normal distribution (Table 1).

Correlation coefficients among these traits after 21- and 28-day growth were presented in Table 2. In this study SFW and SDW were significantly positively related to TLA and LN, and the coefficients between SFW/SDW and TLA (>0.9) were greater than those between SFW/SDW and LN (<0.7), especially in the hydroponic trial of 21-day growth (Table 2), indicating that the elongation of leaves is more important than the number of leaves for rapid early growth of seedlings. The shoot related traits such TLA, SFW, SDW, were significantly positively correlated with RN and RDW, especially after 28-day growth, suggesting their dependence on root system in the

**Table 1. Parental values and population distribution parameters of investigated traits related to early vigor.**

| Trait[§] | Trial | Parents | | RIL population | | | |
|---|---|---|---|---|---|---|---|
| | | Chuanmai 42 | Chuannong 16 | Mean±S.D. | Min - Max | Kurtosis | Skewness |
| LN | 21 days | 4.33 | 4.00 | 3.88±0.21 | 3.30-4.40 | -0.41 | 0.56 |
| | 28 days | 5.00 | 4.67 | 5.14±0.40 | 4.70-6.70 | 0.36 | 0.91 |
| TLA | 21 days | 53.87** | 39.40 | 50.74±5.34 | 38.39-64.58 | -0.41 | 0.04 |
| | 28 days | 76.11* | 72.14 | 92.23±10.10 | 70.05-117.39 | -0.11 | 0.45 |
| SFW | 21 days | 1.35** | 0.72 | 1.11±0.13 | 0.85-1.44 | -0.50 | 0.15 |
| | 28 days | 1.84* | 1.45 | 2.14±0.30 | 1.50-2.88 | -0.25 | 0.40 |
| SDW | 21 days | 0.11* | 0.09 | 0.10±0.01 | 0.08-0.14 | -0.55 | 0.21 |
| | 28 days | 0.17 | 0.15 | 0.21±0.03 | 0.14-0.29 | -0.11 | 0.39 |
| RN | 21 days | 8.67* | 6.00 | 7.05± 0.77 | 5.00-9.70 | 0.45 | 0.15 |
| | 28 days | 10.33* | 7.33 | 9.61±1.12 | 7.30-12.30 | -0.26 | 0.27 |
| RDW | 21 days | 0.02 | 0.02 | 0.02±0.004 | 0.01-0.03 | 0.16 | 0.28 |
| | 28 days | 0.03 | 0.03 | 0.03±0.007 | 0.02-0.06 | 0.61 | 0.58 |
| RGR | 21 days | 0.05* | 0.04 | 0.05±0.006 | 0.03-0.07 | 0.23 | 0.24 |
| | 28 days | 0.05 | 0.05 | 0.06±0.006 | 0.04-0.07 | -0.02 | 0.19 |

[§]LN, number of expanded leaves; TLA, total measured leaf area; SFW, shoot fresh weight; SDW, shoot dry weight; RN, main root number; RDW, root dry number; RGR, relative growth rate;

* And ** indicate significant differences from Chuannong 16 at *P*=0.05 and *P*=0.01, respectively

**Table 2. Correlation coefficients between investigated traits in the RIL population¶.**

| Trait | Trial | LN | TLA | SFW | SDW | RN | RDW | RGR |
|---|---|---|---|---|---|---|---|---|
| LN | 21 days | 0.265** | | | | | | |
| | 28 days | | | | | | | |
| TLA | 21 days | 0.206* | 0.492** | | | | | |
| | 28 days | 0.617** | | | | | | |
| SFW | 21 days | 0.199* | 0.927** | 0.546** | | | | |
| | 28 days | 0.637** | 0.924** | | | | | |
| SDW | 21 days | 0.182* | 0.879** | 0.923** | 0.500** | | | |
| | 28 days | 0.644** | 0.901** | 0.949** | | | | |
| RN | 21 days | 0.322** | 0.461** | 0.417** | 0.409** | 0.510** | | |
| | 28 days | 0.395** | 0.541** | 0.532 ** | 0.517** | | | |
| RDW | 21 days | 0.116 | 0.501** | 0.482** | 0.568** | 0.338** | 0.339** | |
| | 28 days | 0.453** | 0.675** | 0.687** | 0.724** | 0.345** | | |
| RGR | 21 days | 0.288** | 0.381** | 0.595** | 0.641** | 0.473** | 0.703** | 0.645** |
| | 28 days | 0.625** | 0.735** | 0.744** | 0.786** | 0.503** | 0.695** | |

¶Shaded cells represent the correlation coefficients of the same trait between 21 days and 28 days;
*, ** indicate significance at $P = 0.05$ and 0.01, respectively.

late part of the seedling growth stage (Table 2). RGR represented the rate of whole seedling growth, which directly indicated the early vigor and was significantly positively correlated with both shoot and root related traits (Table 2). Moreover, significant positive correlations between traits investigated at different time were also displayed in the shaded cells of Table 2, the coefficients ranged from 0.265 to 0.645, and the coefficient between $RGR_{21}$ and $RGR_{28}$ was the highest one among them (Table 2).

**QTL analysis:**

***Shoot related traits*:** In this study, the number of the all-expanding leaves was investigated on both days 21 and 28, separately. A total of 9 QTL for LN were mapped to chromosome 1D, 2A, 3D, 4D, 5A, 5B, 6A, 6B, and 7A, respectively (Table 3). Among them, 3 QTLs *QLn.saas-5A*, *QLn.saas-6B* and *QLn.saas-7A.2* were detected in both 21- and 28-day growth periods, and genetic distance between their QTL peaks in different growth periods was less than 15 cM (Fig. 2). The detected LOD value of *QLn.saas-6B* rose up greatly with the seedling growing up (Table 3). These 3 QTLs increased LN through Chuanmai 42 alleles, suggesting that Chuanmai 42 alleles in these QTL locus enhanced seedling leaf establishment. TLA is the total area of all-expanding leaves, and positively related with the LN, especially in 28-day growth (Table 2). Among the detected QTLs for TLA, the intervals of TLA QTLs on 5A, 6B and 7A overlapped with QTLs for LN on these chromosomes (Fig. 2). QTL in the interval *Xbarc1466-Xgwm88* of chromosome 6B had the highest LOD value, and Chuanmai 42 allele increased the TLA (Table 2). This QTL *QTla.saas-6B.1* was only detected on days 28, indicating its significant effect on increasing TLA in the growth period from days 21 to days 28. Moreover, the QTL for TLA on chromosome 5A had the LOD value of 3.00 on days 21, and increased TLA through Chuannong 16 allele. SFW and SDW were greatly positively related traits, and most detected QTL intervals for SDW overlapped with those for SFW, such as QTLs on chromosomes 4A, 5A, 5B, 6A and 7A (Fig. 2). For SFW, 3 QTL with LOD values more than 3.00 were mapped to chromosomes 5A, 5B and 6B, respectively. All the 3 QTLs explained more than 12% of the phenotypic variation, and QTLs on 5A and 5B had stronger phenotypic effects in the growth period from day 0 to days 21 while QTL on 6B showed its significant phenotypic effect from days 21 to days 28 (Table 3). Among these 3 QTLs, *QSfw.saas-5B* and *QSfw.saas-6B* enhanced the shoot fresh weight through Chuanmai 42 alleles. For SDW, among the detected QTLs only 2 QTLs were identified with their LOD values more than 3.00 and mapped to chromosomes 5A and 7A, respectively. The RDW QTL on 5A increased the root dry weight through Chuannong 16 allele while *QSdw.saas-7A* allele from Chuanmai 42 enhanced RDW.

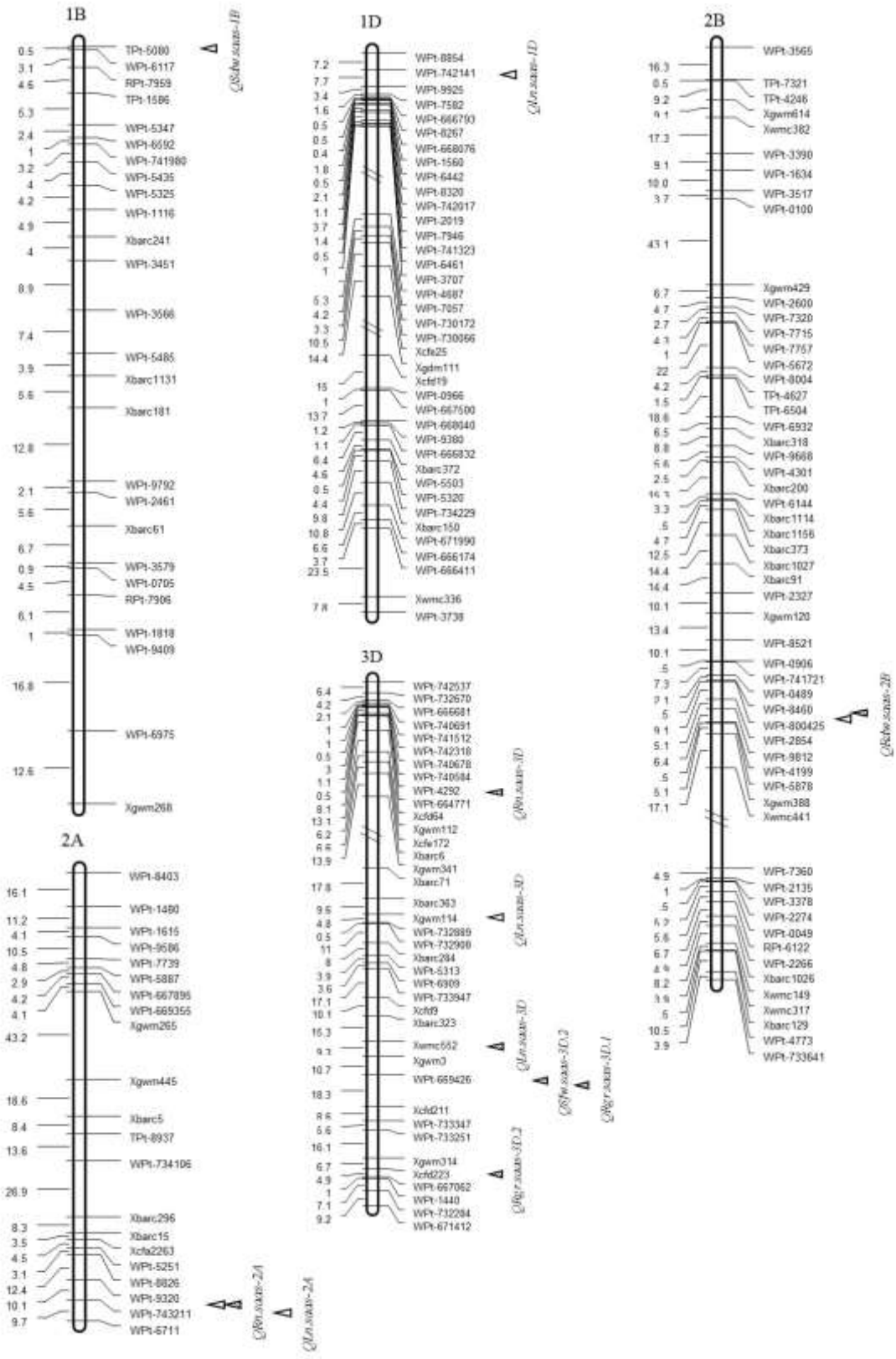
In this QTL map, the regions *Xgwm88-Wpt-0446* of chromosome 6B and *Wpt-4553-Xcfa2293* of chromosome 7A were significantly associated with both leaf-related traits (LN and TLA) and shoot weight (SFW and SDW) (Fig. 2), and the haplotypes of Chuanmai 42 increased early vigor of seedling shoot. And the genomic region in the interval *Xbarc56-Wpt733649* of chromosome 5A from Chuannong 16 increased TLA, SFW and SDW simultaneously (Table 3).

***Traits associated with root*:** Two morphological traits for root system, RN and RDW, were evaluated for QTL analysis. A total of 3 RN QTLs with LOD value more than 3.00 and PVE > 10% were identified on chromosomes 2A, 3D and 4B, respectively. *QRn.saas-2A* and *QRn.saas-4B* were detected in both growing periods, while the LOD value of *QRn.saas-4B* increased greatly in 28-day growth period (Table 3). Among these 3 QTLs, *QRn.saas-2A* and *QRn.saas-3D* increased the number of primary roots through Chuanmai 42 alleles, and the other one was through Chuannong 16 allele. A total of 6 QTLs were detected for RDW, and only one QTL on 2B was identified in both growth periods.

**Table 3. QTLs identified for early vigor related traits in Chuanmai 42 derived RIL population.**

| Trait | Trial (days) | QTL | Marker interval | LOD | $R^2$ (%) | Additive effect[a] |
|---|---|---|---|---|---|---|
| LN | 21 | *QLn.saas-1D* | *WPt-742141-WPt-9925* | 2.12 | 9.03 | 0.095 |
| | | *QLn.saas-2A* | *WPt-743211-WPt-6711* | 2.64 | 12.32 | 0.075 |
| | | *QLn.saas-3D* | *Xgwm114-WPt-732889* | 1.95 | 7.24 | 0.063 |
| | | *QLn.saas-4D* | *Xbarc1183-Xbarc48* | 2.93 | 14.83 | -0.099 |
| | | *QLn.saas-5A* | *Xbarc117-Xbarc56* | 1.63 | 5.60 | 0.054 |
| | | *QLn.saas-5B* | *WPt-6105-WPt-9454* | 2.41 | 8.16 | 0.065 |
| | | *QLn.saas-6A* | *WPt-671561-WPt-5463* | 2.01 | 10.80 | -0.102 |
| | | *QLn.saas-6B* | *Xgwm88-WPt-2000* | 2.62 | 10.42 | 0.076 |
| | | *QLn.saas-7A.2* | *WPt-1706-WPt-4553* | 1.57 | 5.41 | 0.054 |
| | 28 | *QLn.saas-3D* | *Xwmc552-Xgwm3* | 2.34 | 8.54 | 0.111 |
| | | *QLn.saas-5A* | *Xbarc117-Xbarc56* | 1.93 | 5.96 | 0.094 |
| | | *QLn.saas-6A* | *WPt-3091-WPt-2573* | 2.50 | 8.48 | -0.112 |
| | | *QLn.saas-6B* | *WPt-2000-WPt-0446* | 4.03 | 13.89 | 0.144 |
| | | *QLn.saas-7A.1* | *WPt-0808-WPt-5257* | 2.91 | 10.38 | 0.123 |
| | | *QLn.saas-7A.2* | *WPt-4553-Xcfa2293* | 1.89 | 5.77 | 0.092 |
| TLA | 21 | *QTla.saas-5A* | *Xbarc165-WPt-733649* | 3.00 | 14.70 | -2.077 |
| | | *QTla.saas-5B* | *WPt-666939-Xcfe86* | 2.22 | 10.83 | 1.629 |
| | | *QTla.saas-6A* | *Xgwm154-WPt-3855* | 2.29 | 14.56 | -3.060 |
| | 28 | *QTla.saas-6A* | *Xgwm154-WPt-3855* | 1.71 | 6.22 | -2.480 |
| | | *QTla.saas-6B.1* | *Xbarc1466-Xgwm88* | 3.08 | 12.93 | 0.110 |
| | | *QTla.saas-6B.2* | *TPt-8161-WPt-5037* | 1.71 | 6.22 | 2.482 |
| | | *QTla.saas-7A.1* | *WPt-0808-WPt-5257* | 1.71 | 6.11 | 2.465 |
| | | *QTla.saas-7A.2* | *WPt-4553-Xcfa2293* | 2.39 | 9.18 | 3.021 |
| SFW | 21 | *QSfw.saas-4A* | *WPt-6900-WPt-5578* | 2.2 | 6.63 | -0.031 |
| | | *QSfw.saas-5A* | *Xbarc165-WPt-733649* | 4.14 | 20.38 | -0.054 |
| | | *QSfw.saas-5B* | *WPt-666939-Xcfe86* | 3.95 | 15.33 | 0.048 |
| | | *QSfw.saas-6A.1* | *WPt-5463-WPt-3563* | 1.55 | 6.89 | 0.048 |
| | | *QSfw.saas-6A.2* | *Xgwm154-WPt-3855* | 2.05 | 8.44 | -0.065 |
| | 28 | *QSfw.saas-3D* | *WPt-669426-Xcfd211* | 2.06 | 10.02 | 0.095 |
| | | *QSfw.saas-5A* | *WPt-733649-WPt-3509* | 2.20 | 8.02 | -0.084 |
| | | *QSfw.saas-6A.2* | *Xgwm154-WPt-3855* | 1.77 | 6.87 | -0.060 |
| | | *QSfw.saas-6B* | *Xbarc1466-Xgwm88* | 3.08 | 12.93 | 0.110 |
| | | *QSfw.saas-7A.1* | *WPt-0808-WPt-5257* | 1.80 | 6.23 | 0.075 |
| | | *QSfw.saas-7A.2* | *WPt-4553-Xcfa2293* | 2.01 | 6.94 | 0.079 |
| SDW | 21 | *QSdw.saas-1B* | *Tpt-5080-WPt-1586* | 2.41 | 7.43 | 0.005 |
| | | *QSdw.saas-4A* | *WPt-6900-WPt-5578* | 1.64 | 4.29 | -0.003 |
| | | *QSdw.saas-5A* | *Xbarc165-WPt-733649* | 4.80 | 19.33 | -0.006 |
| | | *QSdw.saas-5B* | *WPt-666939-Xcfe86* | 2.96 | 8.79 | 0.004 |
| | | *QSdw.saas-6A.1* | *WPt-5463-WPt-3563* | 2.89 | 10.76 | 0.006 |
| | | *QSdw.saas-6A.2* | *WPt-3855-WPt-7846* | 2.73 | 8.13 | -0.008 |
| | 28 | *QSdw.saas-6A.2* | *Xgwm154-WPt-3855* | 2.22 | 12.29 | -0.016 |
| | | *QSdw.saas-6B.1* | *WPt-2000-WPt-0446* | 2.13 | 7.94 | 0.009 |
| | | *QSdw.saas-6B.2* | *WPt-5037-WPt-9124* | 1.64 | 5.53 | 0.007 |
| | | *QSdw.saas-7A* | *WPt-4553-Xcfa2293* | 3.22 | 12.20 | 0.011 |
| RN | 21 | *QRn.saas-2A* | *WPt-743211-WPt-6711* | 2.73 | 12.81 | 0.272 |
| | | *QRn.saas-4B* | *WPt-6209-Xcfd54* | 1.75 | 6.09 | -0.190 |
| | 28 | *QRn.saas-2A* | *WPt-743211-WPt-6711* | 3.17 | 10.65 | 0.367 |
| | | *QRn.saas-3D* | *Xbarc6-Xgwm341* | 3.35 | 11.01 | 0.404 |
| | | *QRn.saas-4B* | *WPt-6209-Xcfd54* | 3.68 | 11.13 | -0.384 |
| | | *QRn.saas-7A* | *WPt-4553-Xcfa2293* | 1.74 | 4.74 | 0.246 |
| RDW | 21 | *QRdw.saas-2B* | *WPt-9812-WPt-4199* | 2.18 | 8.67 | 0.001 |
| | | *QRdw.saas-5A* | *Xbarc165-WPt-733649* | 2.62 | 11.65 | 0.001 |
| | | *QRdw.saas-5B* | *Xcfe86-WPt-1895* | 2.01 | 7.28 | 0.001 |
| | | *QRdw.saas-6A* | *Xgwm154-WPt-3855* | 2.51 | 16.75 | 0.002 |
| | 28 | *QRdw.saas-2B* | *WPt-9812-WPt-4199* | 2.29 | 7.84 | 0.002 |
| | | *QRdw.saas-5D* | *WPt-3825-WPt-667413* | 2.58 | 9.74 | 0.002 |
| | | *QRdw.saas-6B* | *Xgwm88-WPt-2000* | 2.42 | 10.07 | 0.002 |
| RGR | 21 | *QRgr.saas-5A* | *Xbarc165-WPt-733649* | 1.81 | 6.77 | -0.001 |
| | | *QRgr.saas-6B* | *Wpt-2000-Wpt-0446* | 2.50 | 10.62 | 0.002 |
| | 28 | *QRgr.saas-3D.1* | *Wpt-669426-Xcfd211* | 2.21 | 8.85 | 0.002 |
| | | *QRgr.saas-3D.2* | *Xcfd223-Wpt-667062* | 2.00 | 7.84 | 0.002 |
| | | *QRgr.saas-6A* | *Xgwm154-Wpt-3855* | 1.73 | 6.10 | -0.002 |
| | | *QRgr.saas-6B* | *Wpt-2000-Wpt-0446* | 3.50 | 12.74 | 0.002 |
| | | *QRgr.saas-7A* | *Wpt-0808-Wpt-53574R* | 2.52 | 10.74 | 0.002 |

[a]Positive / negative indicate Chuanmai 42 / Chuannong 16 allele produced larger value, respectively.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4 WPt-3451
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WPt-3566
7.4
WPt-5485
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12.8
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WPt-2461
5.6 Xbarc61
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RPt-7906
6.1
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WPt-6975
12.6
Xgwm268
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2A
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WPt-1480
11.2
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4.8 WPt-7739
2.9 WPt-5887
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43.2
Xgwm445
18.6
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WPt-734106
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1D
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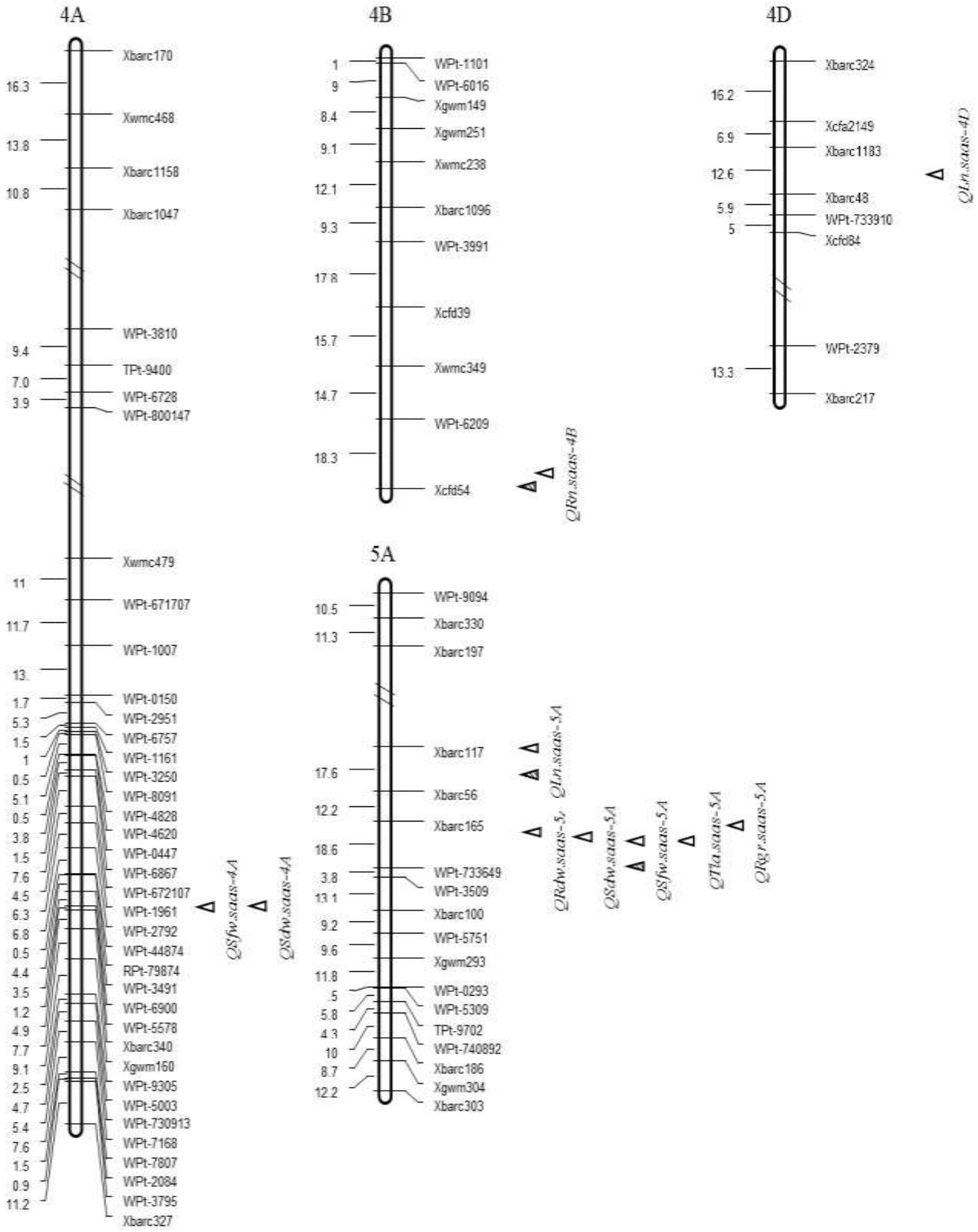
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WPt-1007
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1.7
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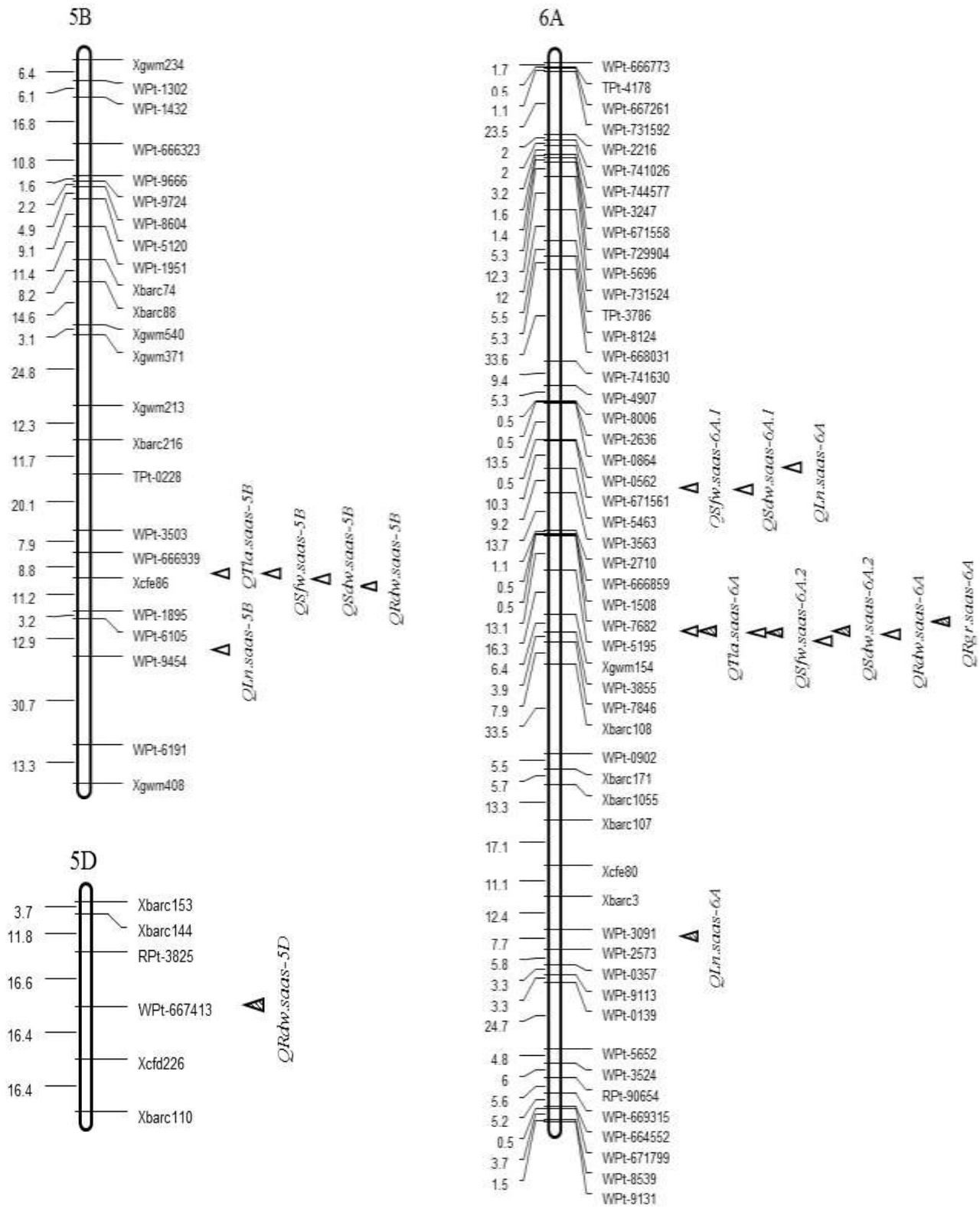
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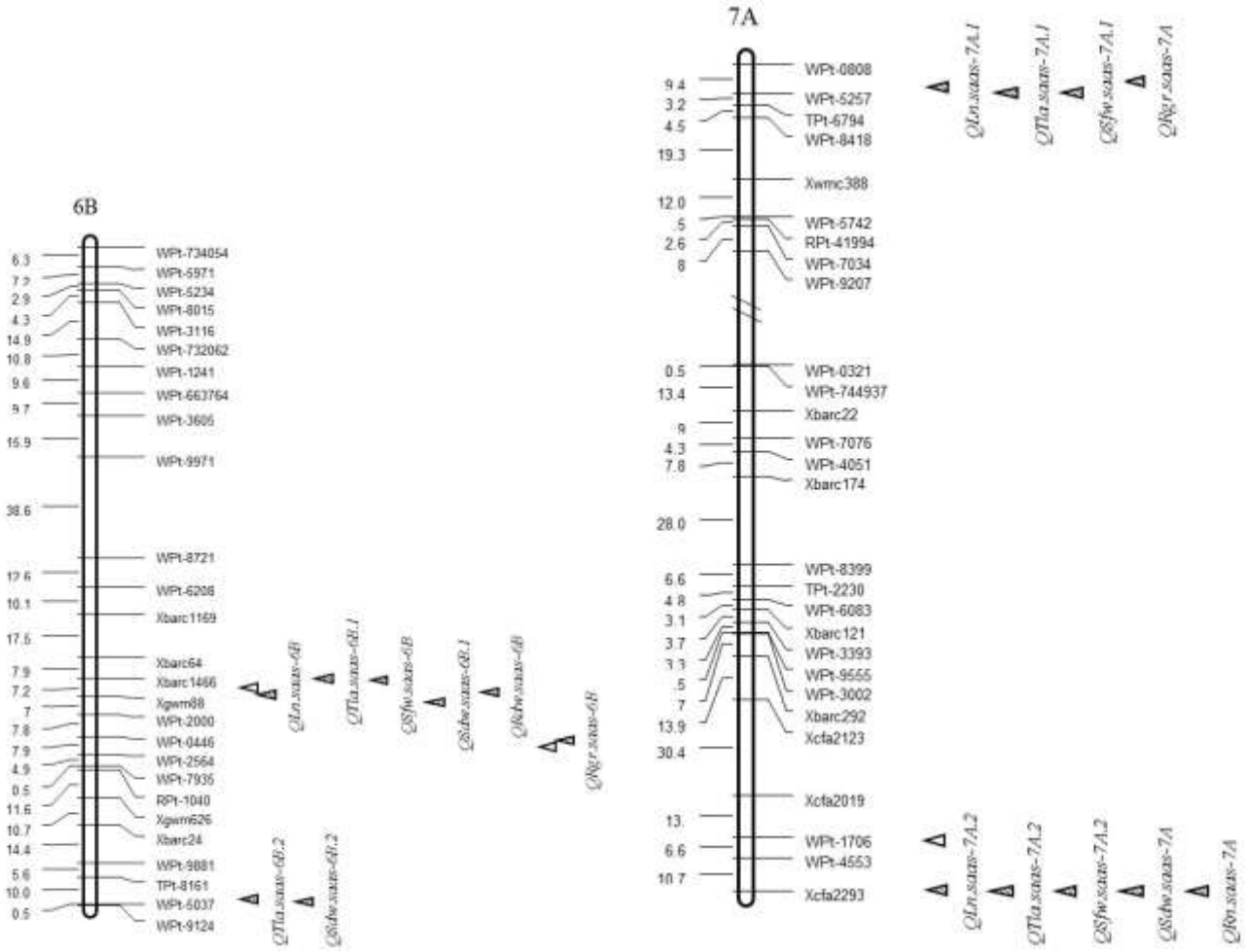


**Figure 2. QTLs for early vigor related traits. The triangle indicates the position of QTL peak.** The dotted triangles indicate QTLs for 28 days, while open triangles represent.

The LOD value of all the detected QTLs for RDW was less than 3.00, and the QTLs on 5A, 6A and 6B explained more than 10% of phenotypic variation (Table 3). In this study, Chuanmai 21 alleles at these loci of detected QTLs increased RDW.

RDW was positively significantly related with shoot weight, especially in 28-day growth period (Table 2), indicating the importance of root system in the late part of the seedling growth stage. In the trial of 28-day growth, detected QTL interval *Xbarc64-Wpt2000* for RDW on chromosome 6B overlapped with QTL for SFW or SDW (Fig. 2), and both QTLs produced positive effects on RDW and SFW/SDW (Table 3).

***Relative growth rate*:** In this study, the dry weight of whole seedling was used to estimate the RGR, considering that root system was necessary for seedling shoot growth to absorb nutrition from the solution. A total of 6 QTLs were mapping to 3D, 5A, 6A, 6B and 7A, respectively. *QRgr.saas-6B* was the only one QTL detected in both growth periods and with the highest LOD value more than 3.00 (Table 3). Both *QRgr.saas-6B* and *QRgr.saas-7A* explained more than 10% of phenotypic variation. At the two QTL loci, Chuanmai 42 carried RGR-increasing alleles.

SDW and RDW were involved in calculating RGR. QTL intervals for SDW and RDW were consistent with QTL intervals for RGR on chromosomes 5A, 6A and 6B, respectively (Fig. 2). QTL intervals on 6A and 6B produced positive effects on SDW, RDW and RGR, explaining the significant positively correlations among them.

In this study, a total of 40 QTLs associated with early vigor were identified on 14 chromosomes with their LOD value more than 2.00 (Table 3; Fig. 2) and 25 QTLs explained more than 10% of the phenotypic variation. Among the 25 QTLs, 17 QTLs increased the phenotypic values through Chuanmai

**Table 4. Reported yield-related QTLs around the intervals for early vigor QTL clusters in Chuanmai 42-derived RILs.**

| Marker interval | QTL for early vigor | Reported yield-related QTLs[§] | Chromosome |
|---|---|---|---|
| *Xbarc56-Wpt733649* | *QTla.saas-5A* | GY (Huang *et al.*, 2004; Cuthbert *et al.*, 2008) | 5AS |
| | *QSdw.saas-5A* | | |
| | *QSfw.saas-5A* | SNP (Jia *et al.*, 2013) | |
| | *QRdw.saas-5A* | GNS (Su *et al.*, 2009) | |
| | *QRgr.saas-5A* | TKW (Cuthbert *et al.*, 2008) | |
| *Xgwm154-Wpt3855* | *QTla.saas-6A* | SSM (Li, 2014) | 6AC |
| | *QSdw.saas-6A.2* | PH (Li, 2014) | |
| | *QSfw.saas-6A.2* | TKW (Huang et al., 2006; Kuchel *et al.*, 2007) | |
| | *QRdw.saas-6A* | | |
| | *QRgr.saas-6A* | | |
| *Xbarc1466-Wpt0466* | *QLn.saas-6B* | GNS (Li, 2014; Su *et al.*, 2009) | 6BL |
| | *QTla.saas-6B.1* | SSM (Li, 2014) | |
| | *QSdw.saas-6B.1* | GY (Tang *et al.*, 2011; Czyczyło-Mysza *et al.*, 2011) | |
| | *QSfw.saas-6B* | | |
| | *QRdw.saas-6B* | | |
| | *QRgr.saas-6B* | | |
| *Wpt0808-Wpt8418* | *QLn.saas-7A.1* | GY (Kumar *et al.*, 2007) | 7AS |
| | *QTla.saas-7A.1* | GNS (Huang *et al.*, 2004; Kumar *et al.*, 2007) | |
| | *QSfw.saas-7A.1* | TKW (Huang *et al.*, 2004) | |
| | *QRgr.saas-7A.1* | | |

[§]GNS, grain number per spike; TKW, thousand-kernel weight; GY, grain yield; SNP, spike number per plant; SSM, spikes per square meter; PH, plant height

42 alleles, whereas Chuannong 16 only had 8 early-vigor-enhancing QTLs (Table 3). A total of 4 genomic regions with clustered QTLs for RGR and other traits were detected on chromosomes 5A, 6A, 6B and 7A, respectively (Fig. 2). The genomic regions *Xbarc56-Wpt3509* on chromosome 5A and *Xgwm154-Wpt7846* on 6A were associated with total leaf area, shoot weight, root dry weight and RGR, and their haplotype enhancing the early vigor was from Chuannong 16. The QTL cluster intervals *Xbarc1466-Wpt0446* on 6B and *Wpt0808-Wpt5257* on 7A were also associated with both shoot-related traits and RGR, and Chuanmai 42 haplotypes in the genomic regions of 6B and 7A produced seedlings with greater early vigor. The average LOD value of detected QTLs in *Xbarc1466-Wpt0466* of 6BL was more than 3.00 and the highest one among these 4 genomic regions, which explained more that 11% of phenotypic variation averagely.

## DISCUSSION

Chuanmai 42 was a SHW-derived cultivar with great early vigor and grain yield, especially in drought-suffering regions. Furthermore, Chuanmai 42-derived cultivar also showed a higher rate of aboveground dry matter accumulation in the early growth period, comparing to these non-Chuanmai 42-derived commercial cultivars (Tang *et al.*, 2015). In this study two groups of 127 Chuanmai 42 x Chuannong 16 RILs and their parents were set up to dissect the molecular basis of great early vigor of Chuanmai 42 for 21- and 28-day growth, respectively. All the traits were investigated destructively from different groups, and the two groups could be also thought as two independent experiments (trials). To measure RGR, kernel weight was used as initial dry weight on day 0, as seed weight was greatly positively associated with early vigor (Zaidman *et al.*, 2010; Moshatati and Gharineh, 2012; Rezapour *et al.*, 2013).

***QTL analysis for early vigor*:** The early vigor related traits was controlled by polygenes and affected greatly by growing period, such as QTLs on 5A and 6B whose LOD values were rather different between 21- and 28-day growth periods. The reported QTLs related to early vigor were distributed throughout almost whole genome of wheat (ter Steege *et al.*, 2005; Landjeva *et al.*, 2008, 2010; Sanguineti *et al.*, 2007; Ibrahim *et al.*, 2012). The LN QTL *QLn.saas-4D* was consistent with the QTL detected by ter Steege *et al.* (2005) by comparing different genetic/bin maps. Spielmeyer *et al.* (2007) identified an interval *Xbarc3-NW3106* for seedling early vigor on chromosome 6A that was associated with leaf width and coleoptile length, and in this study only *QLn.saas-6A* was detected in that genomic interval (*Xbarc3-Wpt3091*). However, we detected another genomic region for early vigor associated with leaf area, shoot weight and RGR on chromosome 6A. Sanguineti *et al.* (2007) identified *Xgwm268* significantly associated with SDW on chromosome 1BL, whereas we detected a SDW QTL on chromosome 1BS.

QTLs for SDW were detected on chromosomes 5A, 5B, 6A and 7A where QTLs for SDW under draught growth condition were also reported in other studies (An *et al.*, 2006; Guo *et al.*, 2012; Genc *et al.*, 2010), indicating that great early vigor was positively related to drought resistance in wheat. QTLs for total leaf area were also identified on these chromosomes. The rapid growth of leaves could reduce evaporative losses from the soil and enhancing the population water-use efficiency (Gregory *et al.*, 2000)

The majority of the detected QTLs related to RDW and RN were not consistent with the chromosome regions of reported QTLs (ter Steege *et al.*, 2005; Sanguineti *et al.*, 2007), possibly due to their sensitiveness to different growth period or environment. On chromosomes 3D, 4B and 7A, RN QTLs were detected in both our study and other studies by Guo *et al.* (2012), Ren *et al.* (2012a) and Ibrahim *et al.* (2012b), but the relationship between these QTLs and reported QTLs was not very clear because of different serviced marker types. And this case also happened to RDW QTLs on chromosome 6A.

RGR was a composite trait that was derived from SDW and RDW on days 21 and 28, In addition to their consistency with QTL intervals for RGR, SDW and RDW on 5A and 6B, the LOD value of *QRgr.saas-6B* rose in the growth period from days 21 to days 28, indicating the significant effect of the 6B genomic region on enhancing the early vigor with the elongation of growth period. And few early vigor related QTLs had been reported on 6B so far.

***Early vigor and yield-related QTLs*:** Seedling growth is one essential physiological process associated with wheat yield establishment. Some early vigor QTLs were reported to overlap with yield-related QTLs such harvest index and spike number (Ibrahim *et al.*, 2010, 2012). In this study, the intervals of QTLs for seedling shoot weight on 4A and LN on 4D were consistent with QTLs for thousand kernel weight (TKW), spike number per plant (SNP) and grain yield (GY) detected by Tang *et al*. (2011) and Li (2014) in the same RILs, respectively. RN QTL on chromosome 4B was located in the interval of reported QTLs for grain number per spike (GNS) (Deng *et al.*, 2011; Jia *et al.*, 2013).

A total of 4 genomic regions for RGR and the other early vigor related traits were mapping to chromosomes 5A, 6A, 6B and 7A in this RILs. Around these genomic regions of QTL clusters, several yield-related QTLs were also reported in this RILs as well as other populations (Table 4). The interval *Xbarc1466-Wpt0466* was the genomic region with the strongest effect on early vigor where QTLs for GNS, spikes per square meter (SSM) and GY were also detected in the same RIL population (Tang *et al.*, 2011; Li, 2014). QTLs for SSM and plant height (PH) were also detected in this population and located in the genomic region of QTL cluster for early vigor on 6A (Li, 2014). Furthermore, Su *et al.* (2009) and Czyczyło-Mysza *et al.* (2011) also mapped QTLs for GNS and GY in this interval, respectively. And the genomic region on 6A was also associated with TKW in other populations (Huang et al., 2006; Kuchel *et al.*, 2007)

On chromosome 5AS, five early vigor related QTLs were mapped to the interval *Xbarc56-Wpt733649* where QTLs for SNP (Jia *et al.*, 2013), GNS (Su *et al.*, 2009), TKW (Cuthbert *et al.*, 2008) and GY (Huang *et al.*, 2004; Cuthbert *et al.*, 2008) were identified in other populations. And the interval for LN, TLA, SFW and RGR on chromosome 7A was consistent with the QTLs for GNS, TKW and GY in other populations (Huang *et al.*, 2004; Kumar *et al.*, 2007). However, no QTLs for yield-related traits were detected in the intervals of 5AS and 7AS from the RILs of this study, and this may be caused by the investigated yield-related traits that were under a well-irrigated condition without any drought stress through the whole growth period (Tang *et al.*, 2011; Li, 2014), while the great early vigor was often positively correlated with drought resistance (Gregory *et al.*, 2000).

Chuanmai 42 was thought to be an elite breeding parent, and at least 19 cultivars were released from its derivations (Yang *et al.*, 2009; Li *et al.*, 2014; Wan *et al.*, 2015). It showed greater early vigor than other cultivars in field trials, and its grain yield was higher than the majority of resent cultivars. Moreover, cultivars derived from Chuanmai 42 also showed greater early vigor and grain yield (Tang *et al.*, 2015). Among the four genomic regions detected for early vigor in this study, two genomic regions enhanced early vigor through Chuanmai 42 haplotypes, including the 6B interval with the strongest phenotypic effect. The other two was from Chuannong 16, including 5A and 6A genomic regions. These QTL alleles from both parents can be used in molecular assistant selection (MAS) for enhancing wheat early vigor in breeding program.

***Acknowledgements*:** This work was partially supported by the NSFC (31401382&31401383),, National Key Research and Development Program of China (2016YFD0100102), and Department of Science and Technology of Sichuan Province (2014TD0014, 2015JQ0022, 2016NYZ0049& 2017JY0077).

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