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ORIGINAL PAPER

QTL mapping for seedling traits in wheat grown under varying concentrations of N, P and K nutrients

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Abstract Nutrient use efficiency (NuUE), comprising nutrient uptake and utilization efficiency, is regarded as one of the most important factors for wheat yield. In the present study, six morphological, nine nutrient content and nine nutrient utilization efficiency traits were investigated at the seedling stage using a set of recombinant inbred lines (RILs), under hydroponic culture of 12 treatments including single nutrient levels and two- and three-nutrient combinations treatments of N, P and K. For the 12 designed treatments, a total of 380 quantitative trait loci (QTLs) on 20 chromosomes for the 24 traits were detected. Of these, 87, 149 and 144 QTLs for morphological, nutrient content and nutrient utilization efficiency traits were found, respectively. Using the data of the average value (AV) across 12 treatments, 70 QTLs were detected for 23 traits. Most QTLs were located in new marker regions. Twenty-six important QTL clusters were mapped on 13 chromosomes, 1A, 1B, 1D, 2B, 3A, 3B, 4A, 4B, 5D, 6A, 6B, 7A and 7B. Of these, ten clusters involved 147 QTLs (38.7%) for investigated traits, indicating that these 10 loci were more important for the NuUE of N, P and K. We found evidence for cooperative uptake and utilization (CUU) of N, P and K in the early growth period at both the phenotype and QTL level. The correlation coefficients (r) between nutrient content and nutrient utilization efficiency traits for N, P and K were almost all significantly positive correlations. A total of 32 cooperative CUU loci (L1–L32) were found, which included 190 out of the 293 QTLs (64.8%) for the nutrient uptake and utilization efficiency traits, indicating that the CUU-QTLs were common for N, P and K. The CUU-QTLs in L3, L7, L16 and L28 were relatively stable. The CUU-QTLs may explain the CUU phenotype at the QTL level.

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Introduction

Nitrogen (N), phosphorus (P) and potassium (K) are often considered as three of the most important mineral nutrient elements limiting plant growth in agricultural systems. To increase the economic output of crops, large amounts of fertilizer have been used to meet the demand for N, P and K. Subsequently, improper practices have caused environmental problems (Giles 2005; Davidson 2009), low use efficiency for fertilizers (Schachtman and Shin 2007) and high annual energy consumption (Ceotto 2005). The high inputs and low use efficiency of fertilizers not only increase the cost of crop production, but also accelerate the exhaustion of non-renewable resources. For example, it has been estimated that P resources will be exhausted worldwide by the end of this century (Vance et al. 2003). It is therefore important to develop crop varieties that use nutrients (especially N, P and K) in more efficient ways.

These new varieties should offer a more cost-efficient solution than relying on fertilizer application alone.

Nutrient use efficiency (NuUE) comprises nutrient uptake and utilization efficiency (Janssen 1998). Considerable work has been undertaken to elucidate the genotypic differences in NuUE for N, P, K and other nutrients (Rengel and Marschner 2005; Ozturk et al. 2005; Tesfaye et al. 2007; Rengel and Damon 2008; White et al. 2010). The development of varieties with high NuUE constitutes a feasible attempt to increase fertilizer use efficiency (Rengel and Marschner 2005; Galloway et al. 2008). To improve NuUE, an elaborate understanding of the genetic basis of traits that manifest at different stages of plant development under varying nutrient conditions is required. In wheat (*Triticum aestivum* L.), genotypic differences in the NuUE of N, P or K have been well documented, suggesting that it is possible to improve NuUE through a genetic approach (Hirel et al. 2001; Ozturk et al. 2005; Harada and Leigh 2006; Laperche et al. 2007; Rengel and Damon 2008). However, the genetic basis of N, P and K uptake and utilization is still poorly understood.

The nutrient-related traits of N, P and K metabolism are complicated quantitative traits. Quantitative trait locus (QTL) analysis provides an effective approach to dissect complicated traits into component loci and study their relative effects on a specific trait (Doerge 2002). In wheat, QTL analysis has mostly been used to study the effects of low and high N levels (Quarrie et al. 2005, 2006; An et al. 2006; Laperche et al. 2006, 2007, 2008; Fontaine et al. 2009), as well as P deficiency and sufficiency levels (Su et al. 2006, 2009; Li et al. 2007b), enabling us to understand NuUE at the QTL level. A QTL analysis was employed to dissect the genetic basis of grain protein, and P, K and other macro/micro-nutrient concentrations in tetraploid wheat (Peleg et al. 2009). To date, there have been only few studies identifying QTLs that allow adaptation to different levels of N, P and K simultaneously under uniform environments.

The objective of this study was to detect QTLs grown at the seedling stage in various concentrations of N, P and K nutrients under hydroponic culture using a population of recombinant inbred lines (RILs) derived from two Chinese winter wheat varieties.

Materials and methods

Plant materials

The population used for QTL analysis consisted of a set of 131 RILs derived from a cross of Chuan 35050 × Shannong 483 (F_{16} in 2008, Li et al. 2007a). Chuan 35050 has been cultivated in the South-western Winter Wheat Region of China. Shannong 483 has been grown in the Huang-huai Winter Wheat Region. Shannong 483 was derived from 'Ai-Meng-Niu', one of the most famous germplasms and backbone parents in Chinese wheat breeding programs. 'Ai-Meng-Niu' was released by Shandong Agricultural University in 1980. Because of the excellent comprehensive yield traits and nice combining ability of this germplasm, more than 16 famous varieties, planted on more than 30 million hectares, have been developed from 'Ai-Meng-Niu'.

Experimental design

Single treatments of N, P or K were administered at different concentration levels, and all combinations of either two or three nutrients were also tested. The nutrient solution was composed of Hoagland's nutrient solution (Hoagland and Arnon 1950) that had been modified to optimize wheat growth (Table 1). Twelve treatments (T1–T12) were designed (Table 2). N was administered at high N (HN), middle N (MN) and low N (LN) levels (An et al. 2006); P at middle P (MP) and low P (LP) levels (Li et al. 2007b); and K at middle K (MK) and low K (LK) levels. The middle N, P and K levels were applied in reformative Hoagland's nutrient solution (Table 1). Because high concentrations of P would cause some micronutrients to be deposited as insoluble phosphates and would have made it difficult to achieve a well-balanced nutrient solution (Zhang et al. 2003), we did not set test a high P treatment. Because K was present in the culture solution mainly as potassium chloride (KCl) and excessive chloride may be toxic (Xu et al. 2000; White and Broadley 2001), it also was not tested at the high level. The two-nutrient combinations were HNLP, HNLK, LNLP, LNLK and LPLK; and the

Table 1 Nutrient solution ingredients for wheat seedling growth

Ingredients	Concentration (mmol/L)	Ingredient	Concentration (μmol/L)
$(NH_4)_2SO_4 \cdot H_2O$	1.0	H_3BO_3	1.0
$Ca(NO_3)_2 \cdot 4H_2O$	1.0	$CuSO_4 \cdot 5H_2O$	0.5
KH_2PO_4	0.2	$ZnSO_4 \cdot 7H_2O$	1.0
KCl	1.8	$MnSO_4 \cdot H_2O$	1.0
$MgSO_4 \cdot 7H_2O$	0.5	FeEDTA	100
$CaCl_2$	1.5	$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	0.1

Table 2 Summary of the 12 treatments of N, P and K nutrients

Treatments		$NH_4^+ + NO_3^-$		$H_2PO_4^-$		K^+	
Code	Name	Times	Concentration (mmol L^{-1})	Times	Concentration (mmol L^{-1})	Times	Concentration (mmol L^{-1})
T1	MNMPMK	1×	4.0	1×	0.2	1×	2.0
T2	HN	3×	12.0	1×	0.2	1×	2.0
T3	LN	1/5×	0.8	1×	0.2	1×	2.0
T4	LP	1×	4.0	1/10×	0.02	1×	2.0
T5	LK	1×	4.0	1×	0.2	1/10×	0.2
T6	HNLP	3×	12.0	1/10×	0.02	1×	2.0
T7	LNLP	1/5×	0.8	1/10×	0.02	1×	2.0
T8	HNLK	3×	12.0	1×	0.2	1/10×	0.2
T9	LNLK	1/5×	0.8	1×	0.2	1/10×	0.2
T10	LPLK	1×	4.0	1/10×	0.02	1/10×	0.2
T11	HNLPLK	3×	12.0	1/10×	0.02	1/10×	0.2
T12	LNLPLK	1/5×	0.8	1/10×	0.02	1/10×	0.2

MNMPMK middle nitrogen/middle phosphorus/middle potassium, *HN* high nitrogen, *LN* low nitrogen, *LP* low phosphorus, *LK* low potassium

three-nutrient combinations were HNLPLK and LNLPLK.

The RILs and their parents were grown in a greenhouse at the Shandong Agriculture University. The experiments adopted random complete block design, with three replications for each treatment. All 131 RILs and their parents were contained in one tray for each of the 12 treatments. Two hundred seeds from each line and their parents [the trial needed to select 108 uniform seedlings (3 [plants] × 12 [treatments] × 3 [replications]) when transferred] were sterilized for 5 min in a 10% solution of H_2O_2, washed with distilled water, and germinated on moist filter paper in Petri dishes for 7 days. For each replicate, three uniform seedlings from each line with both the embryogenic primary root and coleoptile (3–4 cm long) were selected and transferred into holes in trays (the seedlings were attached with a sponge), which were placed on plastic tanks containing 20 L of nutrient solution. The containers and tops for hydroponic culture were opaque so as to produce healthy roots and to discourage the growth of algae. The distances between different lines were 3 × 3 cm. The solution was continuously aerated through rubber tubes connected to an air compressor. The nutrient solution was renewed every 4 days and the pH was adjusted to 6.2 using a dilute NaOH solution (0.5%) every day. The plants were grown for 30 days (from 27 November to 27 December 2008). The temperature, relative humidity and the photoperiod were measured and recorded every 10 min by the ZDR Data Loggers (ZDR, Zhejiang University Electric Equipment Factory, China), and they varied from 5.0 to 33.9°C, 5.7 to 59.5% and 0.1 to 20.0 Klux, respectively.

Trait measurement

The summary of all 24 investigated traits and their measurement methods are listed in Table 3. Nine plants (three replicates) from each line were harvested at the four-leaf stage. The plants were first removed from the plastic tanks. The roots were rinsed in distilled water for at least 10 min, and excess water was soaked up using absorbent paper. The numbers of axial roots (ARN) were counted for each plant, and ARN for each line was calculated as the average of the nine plants. The maximal root length (MRL) or shoot height (SH) was measured with a ruler. All roots and shoots were then separated using scissors, and fresh roots or shoots from the nine sampled plants of each line were combined. All samples were dried at 60°C for 24 h to a constant mass, and the root dry weight (RDW) and shoot dry weight (SDW) were measured using 1/1,000 balances. The total dry weight (TDW) was calculated as RDW + SDW.

All plant samples were milled to determine the N, P and K contents. The total N concentrations were determined by the Kjeldahl method (Kjeldahl 1883) using an NC analyzer (KDY-9820, Tongrun Ltd., China); the plant samples were digested with concentrated H_2SO_4 and H_2O_2 until the mixture was clear. To determine the P and K concentrations, dried tissue samples were digested using the mixed concentrated acids HNO_3:$HClO_4$ (3:1, v/v) until the mixture was clear. The P and K concentrations were analyzed according to the Japanese Industrial Standard Method using a sequential plasma spectrometer (ICPS-7500, Shimadzu Co. Ltd., Kyoto, Japan). The N, P and K contents for the roots or shoots of each plant (RNC and SNC, RPC and

Table 3 Summary of investigated traits and their measurement methods

Abbreviations	Traits	Units	Methods of trait measurement
Morphological traits			
ARN	The number of axial roots	Number	Average number of the nine plants
MRL	Maximal root length	cm	Measured with a ruler
SH	Shoot height per plant	cm	
RDW	Root dry weight per plant	mg plant^{-1}	Dried and weighted using 1/1,000 balances
SDW	Shoot dry weight per plant	mg plant^{-1}	
TDW	Total dry weight per plant	mg plant^{-1}	
Nutrient content traits			
RNC	Root N content per plant	mg plant^{-1}	Kjeldahl method (Kjeldahl 1883) using an NC analyzer (KDY-9820, Tongrun Ltd., China)
SNC	Shoot N content per plant	mg plant^{-1}	
TNC	Total N content per plant	mg plant^{-1}	
RPC	Root P content per plant	mg plant^{-1}	Japanese Industrial Standard Method using a sequential plasma spectrometer (ICPS-7500, Shimadzu Co. Ltd., Kyoto, Japan).
SPC	Shoot P content per plant	mg plant^{-1}	
TPC	Total P content per plant	mg plant^{-1}	
RKC	Root K content per plant	mg plant^{-1}	
SKC	Shoot K content per plant	mg plant^{-1}	
TKC	Total K content per plant	mg plant^{-1}	
Nutrient utilization efficiency traits			
RNUE	Root N utilization efficiency	mg^{2}RDW μg^{-1}RNC	RDW/[RN] = RDW^2/(RNC × 1000)
SNUE	Shoot N utilization efficiency	mg^{2}SDW μg^{-1}SNC	SDW/[SN] = SDW^2/(SNC × 1000)
TNUE	Total N utilization efficiency	mg^{2}TDW μg^{-1}TNC	TDW/[TN] = TDW^2/(TNC × 1000)
RPUE	Root P utilization efficiency	mg^{2}RDW μg^{-1}RPC	RDW/[RP] = RDW^2/(RPC × 1000)
SPUE	Shoot P utilization efficiency	mg^{2}SDW μg^{-1}SPC	SDW/[SP] = SDW^2/(SPC × 1000)
TPUE	Total P utilization efficiency	mg^{2}TDW μg^{-1}TPC	TDW/[TP] = TDW^2/(TPC × 1000)
RKUE	Root K utilization efficiency	mg^{2}RDW μg^{-1}RKC	RDW/[RK] = RDW^2/(RKC × 1000)
SKUE	Shoot K utilization efficiency	mg^{2}SDW μg^{-1}SKC	SDW/[SK] = SDW^2/(SKC × 1000)
TKUE	Total K utilization efficiency	mg^{2}TDW μg^{-1}TKC	TDW/[TK] = TDW^2/(TKC × 1000)

SPC, RKC and SKC, respectively) were calculated by multiplying each sample's concentration by the average plant dry weight. The total N, P and K contents (TNC, TPC and TKC) were calculated as RNC + SNC, RPC + SPC and RKC + SKC, respectively. The N, P and K utilization efficiencies (RNUE, SNUE, TNUE, RPUE, SPUE, TPUE, RKUE, SKUE and TKUE) were calculated by dividing the dry weight by the relative nutrient concentration relatively of the roots, shoots and total plant (Siddiqi and Glass 1981).

Data analysis

The analyses of variance (ANOVA), least significant difference (LSD) test and simple correlation coefficients between traits were calculated using the SAS software. The broad-sense heritability (h_B^2) were calculated using the GLM procedure in SAS according to Knapp et al. (1985). Heritability was calculated using a model where the 12 treatments were regarded as 12 replications and the genotype × treatment interaction as the error term.

An enriched genetic map (Wang et al. 2011) was used in the QTL analysis. The map consisted of 719 markers assigned to 21 chromosomes, giving a total map length of 4,008.4 cM with a marker density of 7.15 cM. The majority of markers were DArTs (Diversity Array Technology), SSRs, EST-SSRs and other molecular and biochemical loci. The software Windows QTL Cartographer 2.5 (Wang et al. 2007) was used to perform the QTL mapping. Composite-interval mapping (CIM) was selected to search for QTL of each trait separately for (i) each of the 12 treatments and (ii) the average value (AV) across 12 treatments. The parameter set-up ''model 6 standard analysis'' was used with a walk speed of 1 cM, ''forward and backward'' regression for the selection of the markers to control for the genetic background, up to five control markers, and a blocked window size of 10 cM to exclude closely linked control markers at the testing site. The threshold for declaring the presence of a significant QTL for each trait–treatment combination was defined by 1,000 permutations at $p \leq 0.05$ (Churchill and Doerge 1994) and the minimum LOD score of 3.0 was chosen.

Stoll et al. (2000) described the concept of a QTL cluster as the nearest two markers flanking the overlapping confidence interval (CI). Thus, we defined a QTL cluster as two or more significant QTLs with overlapping CI, defined as map distances corresponding to LOD $\geq$ 2.5.

Results

Phenotypic variation and correlations between traits

The results of ANOVA showed that the variance for either genotype or treatment effects on all the 24 investigated traits were significant at the $p \leq 0.001$ (Table 4). The LSD test showed that the average values of the investigated traits were in most cases significantly different among the 12 treatments (Table S1 ESM). These results indicated that the treatments and genetic background were very important in explaining the overall phenotypic variation.

The parents of the RIL population, Chuan 35050 and Shannong 483, exhibited distinct differences in most of the investigated traits in the 12 treatments, indicating that the parents had different NuUE for N, P and K. For the RIL population, there was a wide range of variation, with coefficient of variations (CVs = SD/Mean $\times$ 100%) from 4.97% of MRL in T9 to 41.04% of RKC in T8; the CVs for most trait–treatments were more than 20%. Transgressive segregations were observed for almost all of the 288 trait–treatments (Table S1 ESM). All the investigated traits in each trait–treatment exhibited continuous distribution, indicating a quantitative nature of inheritance (Fig. S1 ESM).

The heritability (h_B^2) for the investigated traits ranged from 20.7% (RKUE) to 76.9% (ARN) (Table S1 ESM). For morphological and N content traits, the h_B^2 values were higher and were all over 50.0%; however, the h_B^2 values were relatively lower for nutrient utilization efficiency traits, ranging from 20.7% (RKUE) to 45.1% (SPUE).

The correlation coefficients (r) among the 24 traits were mostly significant at the $p \leq 0.01$ level (Table S2 ESM). Only 84 correlation coefficients for trait–treatments (84/3,360 $\times$ 100% = 2.5%) were not significant; these correlation coefficients primarily described the relationships between ARN and RML/SH, and between MRL and SH/SPUE/SKUE, most of which were related to T1 treatment.

Major characteristics of the located QTLs

For the 24 traits, 380 QTLs were detected in at least one treatment. When the 12 treatments were considered, a total of 655 QTLs were detected; they were scattered across 20 of the 21 chromosomes except for 4D (Fig. 1; Table S3 ESM). Of these, 87, 149 and 144 QTLs for 6 morphological, 9 nutrient content and 9 nutrient utilization efficiency traits were found, respectively. An individual QTL explained between 5.8 (RKUE) and 43.8% (RDW) of the phenotypic variation. The highest LOD value for a single QTL was 10.2 for TDW. Thirty-two relatively high frequency (RHF) QTLs (detected in 190 trait–treatments, 190/655 $\times$ 100% = 29.0%), which were expressed in 4–10 treatments, were located for 19 out of the 24 traits (Table 5). The average contributions of the QTLs ranged from 10.8 (SH) to 18.2% (RKC). Of these, 16 RHF-QTLs, *QArn-1B.1*, *QRdw-1B.1*, *QSdw-1B*, *QTdw-1B.1*, *QSnc-1B*, *QTnc-1B*, *QSpc-1B.1*, *QTpc-1B.1*, *QSkc-1B.1*, *QTkc-1B.1*, *QSkue-1B*, *QSdw-1D*, *QRdw-4A*, *QRpc-4A.2*, *QSh-4B* and

Table 4 Analysis of variance (ANOVA) for the investigated traits under hydroponic culture

Traits	Source of variation		Heritability (h_B^2)	Traits	Source of variation		Heritability (h_B^2)
	Genotypes	Treatments			Genotypes	Treatments	
ARN	41.01***	85.53***	76.9	RKC	8.04***	697.25***	37.0
MRL	19.80***	32.69***	61.0	SKC	9.37***	636.02***	41.1
SH	31.14***	286.90***	71.5	TKC	10.14***	654.71***	43.2
RDW	22.10***	68.43***	63.7	RNUE	10.16***	116.12***	43.5
SDW	21.73***	69.30***	63.3	SNUE	12.23***	122.85***	42.1
TDW	22.30***	52.08***	64.0	TNUE	12.04***	116.91***	42.1
RNC	15.53***	36.52***	54.8	RPUE	7.91***	517.71***	36.5
SNC	20.82***	75.69***	62.3	SPUE	10.87***	482.08***	45.1
TNC	20.07***	43.29***	61.4	TPUE	10.75***	418.79***	44.8
RPC	9.74***	378.86***	42.2	RKUE	4.13***	540.16***	20.7
SPC	7.12***	718.39***	33.8	SKUE	9.82***	407.31***	42.4
TPC	7.92***	657.19***	36.6	TKUE	10.61***	517.78***	44.5

*** Indicates the significance at the $p \leq 0.001$

QArn-7A, were detected in more than six treatments, suggesting that they were more important RHF-QTLs.

Using the data of AV, 70 QTLs were detected for 23 traits (Fig. 1; Table S3 ESM). Of these, 64 QTLs were found in both treatment(s) and AV, and 6 QTLs only in AV. Furthermore, 28 QTLs for AV were located in the same marker region of RHF-QTLs, indicating QTLs in these 28 chromosome regions were relatively stable.

Important QTL clusters

Twenty-six important QTL clusters (C1–C26) with more than five traits were mapped on chromosomes 1A, 1B, 1D, 2B, 3A, 3B, 4A, 4B, 5D, 6A, 6B, 7A and 7B (Table 6). Of these, ten clusters were linked to more than 12 traits, including C1, C2, C3, C7, C14, C15, C17, C18, C23, C25, which involved 147 QTLs ($147/380 \times 100\% = 38.7\%$)

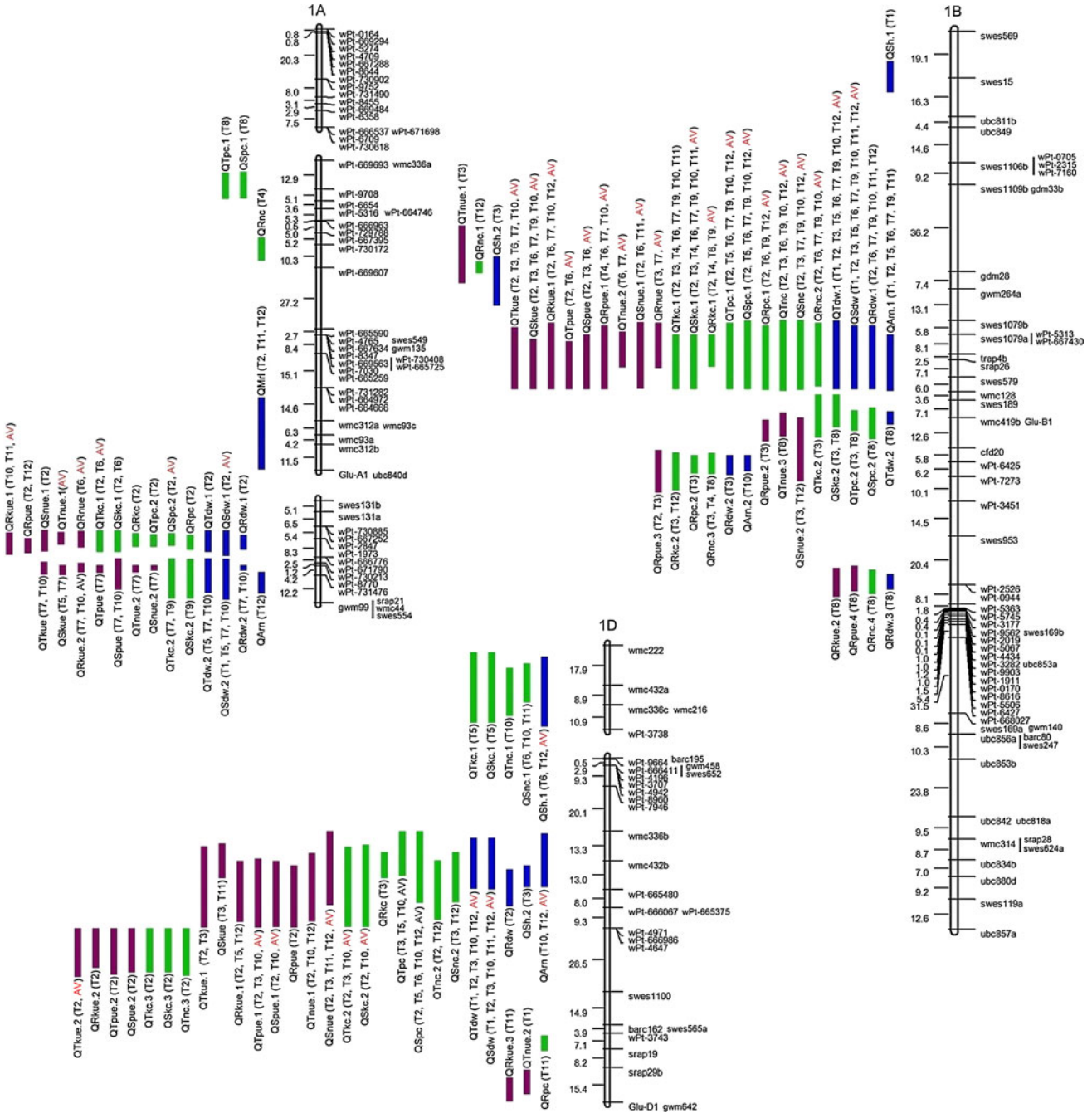

Fig. 1 Locations of QTLs for wheat seedling traits in 12 treatments of N, P and K nutrients based on RILs derived from Chuan 35050 × Shannong 483. QTLs are indicated on the *left side* of each chromosome. QTL intervals were LOD ≥ 2.5 with LOD peak values more than 3.0

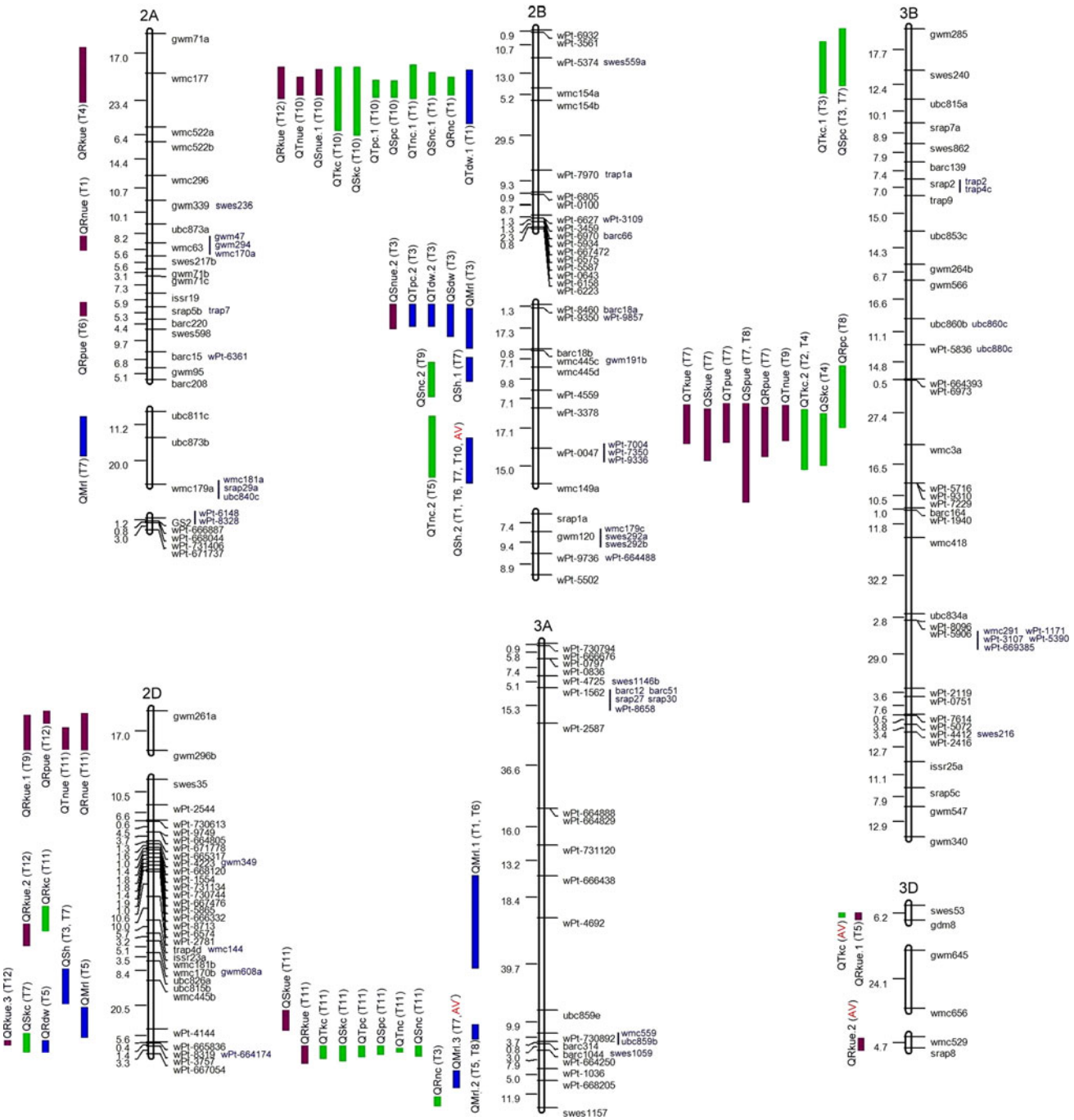

Fig. 1 continued

for investigated traits (Tables 5, 6; Fig. 1), which indicated that the 10 loci were more important for the NuUE of N, P and K.

The most important clusters were C3 and C7, which linked to 22 and 20 traits, respectively. Cluster C3 on chromosome 1B in marker region *swes1079a-swes579* involved 4, 9 and 9 QTLs for morphological, nutrient content and nutrient utilization efficiency traits, respectively, detected in 120 trait–treatments. Out of these, 17 RHF-QTLs (*QArn-1B.1*, *QRdw-1B.1*, *QSdw-1B*, *QTdw-1B.1*, *QRnc-1B.2*, *QSnc-1B*, *QTnc-1B*, *QRpc-1B.1*, *QSpc-1B*, *QTpc-1B.1*, *QRkc-1B.1*, *QSkc-1B.1*, *QTkc-1B.1*, *QRpue-1B.1*, *QRkue-1B*, *QSkue-1B* and *QTkue-1B*) were found. The additive effects of all QTLs were negative,

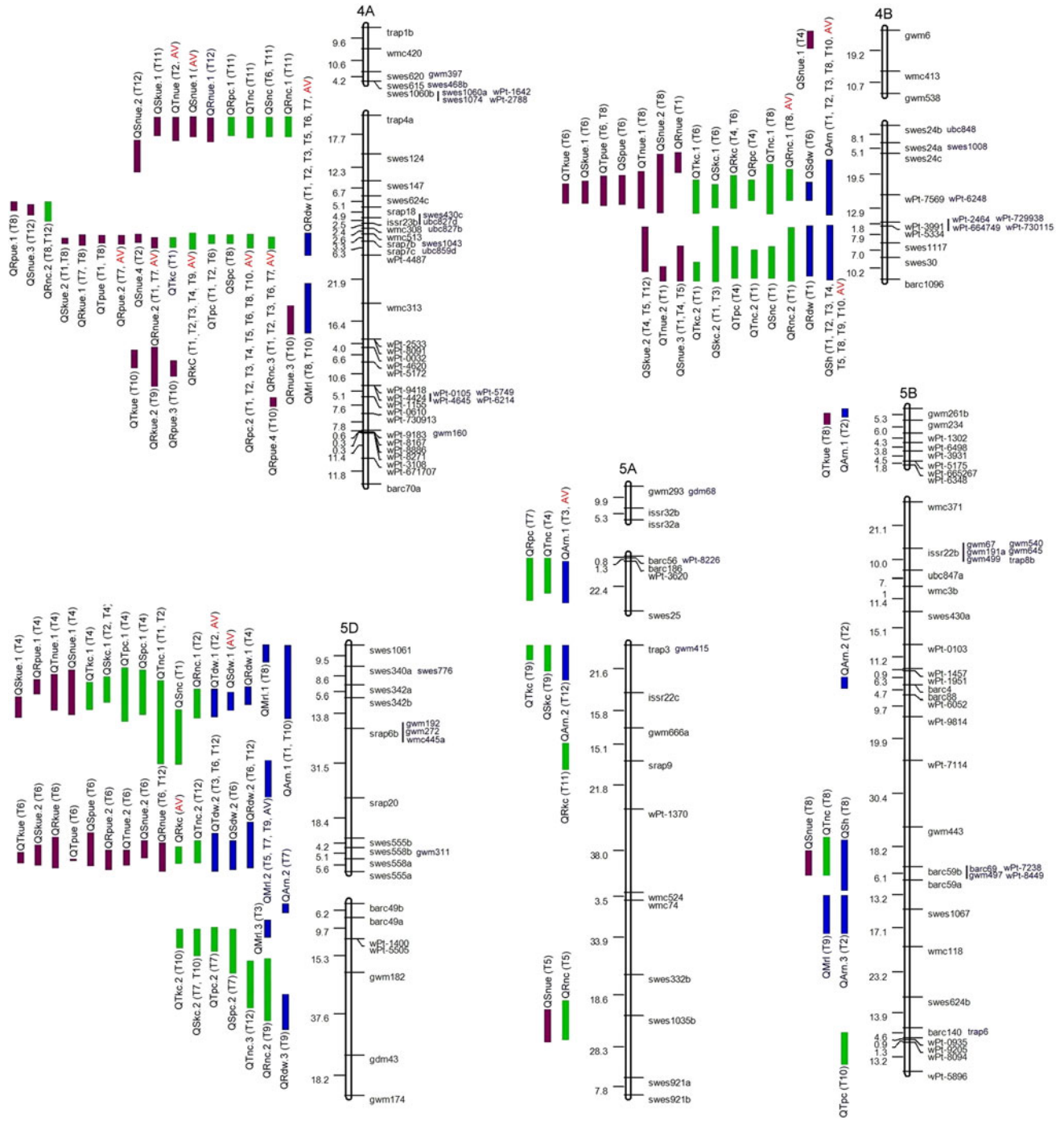

Fig. 1 continued

indicating that Shannong 483 increased the QTL effects. This suggests positive relationships among the QTLs. Cluster C7 on chromosome 1D in marker region *wmc432b-wPt-666067* involved 5, 7 and 8 QTLs for morphological, nutrient content and nutrient utilization efficiency traits, respectively, detected in 52 trait–treatments. Out of these, 4 RHF-QTLs (*QSdw-1D*, *QTdw-1D*, *QSpc-1D* and *QTkue-1D*) were detected. The increasing effects of all QTLs came from Shannong 483, suggesting positive relationships among the QTLs.

For the other eight more important clusters, C1 and C2 on chromosome 1A, and C15 on chromosome 4B involved 13, 13 and 14 QTLs for investigated traits, respectively. Similarly to Clusters C3 and C7, the increasing effects of

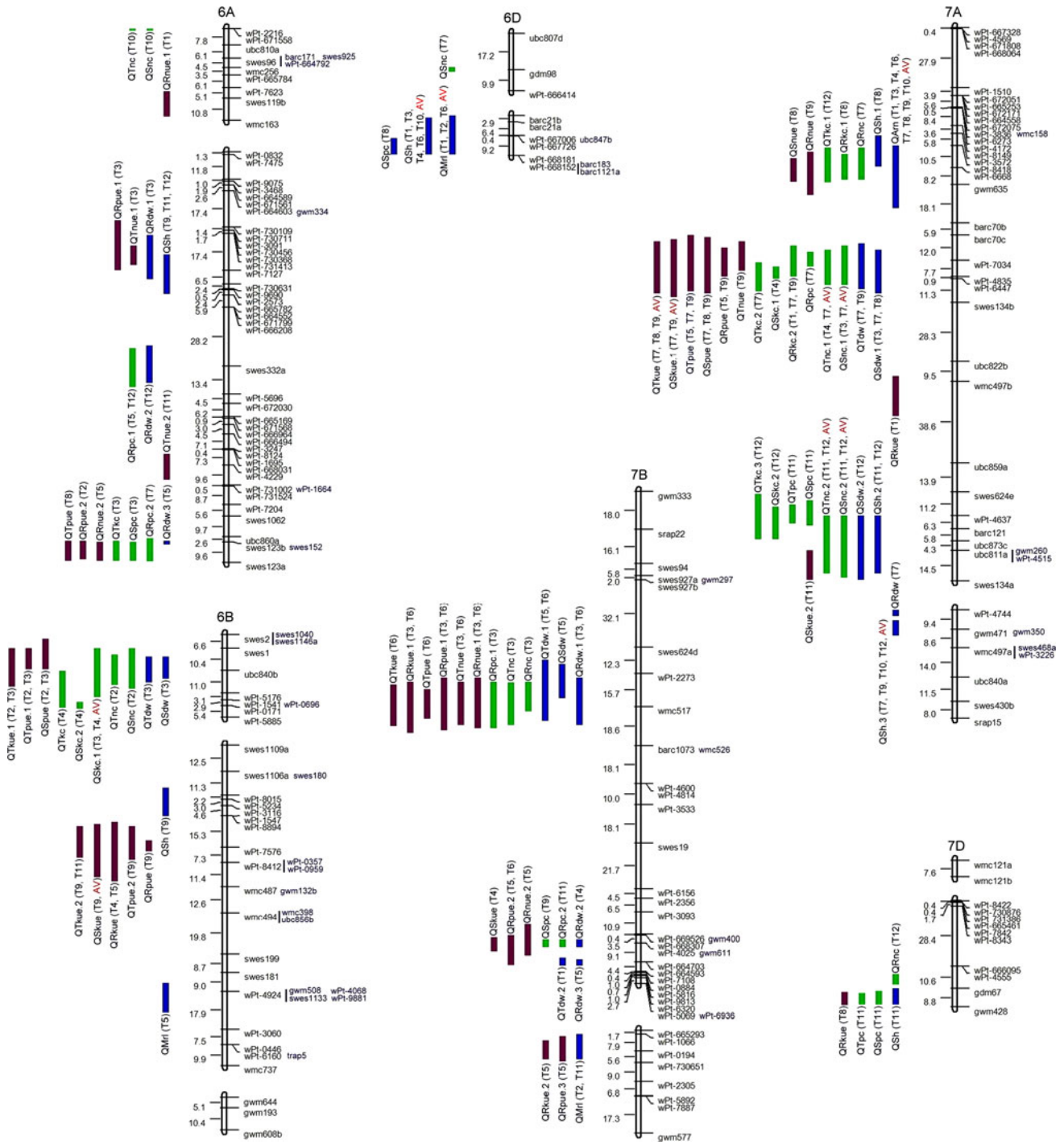

Fig. 1 continued

all QTLs came from Shannong 483, and the relationships among these QTLs were positive. Cluster C14 on 4A, C17 and C18 on 5D, C23 on 7A, and C25 on 7B involved 13, 13, 13, 14 and 12 QTLs for investigated traits, respectively. Chuan 35050 increased the effects of all QTLs, indicating positive relationships among them.

Discussion

QTL location and QTL clusters for NuUE

Some studies of QTL location for wheat traits related to NuUE of N and P have been conducted. The majority of

Table 5 Summary of relatively high frequency QTLs (RHF-QTLs), defined as QTLs detected in at least four treatments

Traits	QTLs	Treatments	LODs	Additive effects		Contributions (%)	
				Range	Average	Range	Average
ARN	*QArn-1B.1*	T1, T2, T5, T6, T7, T9, T11	3.0–6.4	−0.353 to −0.586	−0.484	6.2–16.4	11.0
	QArn-4B	T1, T2, T3, T8, T10	3.0–5.1	−0.387 to −0.570	−0.491	6.9–16.0	11.8
	QArn-7A	T1, T3, T4, T6, T7, T8, T9, T10	4.1–8.3	0.427 to 0.612	0.498	9.3–20.3	13.3
SH	*QSh-2B.2*	T1, T6, T7, T10	3.3–6.2	0.921 to 1.731	1.197	9.5–23.2	13.9
	QSh-4B	T1, T2, T3, T4, T5, T8, T9, T10	3.9–9.1	−0.971 to −1.668	−1.372	11.1–28.4	17.4
	QSh-6D	T1, T3, T4, T6, T10	3.0–5.3	−0.786 to −1.228	−1.079	7.3–14.0	10.9
	QSh-7A.3	T7, T9, T10, T12	3.0–4.5	1.734 to 2.258	1.997	10.1–11.7	10.8
RDW	*QRdw-1B.1*	T2, T6, T7, T9, T10, T11, T12	3.3–7.3	−1.408 to −1.969	−1.741	8.9–19.2	13.9
	QRdw-4A	T1, T2, T3, T5, T6, T7	4.0–5.9	2.572 to 3.867	3.444	10.1–16.0	12.5
SDW	*QSdw-1A.2*	T1, T5, T7, T10	3.5–6.2	−7.019 to −9.756	−7.840	7.7–15.5	11.4
	QSdw-1B	T1, T2, T3, T5, T6, T7, T9, T10, T11, T12	3.4–8.6	−3.914 to −7.584	−5.754	9.0–23.7	13.8
	QSdw-1D	T1, T2, T3, T10, T11, T12	3.0–5.8	−4.238 to −7.164	−5.432	8.2–15.5	12.1
TDW	*QTdw-1B.1*	T1, T2, T3, T5, T6, T7, T9, T10, T12	3.5–10.2	−5.108 to −11.429	−7.663	9.4–27.3	15.1
	QTdw-1D	T1, T2, T3, T10, T12	3.4–5.8	−5.273 to −8.447	−6.831	9.5–14.7	11.9
RNC	*QRnc-1B.2*	T2, T6, T7, T9, T10	3.7–6.4	−0.052 to −0.084	−0.071	9.8–15.9	12.7
	QRnc-4A.3	T1, T2, T3, T6, T7	3.1–5.5	0.129 to 0.170	0.143	9.5–15.4	12.5
SNC	*QSnc-1B*	T2, T3, T7, T9, T10, T12	3.2–7.6	−0.191 to −0.479	−0.280	8.4–18.6	13.6
TNC	*QTnc-1B*	T2, T3, T6, T9, T10, T12	3.6–9.3	−0.253 to −0.590	−0.386	9.1–23.2	17.0
RPC	*QRpc-1B.1*	T2, T6, T9, T12	4.7–6.3	−0.012 to −0.038	−0.023	13.0–17.1	15.4
	QRpc-4A.2	T1, T2, T3, T4, T5, T6, T8, T10	3.6–8.7	0.019 to 0.090	0.056	12.4–22.9	15.8
SPC	*QSpc-1B.1*	T2, T5, T6, T7, T9, T10, T12	3.2–8.5	−0.035 to −0.197	−0.091	10.2–24.1	15.8
	QSpc-1D	T2, T5, T6, T10, T12	3.2–6.3	−0.031 to −0.200	−0.086	10.1–27.3	15.2
TPC	*QTpc-1B.1*	T2, T5, T6, T7, T9, T10, T12	3.6–8.3	−0.052 to −0.236	−0.110	10.4–21.7	17.1
RKC	*QRkc-1B.1*	T2, T4, T6, T9	3.6–5.7	−0.017 to −0.107	−0.070	10.1–15.2	12.5
	QRkc-4A	T1, T2, T3, T4, T9	4.7–9.9	0.042 to 0.234	0.178	11.9–25.4	18.2
SKC	*QSkc-1B.1*	T2, T3, T4, T6, T7, T9, T10, T11	3.3–8.4	−0.133 to −0.567	−0.300	8.6–20.1	11.6
TKC	*QTkc-1B.1*	T2, T3, T4, T6, T7, T9, T10, T11	3.4–8.3	−0.135 to −0.643	−0.364	8.3–20.6	12.7
SNUE	*QSnue-1D*	T2, T3, T11, T12	3.0–4.1	−0.086 to −0.123	−0.102	10.4–11.7	11.0
RPUE	*QRpue-1B.1*	T4, T6, T7, T10	3.5–5.5	−0.275 to −0.328	−0.307	11.8–13.8	12.9
RKUE	*QRkue-1B.1*	T2, T6, T7, T10, T12	4.0–6.0	−0.032 to −0.281	−0.117	9.8–16.7	12.1
SKUE	*QSkue-1B*	T2, T3, T6, T7, T9, T10	3.1–6.0	−0.062 to −0.289	−0.130	7.7–14.8	12.7
TKUE	*QTkue-1B*	T2, T3, T6, T7, T10	3.4–8.9	−0.398 to −1.073	−0.767	7.9–23.3	14.7

QTLs have been detected under conditions of high and low N in hydroponic culture (An et al. 2006; Laperche et al. 2006), pot trials (Habash et al. 2007) and field trials (Quarrie et al. 2005; An et al. 2006; Laperche et al. 2007, 2008; Fontaine et al. 2009); as well as under conditions of P deficiency and sufficiency in pot trials (Su et al. 2006, 2009) and hydroponic culture trials (Li et al. 2007b). To the best of our knowledge, no studies of QTLs for the NuUE of K have been reported. In the present study, a total of 380 QTLs for 24 seedling traits in plants grown under hydroponic culture treatments of N, P and K were located. Some similar QTLs, for N use efficiency under different N concentrations (Quarrie et al. 2005; An et al. 2006; Laperche et al. 2007; Fontaine et al. 2009) and P use efficiency (Su et al. 2006, 2009; Li et al. 2007b) under P deficiency and/or P sufficiency conditions, both seedling traits and yield traits, were reported in adjacent marker regions by previous studies compared to our QTL mapping results (Table 7). In addition, some QTLs for grain N, P and K concentrations (Peleg et al. 2009) or yield traits (Li et al. 2007a) under normal growing conditions were also detected in the adjacent marker regions of our NuUE QTLs (Table 7). However, most QTLs in the present study were mapped in new marker regions, including the important QTL clusters. One possible explanation for this outcome is that the mapping of QTLs was based on different genetic maps and their component markers were very distinct.

In wheat, a large number of QTL clusters have been mapped in the same genomic regions (McCartney et al. 2005; Quarrie et al. 2005, 2006; ter Steege et al. 2005;

Table 6 Important QTL clusters (more than five QTLs)

Cluster codes	Chromosomes	Marker intervals	No. of QTLs	Treatments
C1	1A	*wPt-1973-wPt-671790*	13	T2, T6, T10, T11, T12
C2	1A	*wPt-8770-wPt-731476*	13	T1, T5, T7, T9, T10, T12
C3	1B	*swes1079a-swes579*	22	T1, T2, T3, T4, T5, T6, T7, T9, T10, T11, T12
C4	1B	*wmc419b-cfd20*	8	T3, T8, T12
C5	1B	*wPt-6425-wPt-7273*	6	T2, T3, T4, T8, T10, T12
C6	1D	*wmc222-wmc336c*	5	T5, T6, T10, T11, T12
C7	1D	*wmc432b-wPt-666067*	20	T1, T2, T3, T5, T6, T10, T11, T12
C8	1D	*wPt-4647-swes1100*	7	T2
C9	2B	*wmc154a-wmc154b*	11	T1, T10, T12
C10	2B	*wPt-8460-barc18b*	5	T3
C11	3A	*wPt-664250-wPt-1036*	7	T11
C12	3B	*wPt-6973-wmc3a*	9	T2, T4, T7, T8, T9
C13	4A	*trap4a-swes124*	7	T6, T11, T12
C14	4A	*srap7b-wPt-4487*	13	T1, T2, T3, T4, T5, T6, T7, T8, T9, T10
C15	4B	*swes24c-wPt-3991*	14	T1, T2, T3, T4, T6, T8, T10
C16	4B	*swes1117-barc1096*	11	T1, T2, T3, T4, T5, T8, T9, T10, T12
C17	5D	*swes342a-srap6b*	13	T1, T2, T4, T10
C18	5D	*swes558b-swes555a*	13	T3, T6, T12
C19	6A	*ubc860a-swes123a*	7	T2, T3, T5, T7, T8
C20	6B	*swes1-wPt-5176*	9	T2, T3, T4
C21	6B	*wPt-8894-wPt-8412*	5	T4, T5, T9, T11
C22	7A	*wPt-8418-gwm635*	7	T1, T3, T4, T6, T7, T8, T9, T10, T12
C23	7A	*barc70c-wPt-6447*	14	T1, T3, T4, T5, T7, T8, T9
C24	7A	*wPt-4637-ubc811a*	8	T11, T12
C25	7B	*wPt-2273-wmc517*	12	T3, T5, T6
C26	7B	*wPt-668307-wPt-7108*	6	T4, T5, T6, T9, T11

Crossa et al. 2007; Li et al. 2007a). In the present study, 26 QTL clusters with more than five traits were mapped, of which 10 clusters (C1, C2, C3, C7, C14, C15, C17, C18, C23 and C25) were more important. The QTL clusters were detected in 2–11 treatments, and were found with high frequency in certain treatment(s) except for C5, C6 and C26. Cluster C3 and C7 were detected mainly in 6 and 4 treatments, respectively, suggesting that these cluster were relatively stable. Surprisingly, some clusters, such as C8, C10 and C11, tended to be expressed in one treatment—T2, T3, T11, respectively—showing that these loci responded to specific level of N, P and K (Table 6).

Cooperative uptake and utilization of N, P and K

The extremely complicated and important effects of N, P and K on plant growth have been acknowledged and investigated for a long time (Clárk 1983; Le Gouis et al. 2000; Rengel and Damon 2008). Plant responses to N, P and K limitations differ, which may be due to the different functions of these nutrients in plants (De Groot et al. 2003a, b). Is there a common genetic mechanism for cooperative uptake and utilization (CUU) of N, P and K in plants? In the present study, we administered N, P and K treatments at different concentrations, and measured the N, P and K contents of each treatment simultaneously. This approach facilitated the discovery of CUU-QTLs.

We found evidence for CUU of N, P and K in the early growth period at the phenotypic level. Almost all correlation coefficients (r) among the nutrient content traits of N, P and K were significantly positive correlations (Table S2 ESM), indicating a cooperative uptake relationship for N, P and K. Similarly, the correlation coefficients among the nutrient utilization efficiency traits of N, P and K were also significantly positive correlations, suggesting a cooperative utilization relationship for N, P and K. Furthermore, the correlation coefficients among the nutrient content traits and utilization efficiency traits were largely indicative of significant positive correlations, further demonstrating a CUU relationship for N, P and K.

We also found evidence for a CUU relationship for N, P and K at the QTL level. We defined a cooperative uptake

Table 7 Comparison of the QTL location between previous studies and this study

Chromosomes	Markers	QTLs in this study			QTLs detected in previous study		
		Morphological traits	Uptake efficiency traits	Utilization efficiency traits	Related traits	Treatments	References
1A	*wmc336*	–	*QSpc.1*, *QTpc.1*	–	PUP	High P level in field trial	Su et al. (2009)
1A	*wmc93*	*QMrl*	–	–	BY, PUP, GNE	Low P level in field trial	Su et al. (2009)
1A	*Glu-A1*	*QMrl*	–	–	GPC	High N level in field trial	Laperche et al. (2007)
1B	*Glu-B1*	*QTdw.2*	*QSpc.2*, *QTpc.2*, *QSkc.2*, *QTkc.2*	*QSnue.2*, *QTnue.3*, *QRpue.2*	GY	N stress in field trial	Quarrie et al. (2005)
1D	*wmc432a*	*QSh.1*	*QSnc.1*, *QTnc.1*, *QSkc.1*, *QTkc.1*	–	TKW, SN	Field trial	Li et al. (2007a)
2A	*gwm339*	–	–	*QRnue*	GS, GDH activity	Middle/High N level in field trial	Fontaine et al. (2009)
2A	*gwm339*	–	–	*QRnue*	KNS, FSS	Field trial	Li et al. (2007a)
2A	*wmc179*	*QMrl.2*	–	–	UTEB	Low P level in pot trial High P level in field trial	Su et al. (2009)
2D	*wmc296*	–	–	*QRnue*, *QTnue*, *QRkue.1*	TGW, BY	High/low P level in field trial	Su et al. (2009)
2D	*issr23a*	–	*QRkc*	*QRkue.2*	GY	Field trial	Li et al. (2007a)
2D	*wmc181b*	–	*QRkc*	*QRkue.2*	TN	High level in pot trials	Su et al. (2006)
2D	*wmc181b*	–	*QRkc*	*QRkue.2*	TGW	High P level in field trial	Su et al. (2009)
3B	*gwm285*	–	–	*QSpc*, *QTkc.1*	GPA, GPY, NTOT	High/low N level in field trial	Laperche et al. (2007)
3B	*gwm285*	–	–	*QSpc*, *QTkc.1*	KNS, GY	Field trial	Li et al. (2007a)
3B	*wmc3a*	–	*QSkc*, *QTkc.2*	*QTnue*, *QRpue*, *QSpue*, *QTpue*, *QSkue*, *QTkue*	SN	Field trial	Li et al. (2007a)
5A	*gwm415*	*QArn.2*	*QSkc*, *QTkc*	–	PUP, GNE, EN, BY	High/low P level in field trials	Su et al. (2009)
5A	*gwm415*	*QArn.2*	*QSkc*, *QTkc*	–	NUP	High N level in field trials	An et al. (2006)
5A	*gwm666*	–	*QRkc*	–	SPU, PUE	High/low P level in pot trials	Su et al. (2006)
5B	*wPt-5896*	–	*QTpc*	–	GPC, grain P concentration	Field trial	Peleg et al. (2009)
5D	*swes342a*	*QArn*, *QRdw.1*, *QTdw*	*QRnc*, *QSnc*, *QTnc*, *QSpc.1*, *QTpc.1*, *QSkc.1*, *QTkc.1*	*QSnue.1*, *QTnue*, *QRpue.1*, *QSkue.1*	TKW	Field trial	Li et al. (2007a)

Table 7 continued

Chromosomes	Markers	QTLs in this study			QTLs detected in previous study		
		Morphological traits	Uptake efficiency traits	Utilization efficiency traits	Related traits	Treatments	References
5D	*swes555b*	*QRdw.2*, *QTdw.2*	*QTnc.2*	*QRnue*, *QSnue.2*, *QTnue.2*, *QRpue.2*, *QSpue*, *QTpue*, *QRkue*, *QSkue.2*	TKW	Field trial	Li et al. (2007a)
6A	*swes332a*	*QRdw.2*	*QRpc.1*	–	TKW	Field trial	Li et al. (2007a)
7B	*gwm611*	*QRdw.2*	*QRpc.2*, *QSpc*	*QRnue.2*, *QRpue.2*, *QSkue*	RL, RN	Low P level in hydroponic culture	Li et al. (2007b)
7B	*gwm400*	*QRdw.2*	*QRpc.2*, *QSpc*	*QRnue.2*, *QRpue.2*, *QSkue*	NUP	High N level in hydroponic culture	An et al. (2006)

BY biomass yield per plant, *EN* ear number per plant, *FSS* fertile spikelet number per spike, *GDH* glutamate dehydrogenase, *GNE* grain number per ear, *GPA* grain per area, *GPC* grain protein concentration, *GPY* grain protein yield, *GS* glutamine synthetase, *GY* grain yield, *KNS* kernel number per spike, *NUP* N uptake, *NTOT* total N amount, *PUE* shoot P utilization efficiency, *PUP* P accumulation per plant, *RL* the length of the root, *RN* the number of roots, *SPU* shoot P uptake per plant, *SN* spike number, *TGW* 1,000 grain weight, *TKW* 1,000 kernel weight, *TN* tiller number, *UTEB* P utilization efficiency based on biomass yield

locus when QTLs were detected for more than two elements of the N, P and K contents in roots, shoots or total plants (*QRnc*, *QSnc*, *QTnc*, *QRpc*, *QSpc*, *QTpc*, *QRkc*, *QSkc* and *QTkc*). Analogously, a cooperative utilization locus was defined when QTLs were detected for more than two elements of the N, P and K utilization efficiencies in roots, shoots or total plants (*QRnue*, *QSnue*, *QTnue,* *QRpue*, *QSpue*, *QTpue,* *QRkue*, *QSkue* and *QTkue*). In this study, a total of 32 CUU loci (L1–L32) were found, which included 190 out of the 293 QTLs (64.8%), indicating that the CUU relationships were common for N, P and K (Table S4; Fig. 1). Of these, 4 loci (L12, L22, L24 and L29) were related to cooperative uptake only, 7 (L13, L17, L21, L23, L26, L31 and L32) to cooperative utilization only, and 21 loci to cooperative uptake and utilization simultaneously. Sixteen CUU loci (including L6, L9, L11, L12, L15, L16, L17, L20, L21, L24, L25, L27, L28, L30, L31 and L32) came from Chuan 35050, indicating that the relationships among these QTLs in each locus were positive (Tables S3, S4 ESM). For the other 16 CUU loci (including L1, L2, L3, L4, L5, L7, L8, L10, L13, L14, L18, L19, L22, L23, L26 and L29), the increasing effects of all QTLs came from Shannong 483, and the relationships between these QTLs were also positive (Tables S3, S4 ESM). The QTLs of 13 loci (L1, L2, L3, L4, L7, L16, L18, L19, L20, L25, L28, L29 and L30) were detected for more than two treatments. In the other 19 loci, the CUU-QTLs were found only for one treatment. Moreover, in 19 loci (including L1–L7, L10, L16, L18, L19, L20, L21, L23, L25, L27–L30), 41 out of 87 (47.1%) QTLs for morphological traits were related to CUU-QTLs (Tables S4 ESM). For example, in T2 of the L3, nine cooperative uptake QTLs (*QRnc.2*, *QSnc*, *QTnc*, *QRpc.2*, *QSpc.1*, *QTpc.1*, *QRkc.1*, *QSkc.1* and *QTkc.1*) and six cooperative utilization QTLs (*QSnue.1*, *QSpue*, *QTpue*, *QRkue.1*, *QSkue* and *QTkue*) were located in the same region on chromosome 1B, indicating that this locus was responsible for the uptake and utilization of N, P and K and had expressed morphological effects (*QArn.1*, *QRdw.1*, *QSdw* and *QTdw.1*). The varying CUU-QTLs at this locus were detected simultaneously in treatments T2, T3, T4, T6, T7, T9, T10, T11 and T12, suggesting that the locus was relatively stable and could be expressed under various nutrient conditions. The CUU-QTLs were also relatively stable in L7, L16 and L28. The CUU-QTL may explain the CUU phenotype at the QTL level.

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