Identification and validation of QTLs for kernel number per spike and spike length in two founder genotypes of wheat

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Abstract

Background: Kernel number per spike (KNS) and spike length (SL) are important spike-related traits in wheat variety improvement. Discovering genetic loci controlling these traits is necessary to elucidate the genetic basis of wheat yield traits and is very important for marker-assisted selection breeding.

Results: In the present study, we used a recombinant inbred line population with 248 lines derived from the two founder genotypes of wheat, Bima4 and BainongAK58, to construct a high-density genetic map using wheat 55 K genotyping assay. The final genetic linkage map consists of 2356 bin markers (14,812 SNPs) representing all 21 wheat chromosomes, and the entire map spanned 4141.24 cM. A total of 7 and 18 QTLs were identified for KNS and SL, respectively, and they were distributed on 11 chromosomes. The allele effects of the flanking markers for 12 stable QTLs, including four QTLs for KNS and eight QTLs for SL, were estimated based on phenotyping data collected from 15 environments in a diverse wheat panel including 384 elite cultivars and breeding lines. The positive alleles at seven loci, namely, QKns.his-7D2–1, QKns.his-7D2–2, QSl.his-4A-1, QSl.his-5D1, QSl.his-4D2–2, QSl.his-5B and QSl.his-5A-2, significantly increased KNS or SL in the diverse panel, suggesting they are more universal in their effects and are valuable for gene pyramiding in breeding programs. The transmission of Bima4 allele indicated that the favorite alleles at five loci (QKns.his-7D2–1, QSl.his-5A-2, QSl.his-2D1–1, QSl.his-3A-2 and QSl.his-3B) showed a relatively high frequency or an upward trend following the continuity of generations, suggesting that they underwent rigorous selection during breeding. At two loci (QKns.his-7D2–1 and QSl.his-5A-2) that the positive effects of the Bima4 alleles have been validated in the diverse panel, two and one competitive allele-specific PCR (KASP) markers were further developed, respectively, and they are valuable for marker-assisted selection breeding.

Conclusion: Important chromosome regions controlling KNS and SL were identified in the founder parents. Our results are useful for knowing the molecular mechanisms of founder parents and future molecular breeding in wheat.

Keywords: Kernel number per spike, Spike length, QTL, KASP markers

Background

Wheat (Triticum aestivum L.) is a major cereal crop worldwide. The current yield trend in wheat is insufficient to meet the future demand of a growing world population, and wheat yield and total production must be increased continuously. The formation of wheat yield is a complex trait and is affected by three yield components, e.g., spike number per unit area, kernel weight, and kernel number per spike (KNS). Among them, kernel weight...
and KNS are closely related to spike morphology, which is primarily determined by spike length (SL), spikelet density, and fertile floret number. Previous studies showed that increasing KNS is an effective approach for wheat yield improvements compared to kernel weight [1, 2], and increasing SL without modification of the spikelet density can increase KNS and subsequently raise yield capacity [3]. A positive correlation between SL and yield was also validated in some previous studies [4]. Besides, the long spike is often associated with reduced severity of Fusarium head blight in wheat [5]. Therefore, discovering genetic loci controlling KNS and SL is necessary to elucidate the genetic basis of wheat yield traits and is very important for marker-assisted selection (MAS) breeding.

Like other spike-related traits, KNS and SL are controlled by multiple genes and affected by environments. Quantitative trait loci (QTL) analysis using different genetic populations and diverse wheat panels provides an effective method to study the genes governing these traits. To date, numerous QTLs associated with KNS have been mapped on nearly all the 21 chromosomes in wheat, such as two QTLs identified on 2D and 4A [6], eight QTLs identified on 1A, 1B, 2B, 2D, 3B, 4B, 6A and 7B [7], one QTL identified on 3D [8], one QTL identified on 4A [9], four QTLs identified on 2A, 4B and 7A [10], six QTLs identified on 1D, 2A, 2D, 3A, 4D and 6D [11], three QTLs identified on 1D, 4D and 6B [12], 12 QTLs identified on 1A, 2D, 3B, 4A, 4B, 5A, 5B, 7A and 7B [13], and one QTL identified on 7A [14]. Likewise, many previous studies have proven that almost all the 21 wheat chromosomes harbored factors affecting SL [3, 10, 15–21]. Yao et al. [22] reported that approximately 350 QTLs of SL have been identified currently, and some of them with relatively large effects were distributed on chromosomes 2D, 3A, 4A, 4B, 5A, 6A, 6B, 7A, 7B, and 7D. Briefly, because of the complexity of the wheat genome, although many QTL for KNS and SL have been reported, common QTLs across different mapping populations are limited, and few of them are used in practical wheat breeding.

Founder parents have played particularly crucial roles in the improvement of wheat worldwide. Many QTLs or chromosomal regions associated with important traits have been found in founder genotypes in wheat [23–26]. However, the knowledge of the molecular mechanisms for the formation of founder parents remains unclear. In China, Bima4 is one of the founder parents that played important roles in wheat breeding, used widely in the Yellow and Huai River Facultative Winter Wheat Region between 1950 and 1970 [27]. It was obtained from the cross between another founder parent Mazhamai and Quality from the United States. More than 70 improved cultivars were developed from Bima4, and some of them such as Shijiazhuang54, Jina12, Beijing8 and Taishan1, had annual maximum acreages over 667,000 ha and were grown for at least 12 years. Similarly, BainongAK58 is a famous cultivar released in 2003 by the Henan Institute of Science and Technology, and its maximum acreage was over 13,333,333 ha. It was also widely utilized as a crossing parent in wheat breeding, from which more than fifty improved cultivars were developed.

In the present study, we used a recombinant inbred line (RIL) population with 248 lines derived from the two founder genotypes of wheat, Bima4 and BainongAK58. The QTL analysis was conducted with a high-density genetic map by using the developed wheat 55 K genotyping assay to identify QTLs responsible for KNS and SL. These QTLs detected were further validated in a diverse wheat panel. Furthermore, we analyzed the transmission of Bima4 alleles to its derivative descendants, and two and one KASP markers for two important loci, QKns.his-7D2–1 and QSl.his-5A–2, were developed. This study is useful for knowing the molecular mechanisms of founder parents and future molecular breeding in wheat.

Results

Linkage map construction in the RIL population

Out of 53,063 SNPs in the 55 k Infinium chip, 16,628 SNPs were polymorphic between the two parents and among the RIL population. These 16,628 markers were divided into 2488 bins. Only one marker was chosen to represent each bin for the genetic map construction. The final genetic linkage map consists of 2356 bin markers (14,812 SNPs) representing all 21 wheat chromosomes. Of them, 1147 bins include only one SNP marker, and the remaining comprises two or more SNP markers.

The 2356 bin markers were mapped on 28 linkage maps (Table 1 and Table S1). Each of the chromosomes 1A, 1D, 2D, 3D, 4D, 5D, and 7D was integrated by two linkage groups. The entire map spanned 4141.24 cM with six gaps (>30 cM) distributed on chromosomes 2D, 6A, 4D, 5B, and 7D. The mean of genetic distance among adjacent bin markers across all chromosomes was 1.76 cM and varied among 28 linkage groups from 0.71 (1A2) to 5.98 (7D1). The bin markers mapped on the A genome (37.9%) were more than those on the B (34.2%) and D (28.0%) genome. Similarly, most of the mapped markers including bin and redundant markers were distributed on A (43.0%) and B genome (36.9%), and only 20.0% of the markers were mapped on D genome. The number of bin markers on 21 chromosomes ranged from 51 on 1D to 177 on 7D, however the number of the mapped markers ranged from 168 on 4D to 1479 on 2A.
Phenotypic analysis for KNS and SL in the RIL population
These two traits for the RIL populations and the two parents in the four environments are shown in Table S2. The SL and KNS showed inconsistency between the parental lines over environments, indicating strongly affected by the environment. In the RIL populations, the KNS and SL showed normal distributions in all the environments, suggesting the polygenic inheritance of these traits (Fig. 1). The transgressive inheritance was found in certain lines for SL and KNS (Fig. 2). The two traits showed strong correlations with each other in all environments. The correlation coefficients ranged from 0.86 to 0.96 for SL and from 0.50 to 0.86 for KNS. The SL had a strong positive correlation with KNS at 0.24 (\( P < 0.0001 \)) (Table 2). The SL and KNS showed high broad-sense heritability at 0.95 and 0.85, respectively.

QTL detection for KNS and SL in the RIL population
A total of seven QTLs were detected for KNS on chromosomes 3A, 3D, 4A, 5A, and 7D (Table 3 and Fig. 3). A major stable QTL, \( Q_{kns.his-4A} \), was detected in all four environments and the average value and explained 9.78–24.24% of the phenotypic variance. \( Q_{kns.his-5A-2} \) was identified in three environments and the average value and explained 3.72–7.01% of phenotypic variation. The positive alleles of \( Q_{kns.his-4A} \) and \( Q_{kns.his-5A-2} \) were contributed by Bima4. The two QTLs, \( Q_{kns.his-7D-1} \) and \( Q_{kns.his-7D-2} \), were detected in one environment and the average value and explained 3.72–7.01% of phenotypic variation. The positive alleles of \( Q_{kns.his-7D-1} \) and \( Q_{kns.his-7D-2} \) were contributed by Bima4 and BainongAK58, respectively. The remaining three QTLs, \( Q_{kns.his-3A} \), \( Q_{kns.his-3D} \) and \( Q_{kns.his-5A-1} \), were detected in a single environment, and they

| Chromosome | Group | Number of bin marker | Number of mapped marker | Length (cM) | cM per bin marker |
|------------|-------|----------------------|------------------------|------------|-----------------|
| 1A         | 1     | 8                    | 18                     | 24.69      | 3.09            |
| 1B         | 1     | 73                   | 370                    | 88.96      | 1.22            |
| 1D         | 1     | 42                   | 261                    | 137.95     | 3.28            |
| 2A         | 1     | 102                  | 1479                   | 193.72     | 1.90            |
| 2B         | 1     | 138                  | 765                    | 169.44     | 1.23            |
| 2D         | 1     | 90                   | 402                    | 269.98     | 3.00            |
| 3A         | 1     | 164                  | 994                    | 223.75     | 1.36            |
| 3B         | 1     | 119                  | 1218                   | 159.76     | 1.34            |
| 3D         | 1     | 10                   | 28                     | 76.02      | 7.60            |
| 4A         | 1     | 104                  | 772                    | 171.62     | 1.65            |
| 4B         | 1     | 108                  | 1228                   | 140.04     | 1.30            |
| 4D         | 1     | 5                    | 10                     | 14.64      | 2.93            |
| 5A         | 1     | 165                  | 787                    | 194.44     | 1.18            |
| 5B         | 1     | 160                  | 921                    | 209.27     | 1.31            |
| 5D         | 1     | 70                   | 217                    | 268.53     | 3.84            |
| 6A         | 1     | 55                   | 443                    | 131.77     | 2.40            |
| 6B         | 1     | 103                  | 585                    | 133.25     | 1.29            |
| 6D         | 1     | 91                   | 232                    | 192.00     | 2.11            |
| 7A         | 1     | 170                  | 961                    | 226.19     | 1.33            |
| 7B         | 1     | 104                  | 385                    | 155.31     | 1.49            |
| 7D         | 1     | 13                   | 61                     | 77.72      | 5.98            |
| 2          | 164   | 792                  | 252.46                 | 1.54       |                 |
| Total      | 28    | 2356                 | 14,812                 | 4141.24    | 1.76            |
explain 5.29, 4.22, and 4.01% of the phenotypic variance, respectively.

A total of 18 QTLs were detected for SL on chromosomes 2D, 3A, 3B, 3D, 4A, 4D, 5A, 5B, 5D, 7B, and 7D with phenotypic variations ranging from 2.04 to 22.31% (Table 3 and Fig. 3). Among them, eight QTLs were detected in a single environment, explaining 2.93–4.85% of the phenotypic variance. Two stable QTLs, $Q_{sl.\text{his}-2D1-1}$ and $Q_{sl.\text{his}-5A-2}$, were detected in all four environments and the average values, and the positive alleles were from Bima4. Of these, the major QTL, $Q_{sl.\text{his}-2D1-1}$, explained 11.03–22.31% of the phenotypic variance. Two QTLs, $Q_{sl.\text{his}-4A-1}$ and $Q_{sl.\text{his}-5D1}$, were identified in three environments and the average values. They accounted for 3.43–8.21% of the phenotypic variance and the positive alleles were contributed by BainongAK58. The two QTLs, $Q_{sl.\text{his}-3A-2}$ and $Q_{sl.\text{his}-3B}$, were detected in three environments and the average values, and they explained 2.18–3.65%

Table 2 Correlations among different environments for SL and KNS

| Trait | 2017XI | 2018XI | 2018HU | 2019XI | Average |
|-------|--------|--------|--------|--------|---------|
| SL    |        |        |        |        |         |
| 2017XI| 1.00   |        |        |        |         |
| 2018XI| 0.86a  | 1.00   |        |        |         |
| 2019HU| 0.88a  | 0.88a  | 1.00   |        |         |
| 2019XI| 0.87a  | 0.92a  | 0.89a  | 1.00   |         |
| Average| 0.94a | 0.95a  | 0.96a  | 0.96a  | 1.00    |
| KNS   |        |        |        |        |         |
| 2017XI| 1.00   |        |        |        |         |
| 2018XI| 0.61a  | 1.00   |        |        |         |
| 2019HU| 0.50a  | 0.55a  | 1.00   |        |         |
| 2019XI| 0.63a  | 0.68a  | 0.56a  | 1.00   |         |
| Average| 0.83a | 0.84a  | 0.80a  | 0.86a  | 1.00    |

Average-SL 0.24a

Average-KNS 0.24a

* Significance level at 0.0001
| Trait | QTL      | Environment | Location | Left marker | Right marker | LOD  | PVE (%) | Add   |
|-------|----------|-------------|----------|-------------|-------------|------|---------|-------|
| KNS   | QKns.his-3A | 2019XI      | 58       | AX-111799835 | AX-109274841 | 3.98 | 5.29    | −1.46 |
|       | QKns.his-3D2 | 2019XI      | 190      | AX-109403595 | AX-110202442 | 3.26 | 4.22    | −1.30 |
|       | QKns.his-4A   | Average     | 123      | AX-111600193 | AX-109332913 | 18.16 | 24.24  | −2.80 |
|       | QKns.his-5A-1 | 2018XI      | 2        | AX-111275827 | AX-109926388 | 3.71 | 4.01    | 1.20  |
|       | QKns.his-5A-2 | 2019XI      | 106      | AX-109980237 | AX-110121838 | 2.82 | 3.72    | −1.24 |
|       | QKns.his-7D2–1 | 2018XI     | 3        | AX-110196726 | AX-109475040 | 4.72 | 5.39    | −1.40 |
|       | QKns.his-7D2–2 | Average    | 6        | AX-109475040 | AX-11094913  | 3.38 | 3.82    | −1.07 |
|       | QSl.his-2D1–1 | 2017XI      | 29       | AX-111574926 | AX-110332825 | 11.04 | 11.03  | −0.43 |
|       | QSl.his-2D1–2 | 2019XI      | 131      | AX-109449257 | AX-109264010 | 4.13 | 3.89    | 0.25  |
|       | QSl.his-3A-1   | 2018HU      | 30       | AX-108836084 | AX-109911369 | 11.07 | 11.12  | −0.55 |
|       | QSl.his-3A-2   | 2019XI      | 37       | AX-109911369 | AX-11087066  | 13.95 | 18.65  | −0.62 |
|       | QSl.his-3D2   | 2018XI      | 99       | AX-111537186 | AX-10999958  | 3.97 | 3.66    | −0.25 |
|       | QSl.his-4A-1   | 2019XI      | 58       | AX-109555453 | AX-108994889 | 4.82 | 3.43    | 0.28  |
|       | QSl.his-4A-2   | 2018XI      | 70       | AX-110574688 | AX-109391536 | 6.07 | 5.77    | 0.31  |
|       | QSl.his-4A-3   | 2017XI      | 121      | AX-111071938 | AX-111508583 | 4.85 | 4.53    | −0.29 |
|       | QSl.his-4D2–1 | 2018HU      | 28       | AX-111494342 | AX-109847443 | 2.93 | 2.83    | 0.28  |
of phenotypic variation and the positive alleles were from Bima4.

Validation of the QTL effects in the diverse wheat panel
The allele effects of the flanking markers for 12 stable QTLs, including four QTLs for KNS and eight QTLs for SL, were estimated based on phenotyping data in the diverse wheat panel. T-test analyses were used to compare the two different allele groups in the same locus ($P < 0.05$). For each QTL investigated, the QTL-associated SNP markers for which differences of phenotypic values showed significance in most environments in the diverse wheat panel were analyzed (Table 4). For KNS, three QTL-associated SNP markers of $QKns.his-7D2–1$ were analyzed. The marker AX-110196726 showed significance in 14 environments in the diverse wheat panel, while the other two markers (AX-109924587 and AX-111049786) showed significant differences of KNS only in six environments, indicating that the former was closer to this QTL compared to the latter. The positive allele of AX-110196726 contributed by Bima4 had a more KNS than BainongAK58 allele in the diverse wheat panel. Similarly, two QTL-associated SNP markers (AX-108912162 and AX-111577597) of $QKns.his-7D2–2$ were analyzed. The positive alleles contributed by BainongAK58 showed significant across all 15 environments more KNS at 5.17 and 4.85 than the Bima4 alleles at these two loci in the diverse wheat panel, respectively. In addition, among six QTL-associated SNP markers of $QKns. his-5A-2$ where the favourable alleles were from Bima4, four showed significant differences of KNS in 15 environments, respectively. At the same time, the effects on KNS were inverse among them, i.e., the Bima4 alleles showed negative effects at AX-109980237 and AX-110121838, but positive effects at AX-111104892 and AX-109876198. In the same way, of four QTL-associated SNP markers of $QKns. his-4A$ two markers (AX-111508583 and AX-109332913) showed significant differences of KNS only in 6 environments respectively. At the same time, the effects on KNS were inverse between them.

For SL, six and two QTL-associated SNP markers were analyzed for $QSl.his-4A-2$ and $QSl.his-5D1$, respectively. Only AX-108955453 and AX-110409786 had significant differences of SL in 12 environments in the diverse wheat panel.

### Table 3 (continued)

| Trait | QTL | Environment | Location | Left marker | Right marker | LOD | PVE (%) | Add |
|-------|-----|-------------|----------|-------------|-------------|-----|---------|-----|
| QSl.his-4D2–2 | Average | 57 | AX-110984743 | AX-109924587 | 5.02 | 10.60 | 0.51 |
| 2018HU | 65 | AX-110984743 | AX-109924587 | 5.95 | 10.33 | 0.55 |
| QSl.his-4D2–3 | 2017XI | 89 | AX-169337603 | AX-111601811 | 3.95 | 3.69 | 0.25 |
| QSl.his-5A-1 | 2019XI | 63 | AX-110950060 | AX-111172588 | 3.58 | 2.51 | 0.23 |
| QSl.his-5A-2 | 2018HU | 94 | AX-109622137 | AX-111104892 | 5.08 | 4.84 | −0.37 |
| 2018XI | 95 | AX-110196765 | AX-110437938 | 5.68 | 4.65 | −0.32 |
| 2017XI | 96 | AX-110196765 | AX-110437938 | 8.46 | 8.38 | −0.38 |
| 2019XI | 96 | AX-110196765 | AX-110437938 | 9.63 | 7.24 | −0.41 |
| Average | 96 | AX-110196765 | AX-110437938 | 6.82 | 5.16 | −0.35 |
| QSl.his-5B | 2018HU | 73 | AX-108868689 | AX-109842839 | 4.59 | 4.34 | 0.34 |
| 2019XI | 86 | AX-110502620 | AX-109068105 | 3.01 | 2.06 | 0.21 |
| Average | 85 | AX-108813434 | AX-110502620 | 3.39 | 2.41 | 0.23 |
| QSl.his-5D1 | 2018HU | 151 | AX-110409786 | AX-94969919 | 5.11 | 8.21 | 0.47 |
| 2019XI | 157 | AX-110409786 | AX-94969919 | 3.29 | 3.97 | 0.29 |
| 2018XI | 159 | AX-110409786 | AX-94969919 | 3.75 | 4.75 | 0.31 |
| Average | 156 | AX-110409786 | AX-94969919 | 4.11 | 5.06 | 0.34 |
| QSl.his-7B | 2017XI | 49 | AX-109478552 | AX-110460118 | 2.94 | 2.71 | −0.21 |
| QSl.his-7D2 | 2018XI | 144 | AX-111038335 | AX-110829820 | 3.42 | 2.68 | 0.24 |
| 2017XI | 144 | AX-111038335 | AX-110829820 | 2.82 | 2.55 | 0.21 |
Fig. 3 The genetic map of 11 linkage groups and QTL analysis for KNS (red) and SL (green) in the RIL population
Table 4  Effects of the QTL-associated SNP markers in the diverse wheat panel

| QTL name | Marker | Position | Allele (origin) | Sample size | 2007 SX | 2007 JS | 2007 HB | 2007 SD | 2007 SC | 2008 SX | 2008 JS | 2008 HB | 2008 SD | 2008 SC | 2009 SX | 2009 JS | 2009 HB | 2009 SD | 2009 SC |
|----------|--------|----------|----------------|-------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| Qkns-7D2-1 | AX-110196726 | C/C (M) | 347 | 52.185 | 52.391 | 57.197 | 48.319 | 46.821 | 51.844 | 52.094 | 50.000 | 41.278 | 33.542 | 51.789 | 51.159 | 53.268 | 42.665 | 35.141 |
|    | T/T (N) | 22 | 46.886 | 45.901 | 51.568 | 44.214 | 40.143 | 45.905 | 45.196 | 44.854 | 37.971 | 28.322 | 46.664 | 48.824 | 50.193 | 37.970 | 30.949 |
|    | P value | 0.000 | 0.000 | 0.011 | 0.012 | 0.013 | 0.000 | 0.000 | 0.002 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.005 |
| Qkns-7D2-2 | AX-108912162 | G/G (M) | 170 | 49.392 | 49.051 | 53.359 | 45.375 | 43.675 | 48.710 | 49.125 | 47.614 | 39.999 | 30.759 | 48.493 | 47.112 | 50.408 | 40.163 | 32.548 |
|    | T/T (N) | 187 | 54.036 | 54.804 | 60.503 | 50.546 | 48.860 | 54.015 | 54.224 | 53.326 | 42.148 | 35.288 | 54.022 | 54.245 | 55.895 | 44.492 | 36.932 |
|    | P value | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Qkns-5A-2 | AX-109980237 | C/C (M) | 188 | 49.849 | 49.422 | 54.022 | 45.448 | 43.797 | 49.167 | 49.029 | 47.573 | 39.946 | 30.792 | 48.920 | 47.310 | 50.889 | 40.772 | 32.924 |
|    | T/T (N) | 169 | 53.776 | 54.794 | 60.135 | 50.660 | 49.067 | 53.811 | 54.571 | 53.355 | 42.333 | 35.309 | 54.040 | 54.441 | 55.505 | 44.047 | 36.804 |
|    | P value | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Qkns-5A-4A | AX-109332913 | A/A (M) | 308 | 51.574 | 51.725 | 56.439 | 47.916 | 46.131 | 51.055 | 51.173 | 50.160 | 41.064 | 32.767 | 51.066 | 50.588 | 53.144 | 42.102 | 34.554 |
|    | G/G (N) | 61 | 53.277 | 53.520 | 58.883 | 49.213 | 48.633 | 53.648 | 54.304 | 51.875 | 41.384 | 34.781 | 53.028 | 51.949 | 53.689 | 43.799 | 36.126 |
|    | P value | 0.037 | 0.068 | 0.060 | 0.133 | 0.090 | 0.001 | 0.002 | 0.091 | 0.328 | 0.010 | 0.028 | 0.139 | 0.332 | 0.018 | 0.067 |
|    | A/A (N) | 186 | 51.501 | 51.367 | 55.978 | 47.298 | 46.124 | 50.748 | 50.831 | 49.772 | 41.073 | 33.099 | 50.610 | 50.706 | 52.342 | 42.305 | 34.286 |
|    | P value | 0.249 | 0.193 | 0.039 | 0.039 | 0.459 | 0.017 | 0.030 | 0.099 | 0.373 | 0.429 | 0.024 | 0.448 | 0.027 | 0.379 | 0.083 |
| QTL name | Marker (origin) | Position | Allele | Sample size | 2007 SX | 2007 JS | 2007 HB | 2007 SC | 2008 SX | 2008 JS | 2008 HB | 2008 SC | 2009 SX | 2009 JS | 2009 HB | 2009 SC | 2009 SD |
|----------|----------------|----------|--------|------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| Qsl.his-4A-1 | AX-108955453 | 36,102,562 | G/G (M) | 71 | 8.514 | 9.314 | 9.246 | 9.510 | 8.228 | 8.213 | 9.538 | 8.994 | 9.276 | 7.425 | 8.710 | 9.404 | 8.910 | 8.407 | 8.031 |
|          |              |          | A/A (Na) | 299 | 9.300 | 10.121 | 9.471 | 10.173 | 8.855 | 8.796 | 10.157 | 9.210 | 9.544 | 7.977 | 9.226 | 10.125 | 9.126 | 8.943 | 8.457 |
| Qsl.his-5D1 | AX-110409786 | 446,797,256 | C/C (M) | 229 | 8.907 | 9.833 | 9.388 | 9.852 | 8.611 | 8.544 | 9.891 | 9.150 | 9.388 | 7.709 | 8.942 | 9.803 | 8.996 | 8.728 | 8.287 |
|          |              |          | A/A (Na) | 134 | 9.572 | 10.152 | 9.541 | 10.328 | 8.925 | 8.909 | 10.250 | 9.202 | 9.651 | 8.118 | 9.403 | 10.270 | 9.246 | 8.988 | 8.495 |
| Qsl.his-4D2-2 | AX-109924587 | 168,781,777 | A/A (M) | 116 | 8.752 | 9.699 | 9.135 | 9.559 | 8.317 | 8.458 | 9.726 | 8.669 | 9.310 | 7.524 | 8.994 | 7.425 | 8.710 | 8.407 | 8.031 |
|          |              |          | G/G (Na) | 245 | 9.304 | 10.055 | 9.545 | 10.240 | 8.889 | 8.772 | 10.145 | 9.273 | 9.572 | 8.021 | 9.314 | 10.174 | 9.204 | 8.965 | 8.469 |
| Qsl.his-5B | AX-108886889 | 490,878,581 | C/C (M) | 94 | 8.731 | 9.557 | 9.378 | 9.636 | 8.384 | 8.538 | 9.718 | 9.195 | 9.293 | 7.456 | 8.951 | 9.108 | 8.617 | 8.197 |
|          |              |          | T/T (N) | 265 | 9.288 | 10.103 | 9.427 | 10.160 | 8.867 | 8.728 | 10.142 | 9.158 | 9.564 | 8.011 | 9.151 | 10.093 | 9.077 | 8.903 | 8.453 |
| Qsl.his-5A-2 | AX-109622137 | 506,645,437 | T/T | 198 | 9.241 | 10.152 | 9.689 | 10.082 | 8.927 | 8.823 | 10.221 | 9.466 | 9.578 | 7.942 | 9.236 | 10.156 | 9.307 | 8.981 | 8.353 |
|          |              |          | G/G (N) | 142 | 9.346 | 10.339 | 9.829 | 10.254 | 9.032 | 8.949 | 10.355 | 9.619 | 9.645 | 8.065 | 9.376 | 10.321 | 9.454 | 9.134 | 8.443 |
| Qsl.his-3A-2 | AX-110199675 | 511,102,792 | C/C (M) | 175 | 8.961 | 9.653 | 9.074 | 9.895 | 8.501 | 8.451 | 9.736 | 8.765 | 9.344 | 7.711 | 8.941 | 9.723 | 8.791 | 8.619 | 8.371 |
|          |              |          | T/T (N) | 213 | 8.992 | 9.695 | 9.173 | 9.866 | 8.546 | 8.510 | 9.786 | 8.894 | 9.378 | 7.742 | 8.959 | 9.753 | 8.846 | 8.649 | 8.349 |
| Qsl.his-3A-2 | AX-111618763 | 599,422,098 | C/C (N) | 140 | 9.354 | 10.213 | 9.601 | 10.203 | 8.895 | 8.764 | 10.207 | 9.186 | 9.601 | 8.088 | 9.267 | 10.196 | 9.165 | 8.934 | 8.579 |
|          |              |          | T/T (N) | 227 | 8.965 | 9.778 | 9.329 | 9.896 | 8.630 | 8.601 | 9.882 | 9.140 | 9.406 | 7.711 | 9.000 | 9.833 | 9.028 | 8.759 | 8.255 |
| Qsl.his-3B | AX-110931375 | 47,609,806 | A/A (M) | 322 | 9.030 | 9.856 | 9.435 | 9.974 | 8.663 | 8.607 | 9.915 | 9.122 | 9.468 | 7.784 | 9.080 | 9.887 | 9.048 | 8.754 | 8.333 |
|          |              |          | G/G (N) | 43 | 9.895 | 10.705 | 9.563 | 10.560 | 9.214 | 9.257 | 10.892 | 9.500 | 9.739 | 8.489 | 9.584 | 10.780 | 9.378 | 9.449 | 8.656 |

| P value |              |          |        |        |        |        |        |        |        |        |        |        |        |        |        |        |        |        |        |
**Table 4** (continued)

| QTL name | Marker Position | Sample size | 2007 SX | 2007 JS | 2007 HB | 2008 SX | 2008 JS | 2008 HB | 2008 SC | 2009 SX | 2009 JS | 2009 HB | 2009 SD | 2009 SC |
|----------|-----------------|-------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| QSl.his-2D1-t | AX-110332825 | T/T (M*) | 278 | 8.924 | 9.771 | 9.284 | 9.587 | 8.587 | 9.473 | 9.847 | 9.498 | 9.377 | 7.735 | 8.928 | 9.788 | 8.908 | 8.664 | 8.295 |
| | C/C (N) | 85 | 9.693 | 10.458 | 9.838 | 10.428 | 9.080 | 9.302 | 10.507 | 9.788 | 9.827 | 8.271 | 9.718 | 10.522 | 9.501 | 9.327 | 8.569 |
| | P value | 0.000 | 0.000 | 0.005 | 0.001 | 0.005 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.009 |
| AX-108836084 | 17,230,342 | G/G (M*) | 281 | 8.915 | 9.767 | 9.267 | 9.856 | 8.608 | 8.462 | 9.830 | 8.966 | 9.369 | 7.719 | 8.902 | 9.798 | 8.915 | 8.679 | 8.268 |
| | A/A (N) | 88 | 9.817 | 10.510 | 9.845 | 10.478 | 9.120 | 9.338 | 10.586 | 9.766 | 9.893 | 8.280 | 9.672 | 10.539 | 9.547 | 9.278 | 8.636 |
| | P value | 0.000 | 0.000 | 0.003 | 0.000 | 0.004 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | 0.001 |

* stands for the positive alleles detected in the RIL population; M and N stand for Bima4 and BainongAK58, respectively; SX, JS, HB, SD, and SC stand for Shaanxi, Jiangsu, Hebei, Shandong, and Sichuan, respectively.
wheat panel separately, and the positive alleles contributed by BainongAK58 increased 0.52 cm and 0.33 cm SL across these two loci, respectively. For QSl.his-2D1–1 and QSl.his-5B, two and four QTL-associated SNP markers were analyzed, respectively. Significant differences of SL were found at AX-109924587 and AX-108886889 in 15 and 10 environments in the diverse wheat panel, respectively, and the positive alleles from BainongAK58 increased 0.46 cm and 0.31 cm SL across these two loci, respectively. Four QTL-associated SNP markers of QSl.his-3A-2 were analyzed. Two markers (AX-109622137 and AX-110199675) showed significant differences of SL in 14 and 13 environments in the diverse wheat panel, respectively, and the positive alleles from Bima4 had a higher SL than BainongAK58 alleles. In addition, four QTL-associated SNP markers of QSl.his-3A-2 and QSl.his-3B were analyzed, respectively. Only AX-111618763 and AX-110931375 showed significant differences of SL in 8 and 12 environments separately, while the positive alleles obtained from Bima4 across the two loci were unfavorable in the diverse wheat panel. Likewise, of five QTL-associated SNP markers of QSl.his-2D1–1 analyzed, two had significant differences of SL in 15 environments, whereas the positive alleles from Bima4 across the two loci were unfavorable in the diverse wheat panel.

Tracking of Bima4 allele in its derivatives and development of KASP markers

Of the 12 stable QTLs analyzed above, the positive alleles for 7 QTLs including 3 QTLs of KNS and 4 QTLs of SL were contributed by Bima4 in the RIL population. The transmission of Bima4 alleles in the QTL-associated SNP markers was determined using its 70 descendants. Among the seven QTLs, the transmission of Bima4 alleles at five loci (QKns.his-7D2–1, QSl.his-5A-2, QSl.his-2D1–1, QSl.his-3A-2, and QSl.his-3B) to its derivative descendants showed a relatively high frequency or an upward trend following the continuity of generations. For example, the Bima4 allele at the QTL-associated SNP marker (AX-110199675) of QKns.his-7D2–1 showed an upward trend following the continuity of generations (Fig. 4A). The Bima4 alleles at two QTL-associated SNP markers (AX-109622137 and AX-110199675) of QSl.his-5A-2 also presented a relatively high frequency or an upward trend following the continuity of generations (Fig. 4A). For these two QTLs, the positive effects of Bima4 alleles have been validated in the diverse wheat panel. Furthermore, two flanking SNP (AX-110945813 and AX-111490337) of QKns.his-7D2–1, which were located in the same bin with AX-110196726 and the physical distances between these two markers and AX-110196726 were only 0.11 Mb and 0.20 Mb, were successfully converted to competitive allele-specific PCR (KASP) markers (Table 5). Likewise, a KASP marker was developed from the flanking SNP (AX-108964722) of QSl.his-5A-2, which were located in the same bin with AX-109622137 and the interval between them was only 1.57 Mb. Similarly, for the three SL QTLs (QSl.his-2D1–1, QSl.his-3A–2, and QSl.his-3B), the Bima4 alleles at four markers (AX-110332825, AX-108836084, AX-111618763, and AX-110931375) showed a high frequency in its four derivative generations, respectively (Fig. 4B). In addition, for QKns.his-4A, the Bima4 allele showed a relatively high frequency (100–80.0%) in its four derivative generations at AX-109332913, but a low frequency (30.0%) across all derivatives at the other marker AX-111508583 (Fig. 4C). A similar result could be observed for QKns.his-5A-2, e.g., the Bima4 alleles showed a high frequency or an upward trend following the continuity of generations at two markers (AX-109980237 and AX-110121838) but had a low frequency (50.0%) across all derivatives at another two markers (AX-111102726 and AX-109867198) (Fig. 4D).

Discussion

Comparison of the QTLs identified for KNS and SL with previous studies

Generally, the major QTLs consistent over environments may play a key role in modulating the agronomic traits of wheat cultivars and have great value for MAS in breeding programs. Based on genetic marker sequence flanking for KNS and SL QTLs and the genome sequence from Chinese Spring wheat (IWGSC V1.0) (http://www.wheatgenome.org/), physical positions of these stable QTLs detected in our study were compared with those reported previously. In the present study, four major QTLs, Qkns.his-4A, Qkns.his-5A-2, Qkns.his-7D2–1 and Qkns.his-7D2–2, were identified for KNS. Of these, the locus Qkns.his-4A in the interval 122.03–122.24 cM on 4A was identified in four environments and the average value, and it was located in the interval 642.37–672.88 Mb. Using a 660 K wheat SNP array, Cui et al. [28] identified a major stable QTL, qKns.his-4A, for KNS in the interval 680.40–683.64 Mb. Gao et al. [29] detected a QTL, QKNS.caas-4AL, in the interval 626.32–660.99 Mb using a 90 K wheat SNP array. Kirigwi et al. [9] identified two simple sequence repeat (SSR) loci, Xwm489 and Xwmc420, related to KNS at positions 515.85 Mb and 538.22 Mb, respectively. There were also some other reported QTLs for KNS on 4A in previous studies [6, 13, 30]. Nevertheless, further research is needed to identify whether these genes are identical. Qkns.his-5A-2, mapped in three environments and the average value in the interval 106.50–125.16 cM on 5A in the present study, was located in the interval 549.34–572.81 Mb, whereas only...
a minor QTL for KNS reported by Wang et al. [13] in a single environment in marker interval Xgwm126-Xgwm291 on 5A positioned in the interval 671.39–698.19 Mb, indicating that Qkns.his-5A-2 is likely to be a new KNS QTL. Likewise, Qkns.his-7D2–1 and Qkns.his-7D2–2, mapped in the 2018XI environment and the average values in the interval 3.00–6.00 cM and 159 cM on 7D in the present study separately, were located in the interval 4.39–7.45 Mb and 526.36–530.75 Mb, respectively. There were also some other reported QTLs for KNS on 7D using SSR or RFLP markers [6, 31], but these markers could not be obtained or precisely located in the reference genome. So, we cannot determine whether the loci were nearby or identical with our results or not.

Of 18 QTLs for SL identified in the present study, 10 were detected in at least two environments. Of these, Qsl.his-2D1–1 was identified in all four environments and the average value. The locus Qsl.his-2D1–1 at the interval 29.00–37.00 cM explained 11.03–22.31% of the phenotypic variance and was located on 2D in the interval 13.25–36.89 Mb. Wu et al. [32] identified an SL-associated gene, QSpl.nau-2D, near position 23.02 Mb. Chai et al. [33] identified two QTLs (QPht/Sl.cau-2D.1 and QPht/Sl.cau-2D.2) with pleiotropic effects on plant height and SL. QPht/Sl.cau-2D.1 is a novel QTL located between SNP markers BS00022234.51 and BobWhite_rep_c63957_1472 near position 20.77 Mb, whereas QPht/Sl.cau-2D.2 was located on the same genetic interval of Rht8. In addition, Sourdille et al. [15], Kumar et al. [10] and Suenaga et al. [16] identified one SSR locus, Xgwm261, associated with SL on 2D at position 19.6 Mb. The marker Xgwm261 is linked to the dwarf gene Rht8. Some previous studies [34–36] indicated that Rht8 does not affect SL, but contrasting with other recent studies showing that Rht8 introgression decreased SL.

![Fig. 4 The frequency of Bima4-derived alleles of SNP markers related to the KNS or SL QTLs in four different generations](image)

Table 5 Information of the KASP markers developed in this study

| QTL          | KASP marker   | Primer sequence                               | FAM                              | VIC                              | Common                        |
|--------------|---------------|-----------------------------------------------|----------------------------------|----------------------------------|-------------------------------|
| QKns.his-7D2–1| KASP-AX-110945813 | GTCATT TTT TTCAGGGTTTGTGATG TATG            |                                  |                                  | AAGCAGCACATGTCAGCTTCTCTCTTA   |
|              | KASP-AX-111490337 | CGTCACACTGGACTGTATGTT             |                                  |                                  | GCGGACGTCCATTTTGGACACAA      |
| QSl.his-5A-2 | KASP-AX-108964722 | ACTCGTTTTTTTTCGCGCCGCAA   |                                  |                                  | ACAGAGGTCGACTCCGCGGCAAA      |

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**Table 5** Information of the KASP markers developed in this study
with constant spikelet number [37]. Therefore, further research is needed to identify whether \( Qsl.his-2D1–1 \) is nearby or identical with \( Rht8 \).

In the present study, \( Qsl.his-5A-2 \) was identified in all four environments and the average value. It was at the interval 94.00–96.00 cM explained 4.65–8.38% of the phenotypic variance and was located on 5A at the interval 506.65–524.73 Mb. Fan et al. [38] identified an SL-associated gene, \( qsl-5A.3 \), in the interval 478.65–541.29 Mb. Kumar et al. [10] identified an SSR locus, Xgwm186, related to SL on 5A at position 471.71 Mb. Cui et al. [3] detected two QTLs related to SL on 5A at positions 444.92 and 682.71 Mb, respectively. In addition, Liu et al. [21] found an SNP maker, IAAV8258, related to SL on 5A at position 572.84 Mb. In our study, the locus \( Qsl.his-5D1 \), which accounted for 3.97–8.21% of the phenotypic variance and was identified in three environments and the average value at the interval 151–156 cM, was located on 5D1 in the interval 446.80–475.31 Mb.

At a similar location to \( Qsl.his-5D1 \), marker Xgwm182 (439.22 Mb) on 5D affecting SL was reported by Kumar et al. [10]. Deng et al. [20] also reported a QTL, \( QSLsdau-5D \), linked to SL in marker interval Xbarc1097-Xcfd8 on 5D positioned in the interval 287.41–396.41 Mb.

**QTL effects in the diverse wheat panel**

In this study, we conducted the allelic analysis based on phenotyping data collected from 15 environments in the diverse wheat panel. As the result showed, the positive alleles of \( QKn_his-7D2–1 \), \( QKn_his-7D2–2 \), \( Qsl.his-4A-1 \), \( Qsl.his-5D1 \), \( Qsl.his-4D2–2 \), \( Qsl.his-5B \), and \( Qsl.his-5A-2 \) significantly increased KNS or SL in the diverse panel, suggesting that they are more universal in their effects, suggesting that they are more universal in their effects. These important loci were very beneficial to pyramid breeding in wheat. On the other hand, the positive alleles of \( Qsl.his-2D1–1 \), \( Qsl.his-3A-2 \), and \( Qsl.his-3B \) in the RIL population were unfavorable in the diverse wheat panel, indicating they may be population-specific QTL. In addition, for \( QKn_his-5A-2 \) where the favorable allele was obtained from Bima4 in the RIL population, the Bima4 alleles showed negative effects at two loci (AX-109980237 and AX-110121838), but positive effects at another two loci (AX-111102726 and AX-109876198) in the diverse wheat panel. \( QKn_his-5A-2 \) was mapped at the interval 106.00–125.00 cM and the physical distance between the marker AX-110121838 (549336395) and AX-111102726 (572237027) reached 22.90 Mb. These results indicated that there may be a great distance between these flanking markers and the peak markers for \( QKn_his-5A-2 \).

**Transmission of Bima4 alleles to its derivative descendants**

Bima4 possesses many superior agronomic traits, especially high resistance to stripe rust, and it has played a crucial role in Chinese wheat breeding and production. In this study, the transmission of Bima4 alleles which showed positive effects in the RIL population at five loci (\( QKn_his-7D2–1 \), \( Qsl.his-5A-2 \), \( Qsl.his-2D1–1 \), \( Qsl.his-3A-2 \), and \( Qsl.his-3B \)) to its derivative descendants showed a relatively high frequency or an upward trend following the continuity of generations, suggesting that they underwent rigorous selection during breeding. These important loci in Bima4 had a great effect on the improvement of wheat breeding and should be studied intensively. Our results also accorded with previous reports by Guo et al. [23], Li et al. [25], Russell et al. [39], Pestsova and Röder [24] and Sjakste et al. [40], who found that the alleles selected preferentially in progeny were associated with advantageous traits. More importantly, the positive effects of the Bima4 alleles at these two loci \( QKn_his-7D2–1 \) and \( Qsl.his-5A-2 \) have been validated in the diverse panel. We further developed two and one KASP markers for these two loci, which are valuable for MAS breeding. Similarly, a few KASP markers were developed in some studies for yield-related traits such as thousand kernel weight [41], grain length [42], productive tiller and fertile spikelet numbers [43], and plant height, SL, and total spikelet number per spike [26]. Compared with conventional molecular markers such as SSR, these KASP markers are more accurate and high-throughput, which can greatly improve the speed and efficiency of genomic selection for MAS breeding [44, 45].

**Conclusions**

A high-density genetic map, consisting 2356 bin markers (14,812 SNPs) and spanning 4141.24 cM, was constructed using the wheat 55 K genotyping assay in the RIL population with 248 lines derived from the two founder genotypes of wheat, Bima4 and BainongAK58. A total of seven and 18 QTLs were identified for KNS and SL, respectively, and they were distributed on 11 chromosomes. The allele effects of the flanking markers for 12 stable QTLs including four KASP markers for these two loci, which are valuable in breeding lines. The positive alleles at seven loci significantly increased KNS or SL in the diverse panel, suggesting that they are more universal in their effects and are valuable for gene pyramiding in breeding programs. The transmission of the Bima4 alleles indicated that the favorable alleles at five loci showed a relatively high frequency or an upward trend following the continuity of generations, suggesting that they underwent rigorous selection during breeding. The positive effects of the Bima4 alleles at two loci \( QKn_his-7D2–1 \) and \( Qsl.his-5A-2 \) have been validated in the diverse panel, and two and one KASP markers were developed for these two loci. Our results are useful for knowing
the molecular mechanisms of founder parents and future molecular breeding in wheat.

Methods

Plant materials

The QTL mapping population containing 248 RILs (F2) were derived from the F2 population of the cross BainongAK58 × Bima4 by the single seed descent method. Bima4 is both an important founder genotype and a widely grown cultivar with high yield potential and wide environmental adaptability. BainongAK58 has many important traits such as lodging resistance, disease resistance, and yield potential. A diverse wheat panel containing 384 elite cultivars and breeding lines was used for QTL validation in this study, and detailed information was described in Li et al. [46]. Seventy cultivars derived from Bima4 were also included (Table S3), and there are 12, 35, 18, and 5 accessions in the first, second, third, and fourth generations of the derivatives, respectively. Seeds of all accessions were provided by the National Crop Gene Bank, Chinese Academy of Agricultural Sciences, Beijing.

Field trials and data analysis

Field experiments for the RIL population were performed at Xinxiang (117.17°E, 40.69°N) in 2017, 2018 and 2019 (2017XI, 2018XI, and 2019XI) and Huixian (116.41°E, 39.91°N) in 2018 (2018HU) in Henan province in a randomized block design. Thirty seeds for each line were evenly planted in two rows of 2 m in length and 25 cm between rows. The main spikes of at least 6 plants in each plot were measured to investigate the SL and KNS when ripening. Broad-sense heritability across different environments was calculated based on the ANOVA model as described by Wu et al. [47].

The diverse wheat panel was planted in randomized complete blocks with two or three replicates in five major wheat ecological regions of China in the 2007, 2008, and 2009 planting seasons as described previously [46], including Yangling (108.08°E, 34.27°N) in Shaanxi Province, Tai’an (117.09°E, 36.21°N) in Shandong Province, Shijiazhuang (114.52°E, 38.05°N) in Hebei Province, Chengdu (104.08°E, 30.66°N) in Sichuan Province, and Yangzhou (119.42°E, 32.40°N) in Jiangsu Province. Two hundred seeds for each cultivar were evenly planted in five rows 2 m long and spaced 30 cm apart. The SL and KNS traits were assessed from 10 spikes randomly sampled from the centre of each plot before harvesting.

SNP genotyping, linkage map construction and QTL detection

The RIL lines and two parents were genotyped with the high-density Illumina Infinium iSelect 55 K SNP array by China Golden Marker (Beijing, China). The diverse wheat panel was also genotyped using the same SNP array [46]. After excluding the monomorphic markers in the RIL population, markers retained were analyzed using the BIN function of IciMapping 4.2 (http://www.isbreeding.net) based on their segregation patterns with the parameters of “Missing Rates” and “Distortion Value” being set as 20 and 0.001, respectively. Only one marker with the least “Missing Rate” was chosen to represent each bin for constructing genetic maps and QTL mapping in this study. Linkage analysis was performed with IciMapping 4.2 using the default mapping function, and the resulting genetic map was displayed with MapChart v2.2 (http://www.biometris.nl/uk/Software/MapChart/). QTLs for SL and KNS in each environment and the average values across all environments were detected using the inclusive composite interval mapping (ICIM) function of IciMapping 4.2 and LOD score values ≥2.5.

QTL validation and development of KASP markers

For certain stable QTLs identified for SL and KNS in the RIL population, the QTL-associated flanking markers were validated using the diverse wheat panel. Furthermore, of the stable QTLs analyzed at which the positive alleles were contributed by Bima4 in the RIL population, the transmission of Bima4 alleles at the QTL-associated SNP markers were also determined using its 70 descend- ants. SNP markers highly associated with a specific QTL were selected and converted to KASP markers.

Abbreviations

KNS: Kernel number per spike; SL: Spike length; QTL: Quantitative trait loci; RIL: Recombinant inbred line; KASP: Kompetitive allele-specific PCR; MAS: Marker-assisted selection.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-022-03544-6.

Additional file 1: Table S1. Genetic map of wheat developed using the RIL population derived from the cross between BainongAK58 and Bima4.

Table S2. Phenotypic variation for SL and KNS in the RIL population.

Table S3. Seventy wheat cultivars derived from Bima4.

Acknowledgments

Not applicable.

Authors’ contributions

XX and XL designed the experiments, analyzed all data, and wrote and extensively revised this manuscript. DZ and JZ participated in phenotype measurement. XH and HS participated in data analysis. ZR guided the experiment. All authors approved the final version of the manuscript.

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Availability of data and materials
The main datasets supporting the conclusions of this article are included within the article and its additional file. A small piece of data used for QTL validation in this study, including the diverse wheat panel and their phenotype and SNP genotyping data, is available in this reference which we published before (Li X, Xu X, Liu W, Li X, Yang X, Xu Z, Li L. Dissection of superior alleles for yield-related traits and their distribution in important cultivars of wheat by association mapping. Front Plant Sci. 2020;11:175. DOI:https://doi.org/10.3389/fpls.2020.00175). All datasets are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
This study on plants complies with relevant institutional, national, and international guidelines and legislation, including the collection of plant material.

Consent for publication
Not applicable.

Competing interests
The authors declare that there are no competing interests.

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