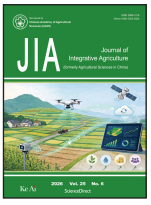
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RESEARCH ARTICLE

Multi-dimensional comprehensive evaluation reveals the quality trait characteristics of wheat cultivars in the Huang-Huai wheat region of China

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Highlights

- The stability time (ST), stretch area (SA), and maximum resistance (MAXR) were identified as key factors influencing wheat quality in the Huang-Huai wheat region of China.
- The subunit types of *Glu-D1* and *Sec-1* are important factors in determining the quality classifications of wheat cultivars.
- A multi-dimensional comprehensive method for assessing wheat quality was developed that incorporates both phenotypic data and molecular marker detection results for the major genetic loci.

Abstract

Wheat (*Triticum aestivum* L.) quality is a major focus of wheat breeding that is influenced by multiple factors. The Huang-Huai wheat region is one of the main wheat-producing areas in China, and it has favorable conditions for cultivating wheat cultivars with strong-gluten and medium-strong-gluten. In this study, a systematic assessment of seven crucial quality traits and two important genetic loci (*Glu-1* and *Sec-1*) in 436 wheat cultivars in the Huang-Huai wheat region of China by principal component analysis (PCA) and fuzzy comprehensive evaluation (FCE) methods identified the stability time (ST), stretch area (SA), and maximum resistance (MAXR) as three key factors which significantly influence wheat quality. *Glu-1* and *Sec-1* primarily impacted these three traits and subsequently influenced wheat quality. Compared to *Glu-A1* and *Glu-B1*, *Glu-D1* has a more significant impact on the comprehensive evaluation value *D*, principal components PC1–PC3, and the main traits ST, SA and MAXR of PC1. Wheat cultivars carrying the high-molecular-weight glutenin subunit (HMW-GS) *Dx5+Dy10* exhibited notable improvements in the ST, SA, and MAXR traits compared with those carrying HMW-GS *Dx2+Dy12*, suggesting that *Dx5+Dy10* may enhance wheat quality by improving those traits. By combining the results of the *D* value, genotype by yield×trait (GYT) index, and HMW-GS score, 20 high-quality and high yielding wheat cultivars were identified, which can be used as elite parents for wheat quality breeding.

Keywords: wheat quality, comprehensive evaluation value, high-molecular-weight glutenin subunits, *Sec-1* locus, genotype by yield×trait

1. Introduction

Wheat (*Triticum aestivum* L.) is a vital staple crop that provides approximately 20% of the calories and 25% of the protein for human consumption worldwide (Wang *et al.* 2021). Protein comprises a substantial proportion of the organic compounds in wheat seeds, accounting for 10–12% of seed weight (Goesaert *et al.* 2005). The storage proteins gliadin and glutenin constitute approximately 75–80% of total wheat proteins. These two proteins combine with each other to form

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unique wheat glutens that produce a network structure upon the hydration and mixing of wheat flour (Delcour and Hoseney 2010; Ooms and Delcour 2019). It is well established that gliadin proteins influence dough viscosity and extensibility, whereas glutenin proteins contribute to dough cohesiveness and elasticity; and their relative proportions determine the distinct characteristics of the gluten (Biesiekierski 2017; Chen *et al.* 2018; Gao *et al.* 2021). Notably, glutenin proteins that make up the polymeric protein network play pivotal roles in determining wheat quality (Jin *et al.* 2015; Wang *et al.* 2018).

Wheat quality is a complex trait determined by multiple quality indexes (Ooms and Delcour 2019), including crude protein content (CPC), wet gluten content (WGC), water absorption (WA), stability time (ST), maximum resistance (MAXR), stretch area (SA), and bulk density (BD). The content and composition of the glutenin proteins play a pivotal role in determining various quality traits (Weegels *et al.* 1996; Lafiandra and Shewry 2022). Wheat glutenin primarily consists of high-molecular-weight glutenin subunits (HMW-GS) linked with low-molecular-weight glutenin subunits (LMW-GS) *via* disulfide bonds (Zang *et al.* 2022). Different types of HMW-GS and LMW-GS exert differential effects on gluten quality, leading to variation in wheat quality-related traits (Goesaert *et al.* 2005; Gao *et al.* 2016; Sherman *et al.* 2018; Jiang *et al.* 2019). Despite accounting for only approximately 10% of total gluten proteins, HMW-GS can explain 45–55% of the phenotypic variation in gluten strength (Gianibelli *et al.* 2001; Li *et al.* 2019).

The HMW-GS are encoded by the *Glu-1* loci located on the long arms of Group I chromosomes 1A, 1B, and 1D, which are designated as *Glu-A1*, *Glu-B1*, and *Glu-D1*, respectively (Payne *et al.* 1980; Shewry *et al.* 2003). Various types of HMW-GS have been shown to have differential impacts on gluten quality as well as end-use quality related traits (Jiang *et al.* 2019; Li *et al.* 2019). The *Glu-A1*, *Glu-B1* and *Glu-D1* genes make different contributions to end-use quality, with variations in *Glu-D1* providing a greater contribution than variation in *Glu-B1* or *Glu-A1* (Morris 2021). Previous studies have demonstrated that the use of molecular marker detection for identifying HMW-GS types can effectively predict end-use quality and confirmed that elite glutenin subunits exhibit a superposition effect during the formation process that determines end-use quality (Yang *et al.* 2014; Zhang *et al.* 2016). These findings provide valuable insights for molecular breeding aimed at improving wheat quality and serve as a theoretical foundation for the genetic improvement of wheat quality. Therefore, the identification of HMW-GS types is crucial for predicting and evaluating wheat quality traits.

The global utilization of wheat-rye 1RS translocations has played an important role in improving disease resistance and yield-related traits in modern wheat cultivars (Hurni *et al.* 2013; Howell *et al.* 2014; Li J J *et al.* 2023). However, the substitution of rye chromosome arm 1RS for wheat chromosome arm 1BS results in the deletion of *Glu-3*, which encodes LMW-GS, potentially impacting end-use quality due to the introduction of the *Sec-1* locus encoding ω-secalins on 1RS (Szakács *et al.* 2020; Li *et al.* 2021). In addition, environmental conditions, cultivation practices, and other genetic factors can influence wheat quality (Hellemans *et al.* 2018; Zörb *et al.* 2018). Therefore, a comprehensive evaluation encompassing HMW-GS types and *Sec-1* locus detection combined with phenotypic analysis is necessary for a comprehensive assessment of wheat quality.

Previous studies on wheat quality traits have mainly focused on specific environments, but large-scale secondary analysis studies are needed to analyze the changes on both spatial and temporal scales. Therefore, comprehensive analysis based on multiple quality-related traits is an ideal method for evaluating wheat quality. PCA and FCE are two essential methods for achieving those objectives. PCA reduces the dimensionality of multiple complex traits, transforming them into a few principal components while clarifying the contribution of each trait to each component (Jolliffe and Cadima 2016; Souza *et al.* 2024). FCE, an evaluation method based on fuzzy mathematics, is well-suited for cases where the relationships among factors are complex and evaluation criteria are challenging to quantify (Xu *et al.* 2021). It has been widely employed in various fields (Xu *et al.* 2021; Li J J *et al.* 2023), and this method integrates multiple indicators for comprehensive analysis, thus avoiding the limitations of single-index assessments.

The Huang-Huai wheat region is one of the main wheat-producing areas in China. The wheat grown in this region mainly includes strong-gluten, medium-strong-gluten, and medium-gluten cultivars (He *et al.* 2002). In the present study, a comprehensive analysis of the quality traits of 436 wheat cultivars released in the Huang-Huai wheat region during 2016–2023 was conducted. The effects of different glutenin subunits and the *Sec-1* locus on wheat quality traits were elucidated to provide a multi-dimensional comprehensive method of assessment for wheat quality that incorporates both phenotypic data and molecular marker detection results for the major genetic loci. Furthermore, 20 wheat cultivars with desirable high-quality characteristics and high yields were identified as elite parents for wheat quality breeding.

2. Materials and methods

2.1. Experimental design

As a temporal scale comprehensive analysis for evaluating wheat quality, a comprehensive analysis of seven crucial quality traits of the 436 wheat cultivars released in the Huang-Huai wheat region during 2016–2023 was conducted. Notably, this study provides a multi-dimensional systematic assessment method for wheat quality that incorporates both phenotypic data and molecular marker detection results for the major genetic loci (Appendix A).

2.2. Data sources

The phenotypic data of 436 approved wheat cultivars released in the Huang-Huai wheat region during 2016–2023 (Appendix B) were analyzed for seven quality-related traits and one yield trait (Table 1). The data were extracted from the official report for wheat cultivar approval through the Big Data Platform for Seed Industry of China (http://202.127.42.47:6010/SDSite/Home/Index). The phenotypes of all traits were averaged over multiple years.

Table 1 Wheat quality traits examined in this study

Trait	Description	Unit
Crude protein content (CPC)	Content of crude protein in grains determined by the Kjeldahl method	%
Wet gluten content (WGC)	Wet gluten content at a 14% wet base	%
Water absorption (WA)	Water absorption per 100 g flour under a 14% wet base	mL
Stability time (ST)	Stabilization time, mainly used to indicate the ability of flour to tolerate mechanical stirring after it forms dough	min
Maximum resistance (MAXR)	Ability of dough to limit outward expansion under external forces	EU
Bulk density (BD)	Weight of wheat grain in a unit volume	g L^{-1}
Stretch area (SA)	Area included in the stretch curve, used to characterize the energy required in the stretch test of the dough	cm^2
Grain yield (GY)	Average yield per mu of wheat cultivars in regional and production trials	kg m^{-2}

2.3. Descriptive statistics and correlation analysis

All data were analyzed using the SPSS 19.0 software (IBM, Chicago, USA). Descriptive statistics were employed to assess the variability of the examined parameters (i.e., the means, maxima, minima, and standard deviations). Coefficients of variation (CV) were also calculated as part of the analysis of variation. One-way ANOVA (analysis of variance) was used to analyze the significance of differences between different years, and Duncan's test was used for multiple comparisons at α=0.05. Spearman's rank correlation method was applied to seven quality traits among the 436 wheat cultivars.

2.4. Principal component analysis (PCA)

To comprehensively evaluate the quality traits of the 436 wheat cultivars, PCA was conducted after using the *z*-score method (Guo *et al.* 2024) to standardize the data of the seven quality traits using SPSS 19.0 software (IBM, Chicago, USA). The principal components describing trait interactions were determined based on criteria of eigenvalue>1 and cumulative contribution rate≥80% as thresholds. Missing values were imputed using the mean of values corresponding to each trait.

2.5. Comprehensive evaluation of wheat quality traits

Based on the results of PCA, the quality traits of 436 wheat cultivars were quantified using the FCE method (Li X F *et al.* 2023) and expressed as the comprehensive evaluation value *D*. The membership function value was calculated as follows:

$$\mu(X_{j,i})=\frac{(X_{j,i}-X_{j\min})}{X_{j\max}-X_{j\min}},\ j=1, 2, 3 \quad (1)$$

In the formula, μ is the membership function value; $X_{j,i}$ is the *i*th comprehensive index value of the *j*th wheat cultivar; and $X_{j\min}$ and $X_{j\max}$ are the minimum and maximum values of the *j*th comprehensive index, respectively.

The principal component weighting analysis was conducted as follows:

$$W_j=\frac{P_j}{\sum_{j=1}^{3}P_j},\ j=1, 2, 3 \quad (2)$$

where W_j and P_j represent the weight and contribution rate of the *j*th comprehensive index among all comprehensive indexes, respectively.

The comprehensive evaluation value *D* was derived as follows:

$$D=\sum_{j=1}^{3}[\mu(X_{j,i}\times W_j)],\ j=1, 2, 3 \quad (3)$$

A cluster analysis of 436 wheat cultivars was carried out by using the *k*-means clustering analysis method (Yu *et al.* 2016) with the *D* value as a variable.

2.6. Molecular marker detection of *Glu-1* and *Sec-1* loci

To identify the gluten subunits and the presence of the *Sec-1* locus, molecular marker detection was conducted using diagnostic markers for the *Glu-1* and *Sec-1* loci (Appendix C). The PCR reaction system referred to our previous study (Liu *et al.* 2022).

2.7. Evaluation score of HMW-GS

The types and compositions of HMW-GS of the 436 wheat cultivars were quantitatively scored according to the methods described by Payne *et al.* (1987) and Rogers *et al.* (1989) (Appendix D). To mitigate the impact of the *Sec-1* locus on the quality traits, the final score of the *Glu-1* locus in wheat cultivars carrying the *Sec-1* locus was adjusted based on Payne *et al.* (1987) (Appendix E).

2.8. Analysis of the genotype by yield×trait

The principal component scores of wheat cultivars were used as the phenotypes to calculate the genotype by yield×trait (GYT) index using the following eq. (Yan *et al.* 2021):

$$P_i=\sum_{j=1}^{3}[W_j(y_i\ x_{ij})],\ j=1, 2, 3 \quad (4)$$

where P_i represents the GYT index; W_j represents the weight of quality traits; y_i is the mean yield of wheat cultivars; and x_{ij} represents the value of cultivar *i* on principal component *j*. The results were all standardized by the *z*-score method (Guo *et al.* 2024).

3. Results

3.1. Analysis of variation of wheat quality traits

To analyze the phenotypic data of the 436 wheat cultivars for seven quality traits, the mean value, extreme value, standard deviation (SD), CV, and data absence rate were calculated for CPC, WGC, WA, ST, MAXR, SA and BD (Fig. 1-A). The absence rate represents the percentage of cultivars lacking a corresponding trait index. Based on the analysis of quality trait variation, BD had the lowest CV at 3.6%, followed by WA at 5.3%, CPC at 6.2%, and WGC at 8.8%, which were

A

Trait	Mean	Maximum	Minimum	SD	CV (%)	Data absence rate (%)
Crude protein content (%)	14.5	17.9	10.5	0.9	6.2	–
Wet gluten content (%)	30.8	40.9	22.1	2.7	8.8	–
Water absorption (mL)	59.9	67.6	51.0	3.2	5.3	–
Stability time (min)	6.6	40.0	1.1	5.2	78.8	–
Maximum resistance (EU)	297.2	870.0	55.5	30.5	10.3	3.7
Stretch area (cm^2)	61.2	192.0	11.5	30.5	49.8	3.7
Bulk density (g L^{-1})	799.2	846.5	402.0	28.9	3.6	3.7

B

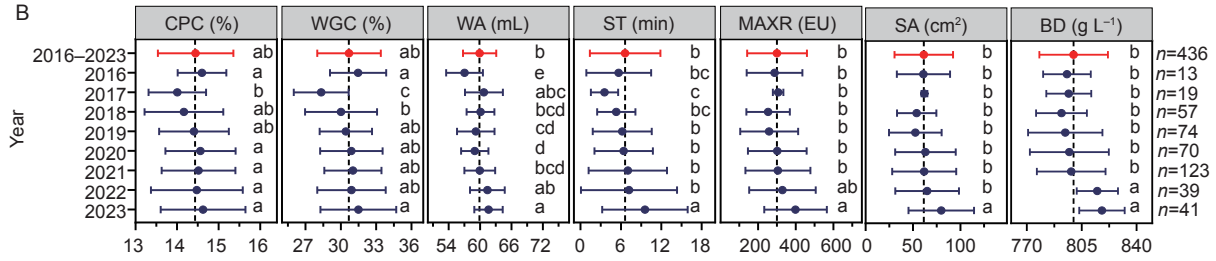


Fig. 1 Descriptive statistics of the seven wheat quality-related traits in this study. A, statistical analysis of quality traits of the 436 wheat cultivars. SD and CV represent the standard deviation and coefficient of variation, respectively. B, annual changes in the quality traits of 436 wheat cultivars in the Huang-Huai wheat region during 2016–2023. The dashed vertical lines represent the mean value of each trait in 2016–2023. The dot and line segments represent the average value and standard deviation of the traits in the corresponding year, respectively. CPC, crude protein content; WGC, wet gluten content; WA, water absorption; ST, stability time; MAXR, maximum resistance; SA, stretch area; BD, bulk density. Bars mean SD. Values with either different or the same letters for each trait indicate significant differences (P<0.05) or non-significant differences (P>0.05) according to Duncan's test.

all below 10%. However, the three traits MAXR, SA, and ST had CVs exceeding 10%, with CVs as high as 49.8% for SA and 78.8% for ST (Fig. 1-A).

To elucidate the annual changes in quality traits among wheat cultivars released from 2016 to 2023, their distribution patterns were analyzed by year (Fig. 1-B). The results revealed consistent trends for CPC, WGC, and ST during this eight-year period; and their mean values tended to be greater before and after they declined in 2017 (Fig. 1-B). Notably, the mean value of ST for wheat cultivars released in 2023 exhibited a significant increase of 47.3% compared with the mean of the eight years from 2016 to 2023 (Fig. 1-B). Moreover, WA started to increase from 2021, after showing a decline between 2018 and 2020, with its mean value being higher by 2.7% in 2023 than that observed during the eight-year period from 2016 to 2023 (Fig. 1-B). In addition, MAXR, SA and BD significantly increased in 2022 and 2023, with their mean values rising by 36.6, 30.8 and 1.6% in 2023, respectively, when compared with their values in 2016 (Fig. 1-B).

3.2. Correlation analysis of wheat quality traits

The degrees of correlation among the seven quality traits were further analyzed using the Spearman's rank correlation method (Appendix F). The results revealed positive correlations between all seven quality traits. Notably, the correlation coefficient between CPC and BD was 0.078, which did not quite reach significance (P>0.05). Similarly, a statistically no significant correlation of 0.098 (P<0.05) was observed between CPC and WA, while the remaining correlations coefficients ranged from 0.124 to 0.961, all of which were highly significant (P<0.01) (Appendix F).

3.3. PCA of wheat quality traits

Strong correlations were observed among the seven quality traits of the 436 wheat cultivars, indicating complex multi-collinearity. To enhance the data interpretation, PCA was used to reduce the dimensionality of those traits. Based on their interrelationships, the traits were consolidated into seven principal components (PC1–PC7). Among them, PC1, PC2, and PC3 exhibited eigenvalues greater than 1, with values of 3.19, 1.53, and 1.07, respectively (Fig. 2-A). PC1 accounted for 45.7% of the phenotypic variance while PC2 and PC3 contributed 21.9 and 15.4%, respectively, so all three cumulatively explained 82.9% of the variation in the quality traits among the analyzed wheat cultivars (Fig. 2-B). Therefore, PC1, PC2, and PC3 accounted for most of the variation in the quality traits for the 436 wheat cultivars. Based on these findings, a biplot was constructed illustrating the PCA for the seven quality traits of the 436 wheat cultivars (Fig. 2-C). The eigenvalues corresponding to each eigenvector were determined based on their projections onto the different principal components (Fig. 2-D). The PCA of PC1 revealed that SA, MAXR, and ST displayed higher loadings than the other four traits and they displayed significant correlations with each other (Fig. 2-C and D), which collectively accounted for more than 20% of the phenotypic contribution (Fig. 2-E). For PC2, CPC and WGC exhibited higher loadings than the other five traits on this component, at 0.62 and 0.48, accounting for approximately 38.4 and 23.5% of the phenotypic contribution, respectively (Fig. 2-D and E). Regarding PC3, the loadings for BD, WA, and CPC were 0.61, 0.59 and 0.47, respectively, which collectively accounted for 94.7% of the phenotypic contribution (Fig. 2-D

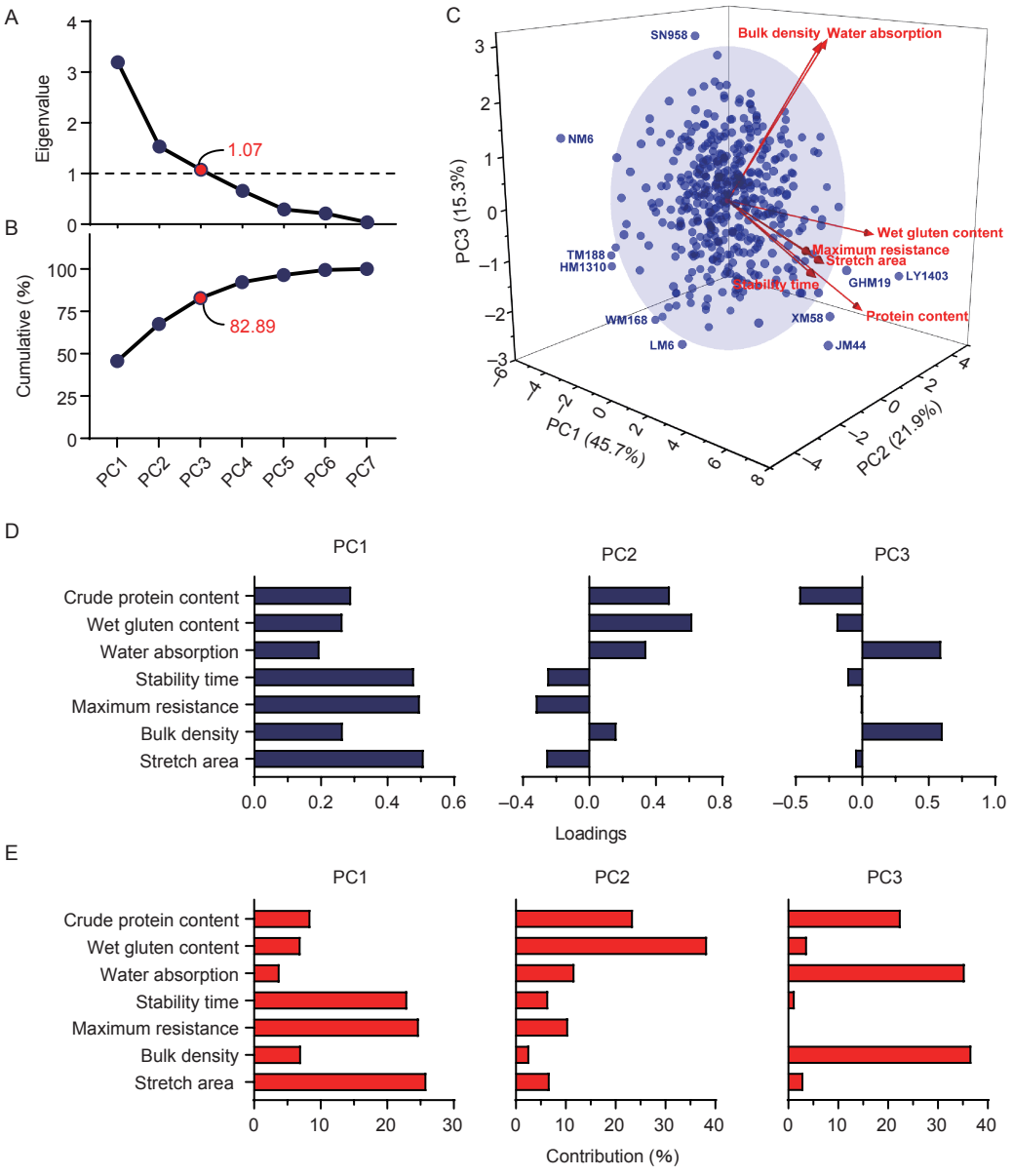


Fig. 2 Principal component analysis (PCA) of quality traits in the 436 wheat cultivars. A, eigenvalues of the different principal components (PCs). The dashed line represents the critical value for selecting the PCs. B, cumulative contribution value of the PCs. C, biplot of the PC analysis. The blue dots represent the position of the score of each cultivar in the space, the blue area represents the 95% confidence interval of the wheat cultivar score distribution range, the dots labeled with cultivar names represent the wheat cultivars outside the confidence interval, and the red lines represent the orientations of the variables on the three PCs. D and E, loadings (D) and phenotypic contribution rates (E) of the seven quality traits on each PC.

and E). Therefore, SA, MAXR, and ST primarily determined PC1; WGC and CPC mainly contributed to PC2; while WA, BD, and CPC were the main determinants of PC3.

3.4. Comprehensive evaluation and cluster analysis of the wheat quality traits

To comprehensively evaluate the quality traits of the 436 wheat cultivars, the FCE method was used to obtain their comprehensive evaluation value *D* based on the three principal component eigenvalues (Appendix B). A higher *D* value indicates better quality in the corresponding wheat cultivars. The *k*-means cluster analysis classified the *D* values into four clusters, consisting of 67, 177, 131, and 61 cultivars, respectively (Table 2). The ranking of quality among these clusters was Cluster IV>Cluster III>Cluster II> Cluster I. Notably, the wheat cultivars in Cluster I exhibited a significantly higher dispersion degree in the *D* values than the other clusters, with a CV reaching up to 250.7% (Table 2).

To elucidate the distribution disparities among the different wheat cultivars over the years, a year-by-year analysis of the proportions of the four clusters during 2016–2023 was conducted (Fig. 3-A). The results showed that from 2016 to 2023, clusters I, II, III, and IV accounted for 15, 41, 30, and 14% of the 436 wheat cultivars, respectively. However, notable fluctuations in the cluster proportions were observed across different years (Fig. 3-A). Overall, a gradual decline

Table 2 Cluster analysis of the 436 wheat cultivars based on the comprehensive evaluation value *D* of quality traits

Cluster	Mean	Maximum	Minimum	SD	CV (%)	Number of cultivars
I	–0.04	0.07	–0.30	0.09	250.72	67
II	0.18	0.26	0.07	0.05	29.00	177
III	0.34	0.43	0.26	0.05	14.66	131
IV	0.52	0.87	0.44	0.08	14.85	61

was observed in the proportions of Cluster I and Cluster II, and Cluster II experienced a significant reduction to approximately 37%. Conversely, an incremental rise was observed in both clusters III and IV, and Cluster IV exhibited a substantial increase to approximately 36% from 2016 to 2023 (Fig. 3-A).

The four clusters exhibited significant differences in the seven quality traits, with the phenotypic mean values ranking from highest to lowest as clusters IV>III>II>I (Fig. 3-B). Except for ST, which showed no significant difference between clusters I and II, the other six traits of CPC, WGC, WA, MAXR, SA, and BD exhibited significant differences among the four clusters (Fig. 3-B). By comparing these traits with the requirements specified in the GB/T 17320-2013 (2013), more than 60% of the wheat cultivars in Cluster IV met the standard for strong-gluten wheat based on the traits CPC, WGC, WA, ST, MAXR, and SA (Fig. 3-C). Overall, the wheat quality in Cluster IV conformed to the standards required for strong-gluten wheat. Except for SA, more than 50% of the wheat cultivars in clusters III and II met the standards for medium-strong-gluten and medium-gluten wheat, respectively (Fig. 3-C). However, note that over 75% of the wheat cultivars among all clusters met the standard for medium-strong-gluten wheat in terms of CPC. In clusters I, II, and III, ranges of 22–65, 26–79, and 16–53% of the wheat cultivars had lower MAXR, SA, and ST than the standard for medium-gluten wheat, respectively (Fig. 3-C).

To demonstrate the association between the comprehensive evaluation value *D* and the three principal components, a correlation analysis was performed using the Spearman's rank correlation method (Fig. 4). Overall, highly significant positive correlations (P<0.01) were observed between the *D* value and all three principal components. However, notable variations in this correlation were observed among the different clusters. Specifically, wheat cultivars from clusters I to IV exhibited highly significant positive correlations between PC1 and their *D* values (Fig. 4-A). However, for PC2 and PC3, only the wheat cultivars in clusters I and II displayed highly significant and significant positive correlations with their *D* values, respectively, and no significant correlations were observed for wheat cultivars in clusters III and IV (Fig. 4-A).

Considering the highly significant positive correlation between the PC1 of clusters I to IV and the *D* value, an examination of the correlations between the *D* value and phenotypes of MAXR, SA, and ST showed that they had phenotypic contribution rates exceeding 20% (Fig. 4-B). Variations were observed in the correlations between MAXR, SA, ST, and the *D* value among the different clusters. Specifically, no significant correlations were detected between the *D* value and the three traits MAXR, SA, and ST within Cluster I, but only ST showed no significant correlation with the *D* value in Cluster II (P>0.05). Conversely, MAXR, SA, and ST all displayed highly significant positive correlations with the *D* value in Cluster III (P<0.01), but only MAXR showed a significant positive correlation with the *D* value in Cluster IV (P<0.05) (Fig. 4-B). Therefore, MAXR, SA and ST are the main traits determining wheat gluten quality.

3.5. Molecular marker detection results for HMW-GS and the *Sec-1* locus

The types and scores of HMW-GS and distribution of the *Sec-1* locus in the 436 wheat cultivars were identified and analyzed using molecular markers (Fig. 5). The predominant subunits on the *Glu-A1*, *Glu-B1* and *Glu-D1* loci were *Ax1* (84.4%), *By9* (52.1%) and *Dx2*+*Dy12* (71.8%). The highest occurrence was observed with these three subunit combinations, accounting for 35.3% (Fig. 5-B). Among the 436 wheat cultivars, a total of 208 cultivars were shown to carry *Sec-1*, accounting for 48.8%.

The subunit scores for each wheat cultivar were calculated based on the corresponding HMW-GS scores. The results revealed that the original HMW-GS scores of the 436 wheat cultivars ranged from 5 to 10 points, with 64.1% of them scoring between 7 and 8 points (Fig. 5-C). After adjusting the HMW-GS score based on the distribution of *Sec-1*, the scores ranged from 3 to 8, with most of the wheat cultivars having a scoring of 5 (36.7%) (Fig. 5-C). Before and after adjustment, highly significant positive correlations were observed between the HMW-GS score and the *D* value (P<0.001), and a greater correlation coefficient was observed for the adjusted scores, indicating a significant influence of *Sec-1* on the *D* value (Fig. 5-D). The average adjusted scores in clusters I and II were lower than the overall average both before and after adjustment. Conversely, clusters III and IV exhibited higher average scores before and after adjustment compared with the overall average across the four clusters (Fig. 5-C, E–H). Moreover, the differences between adjusted and original scores of clusters III and IV were lower than those of clusters I and II.

3.6. Influence of *Glu-1* and *Sec-1* on the comprehensive evaluation of the wheat quality traits

Based on molecular marker detection of the *Glu-1* and *Sec-1* loci in 436 wheat cultivars, the association between the *D* value and *Glu-1* or *Sec-1* was analyzed (Fig. 6-A; Appendix G). The results indicate that there were no significant differences in the *D* values among cultivars carrying different alleles of *Glu-A1*. However, for *Glu-B1*, the *D* value of cultivars carrying the *By16* allele was significantly higher than those of cultivars carrying the other alleles. The scores of PC1, PC2, and PC3 for cultivars with different *Glu-B1* alleles showed no significant differences. Further analysis of the effects of allele combinations of *Glu-A1*, *Glu-B1*, and *Glu-D1* on the *D* value and its components (PC1–PC3) revealed that the favorable alleles *Dx5*+*Dy10* of *Glu-D1*, when combined with favorable alleles of *Glu-A1* or *Glu-B1*, resulted in higher *D* values and PC1 scores compared to other combinations,

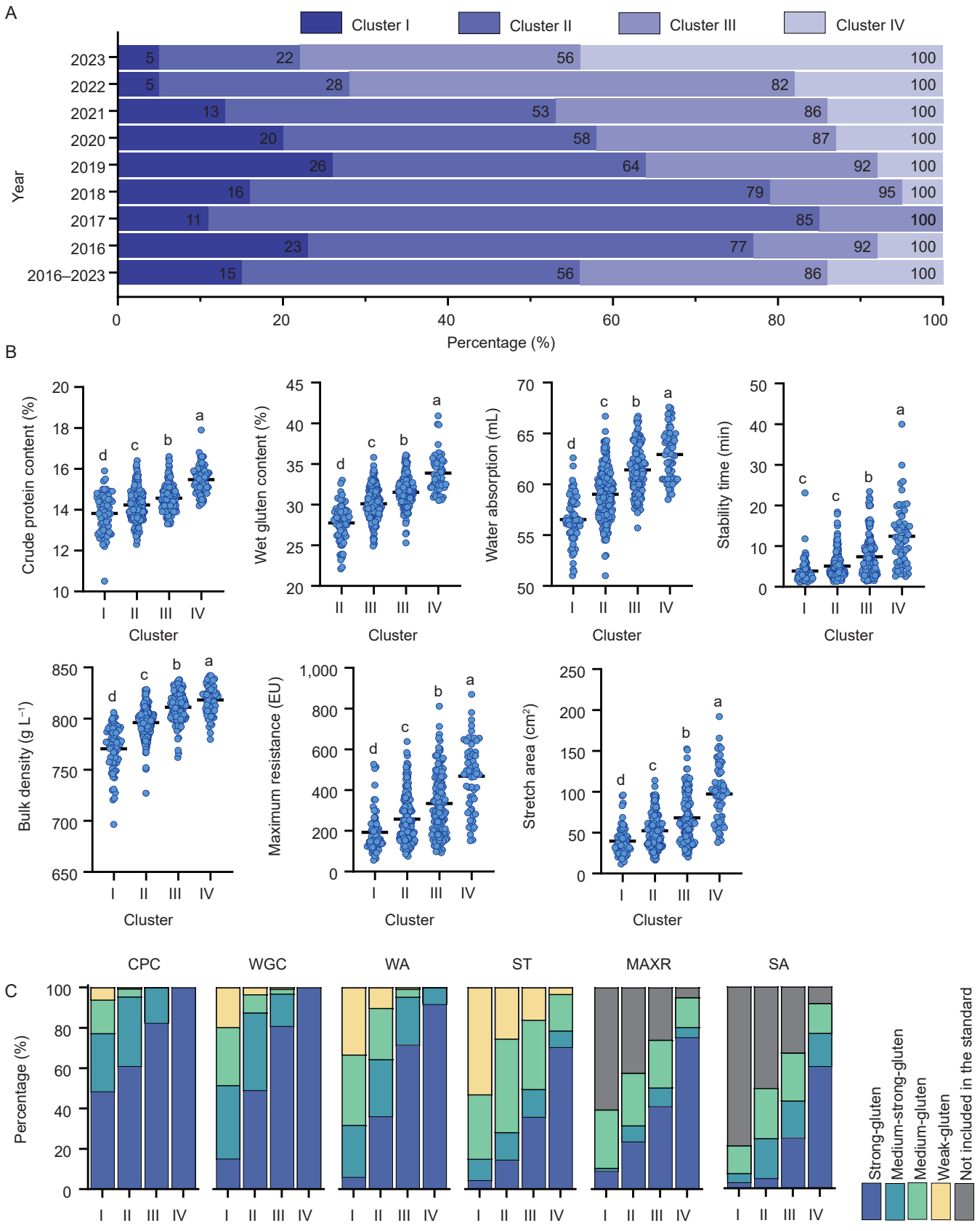


Fig. 3 Cluster analysis of the 436 wheat cultivars based on the comprehensive evaluation value *D* of quality traits. A, distributions of the four clusters in different years based on the cluster analysis of comprehensive evaluation value *D*. B, phenotypic distributions of crude protein content (CPC), wet gluten content (WGC), water absorption (WA), stability time (ST), bulk density (BD), maximum resistance (MAXR), and stretch area (SA) across the four clusters. Values with either different or the same letters for each trait indicate significant differences ($P<0.05$) or non-significant differences ($P>0.05$) according to Duncan's test. C, current status of CPC, WGC, WA, ST, MAXR and SA in relation to the GB/T 17320-2013 (2013) across the four clusters.

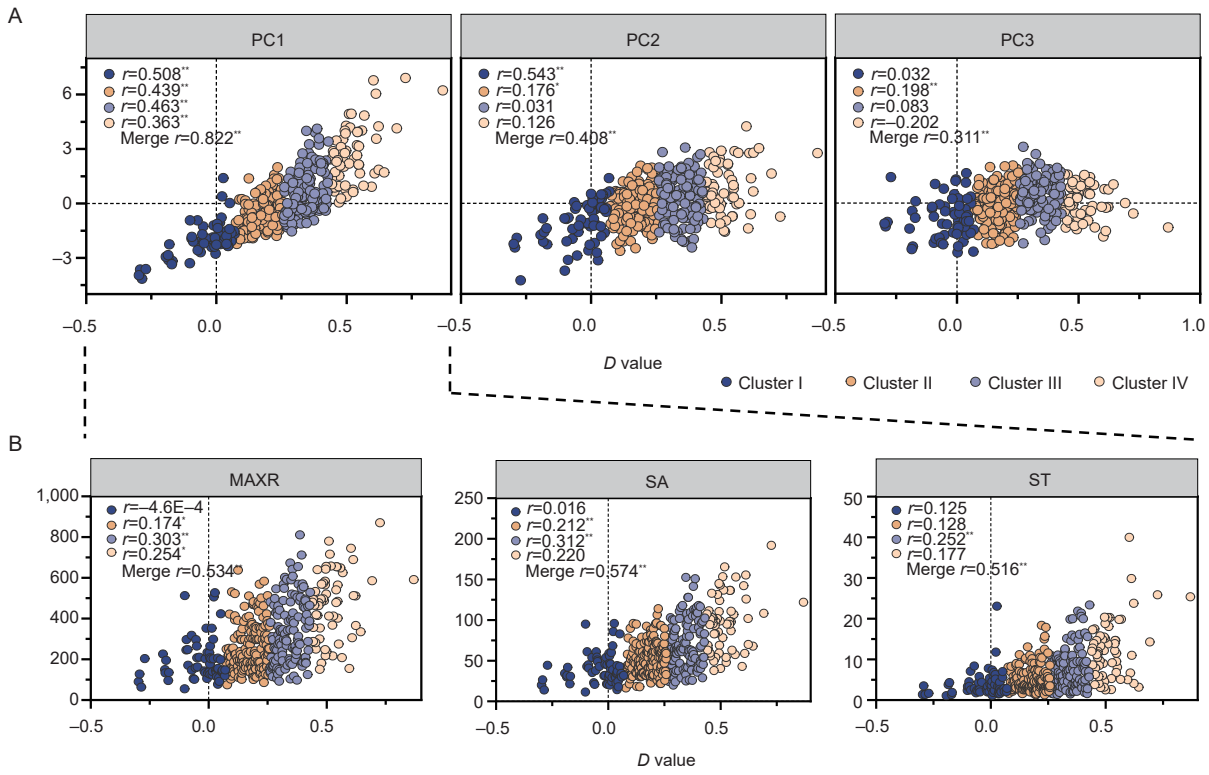


Fig. 4 Correlations between the comprehensive evaluation value *D* of the 436 wheat cultivars and the principal components (PCs) as well as primary constituent traits. A, correlations between the comprehensive evaluation value *D* and the PC1, PC2 and PC3. B, correlations between the comprehensive evaluation value *D* and the principal components of PC1. Merge denotes the correlation between *D* values and the corresponding principal components without distinguishing clusters. Clusters I–IV represent four kinds of wheat cultivars based on a cluster analysis of the comprehensive evaluation value *D* of their quality traits. The Spearman's rank correlation method was used for conducting the correlation analysis. Correlation coefficient is denoted as "*r*". * and ** indicate $P<0.05$ and $P<0.01$, respectively.

with the differences reaching significance (Appendix G). This indicates that *Glu-D1* is a major factor affecting the *D* value and PC1 scores of wheat cultivars.

For *Glu-D1*, the average *D* value of the wheat cultivars carrying *Dx5+Dy10* was significantly higher than that of wheat cultivars carrying *Dx2+Dy12* ($P<0.001$). Wheat cultivars carrying *Sec-1* had a significantly lower average *D* value compared with those lacking *Sec-1* ($P<0.001$) (Fig. 6-A). Further analysis regarding the relationship between the principal component scores of the 436 wheat cultivars and the subunit types of *Glu-D1* or *Sec-1* revealed that PC1 (mainly determined by SA, MAXR and ST) displayed significant differences among the different subunit types of *Glu-D1* ($P<0.01$), while PC2 (primarily determined by WGC and CPC) and PC3 (mainly determined by WA, BD and CPC) showed no significant differences among the different subunit types of *Glu-D1* (Fig. 6-B). Similarly, wheat cultivars with or without *Sec-1* also followed this pattern. For PC1 scores, wheat cultivars carrying *Sec-1* had significantly lower values than those without it ($P<0.01$), whereas there were no significant differences in terms of the PC2 and PC3 scores between these two groups ($P>0.05$) (Fig. 6-B). These results suggested that both the *Glu-D1* and *Sec-1* loci predominantly impact the *D* value through their influence on PC1, which is determined by SA, MAXR, and ST.

To further investigate the influences of *Glu-D1* and *Sec-1* on the PC1 scores in the 436 wheat cultivars, an analysis was conducted on the relationship between the quality phenotypes that showed a phenotypic contribution rate exceeding 20% in PC1 and the subunit types of *Glu-D1* or *Sec-1* (Figs. 2-E and 6-C). Among these traits, wheat cultivars with *Dx5+Dy10* exhibited significantly higher average scores for SA, MAXR and ST compared to those with *Dx2+Dy12* (Fig. 6-C). For SA and MAXR, *Sec-1* significantly reduced their mean phenotypic values regardless of the subunit types of *Glu-D1* ($P<0.001$); while for ST, *Sec-1* only significantly reduced the phenotypic value of cultivars carrying *Dx5+Dy10* ($P<0.001$) (Fig. 6-C). These results indicated that *Glu-D1* and *Sec-1* contributed to the differences in PC1 scores by influencing SA, MAXR and ST, which further affected the *D* value of the wheat cultivars. Moreover, the effect of *Sec-1* on *Dx5+Dy10* was greater than that on *Dx2+Dy12*.

Given the important influences of *Dx5+Dy10* and *Sec-1* on wheat quality traits, a further analysis was conducted on the distribution frequencies of these two factors among the approved wheat cultivars across different years (Fig. 6-D). From 2016 to 2023, the distribution frequency of *Dx5+Dy10* exhibited an increasing trend, but it did not surpass 50% (Fig. 6-D). In contrast, the distribution frequency of *Sec-1* displayed a declining pattern, which remained unaffected by variations in the number of cultivars (Fig. 6-D and E), indicating increased selection for *Dx5+Dy10*, but reduced

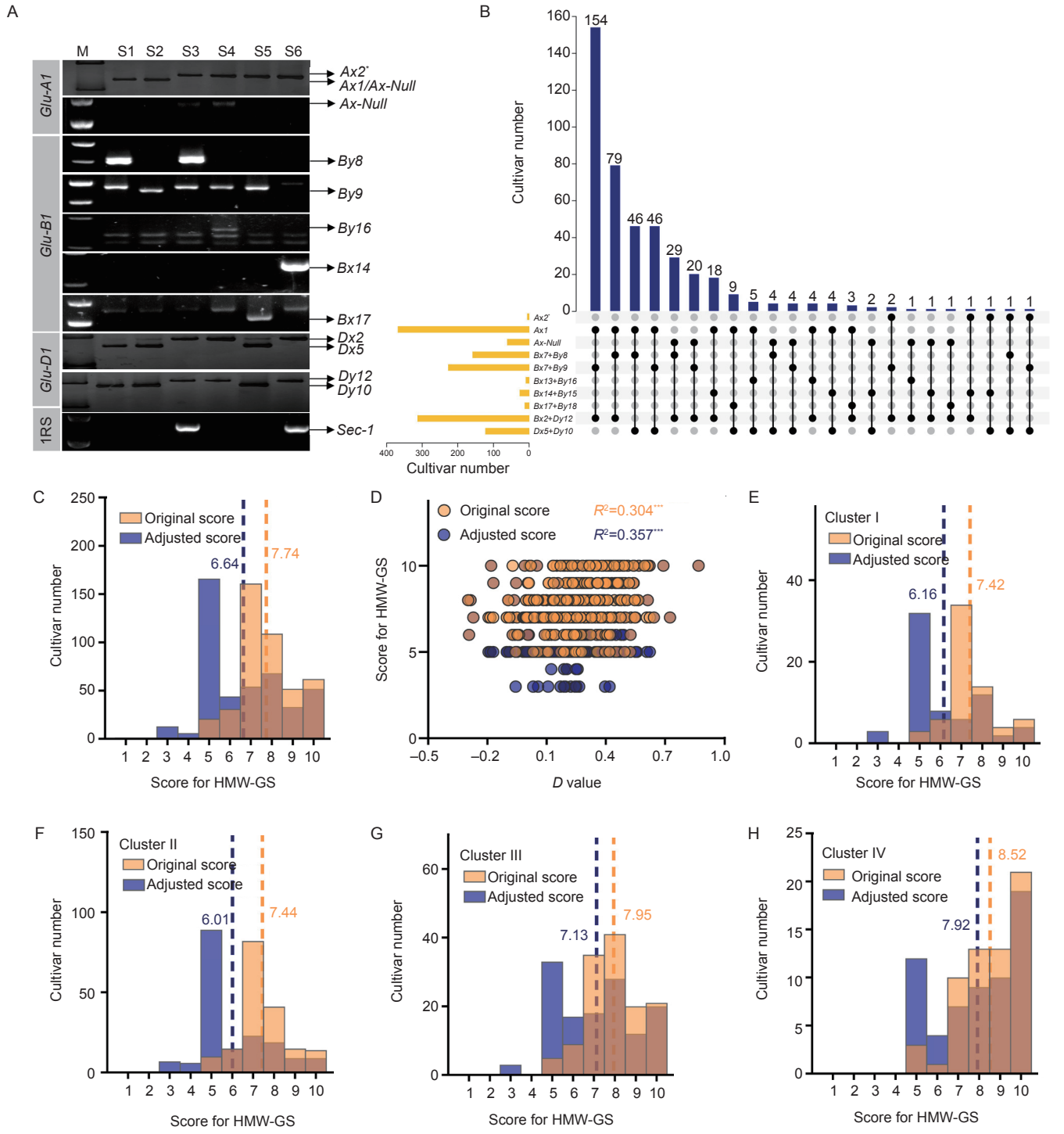


Fig. 5 Distributions and scores of high-molecular-weight glutenin subunits (HMW-GS) in the 436 wheat cultivars. A, molecular marker detection results of selected wheat cultivars. S1–S6, cultivars Luyan 1403, Fuzhao 6002, Hengmai 26, Tunmai 257, Shannong 41, and Xingmai 20. B, combinations of HMW-GS types in the 436 wheat cultivars. C, distributions of HMW-GS scores before and after adjustment. D, correlations between the HMW-GS scores before and after adjustment and the *D* value. E–H, distributions of HMW-GS scores of wheat cultivars in clusters I–IV before and after adjustment.

selection for *Sec-1* following the progress in breeding in the Huang-Huai wheat region. Among the wheat cultivars in clusters I to IV, a gradual increase was observed in the proportion of cultivars carrying *Dx5+Dy10*. Similarly, this trend also was observed for cultivars carrying only *Dx5+Dy10* without *Sec-1*. However, the proportion of cultivars which carried *Sec-1* gradually decreased over time (Fig. 6-F).

3.7. Effect of yield on the wheat quality traits

Based on the results of a cluster analysis of the *D* value and the quality character requirements outlined in the GB/T 17320-2013 (2013), the GYT index was used to investigate the impact of yield on the comprehensive evaluation value *D* for wheat cultivars that conform to the standards for strong-gluten (Cluster IV), medium-strong-gluten (Cluster III), and medium-

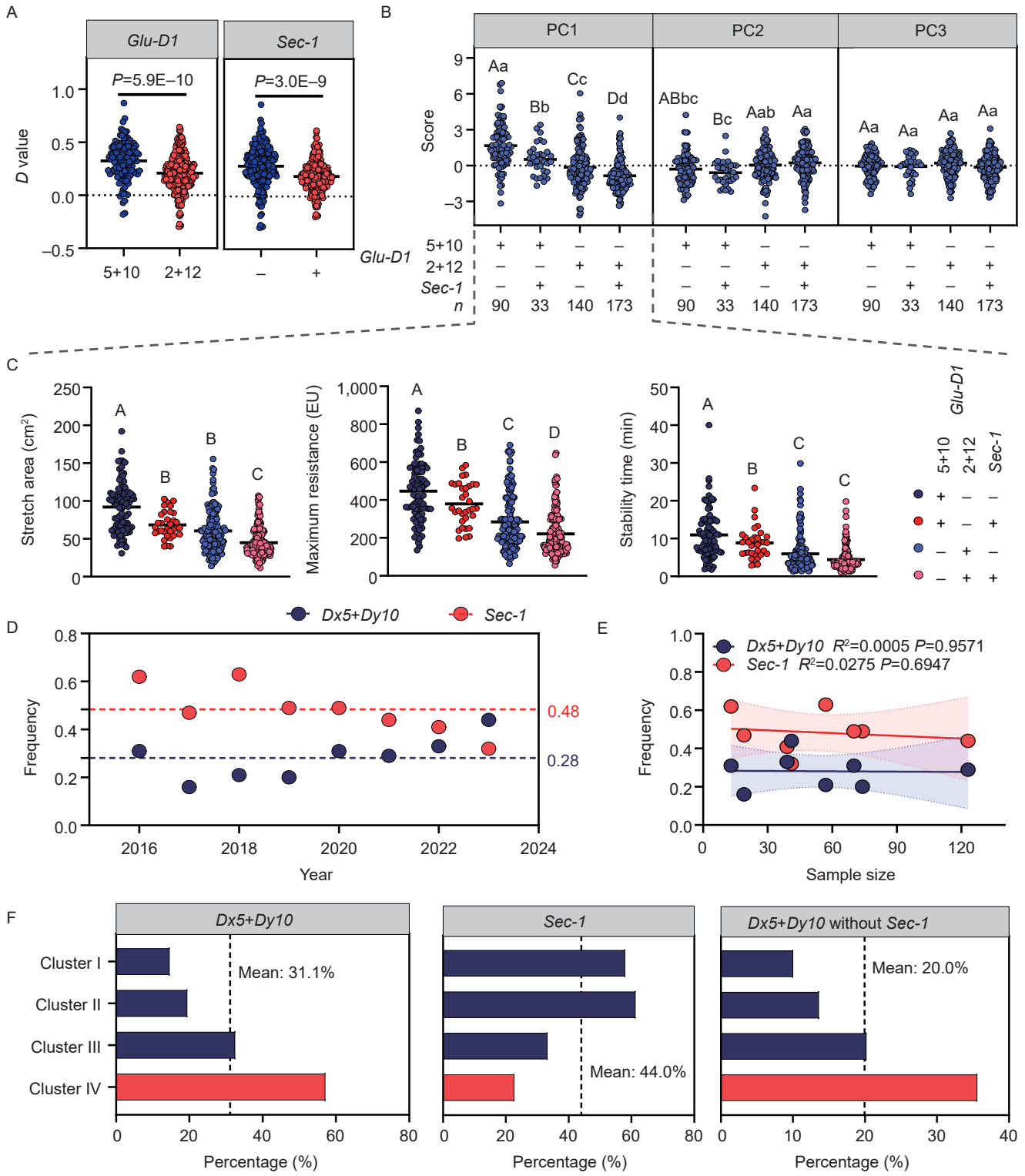


Fig. 6 Influence of the *Glu-D1* and *Sec-1* loci on the comprehensive evaluation of wheat quality traits. A and B, the influences of different subunit types of the *Glu-D1* and *Sec-1* loci on the comprehensive evaluation value *D* (A) and principal component scores (B) of the 436 wheat cultivars. C, influences of different subunit types of the *Glu-D1* and *Sec-1* loci on the principal component traits of PC1. D and E, the distribution frequency (D) of *Dx5+Dy10* on the *Glu-D1* and *Sec-1* loci in the 436 wheat cultivars across different years and their correlations (E) with the number of cultivars. F, distribution frequencies of *Dx5+Dy10* and *Sec-1* in clusters I–IV. Upper- and lower-case letters within each graph indicate very significant (P<0.01) and significant (P<0.05) differences, respectively.

gluten (Cluster II) (Fig. 7; Appendix B). Among the three clusters, there was a highly significant positive correlation between the *D* value and the GYT index. Notably, Cluster IV exhibited a higher correlation coefficient of 0.67 compared with Cluster III and Cluster II (Fig. 7-A). Further analysis of the impact of *Sec-1* on yield and the GYT index across the

different clusters of wheat cultivars revealed that *Sec-1* had a significant effect only on the yield and GYT index in Cluster IV (Appendix H). Although *Sec-1* significantly increased the average yield of Cluster IV cultivars, the GYT index was higher in wheat cultivars without *Sec-1* (Appendix H). Consequently, an analysis was conducted on the 61 wheat cultivars in Cluster IV by integrating the GYT index and HMW-GS scores. The results showed that 27 wheat cultivars (44.3%) in Cluster IV surpassed the mean GYT index value, and 38 cultivars (62.3%) had HMW-GS scores ranging from 8 to 10 points (Fig. 7-B). Based on these results, 20 cultivars (32.8%) were identified with both a GYT index exceeding the mean value of Cluster IV and HMW-GS scores within the range of 8–10 points (Fig. 7-B; Table 3).

4. Discussion

4.1. Current status and strategy for improving the main quality traits in the Huang-Huai wheat region

The Huang-Huai wheat region is one of the major wheat-producing areas in China. In this study, a systematic analysis was conducted on seven crucial wheat quality traits for the 436 wheat cultivars released in the Huang-Huai wheat region during 2016–2023. The results revealed that the four traits, CPC, WGC, WA, and BD, demonstrated stable phenotypes with CVs below 10% (Fig. 1-A). These findings were consistent with those reported by Ma *et al.* (2021), indicating that there was strong positive selection for these four traits in the breeding practices within the Huang-Huai wheat region. Conversely, traits ST, SA, and MAXR displayed CVs above 10% indicating significant variation in ranking among the 436 wheat cultivars analyzed for those traits. That result also agreed with the findings of Ma *et al.* (2021), suggesting that substantial genetic improvements are still needed for these three traits. Notably, significant correlations were observed among all traits except BD and CPC. Previous studies have indicated that the CPC and WGC in wheat determine the formation of the gluten network, which further influences dough strength and stability by enhancing dough WA and BD (Shewry *et al.* 2003; Sherman *et al.* 2018; Hu *et al.* 2021). In addition, ST, SA, and MAXR are interrelated during dough mixing, collectively impacting the overall processing suitability of wheat (Shewry *et al.* 2003). Consistent with the findings of this study, there are complex associations among these seven traits, and employing effective methods to simplify this complexity is essential for identifying the key indicators affecting wheat quality.

In this study, the PCA and FCE methods were used to identify ST, SA, and MAXR as the three key factors which significantly influenced wheat quality and produced obvious improvements in 2022 and 2023 (Figs. 2-E, 4 and 6-C). As the primary traits in the comprehensive evaluation of wheat quality, SA, MAXR and ST participated in the core principal component PC1 that represents gluten quality (Fig. 2-D and E). In Cluster IV, although no significant correlation was observed between the *D* value and SA or ST, there was a significant positive correlation between the *D* value and PC1 (Fig. 3-A; Appendix F), indicating that multiple important traits interacted to reduce the dispersion degree of gluten quality-related traits among the cultivars within Cluster IV (Fig. 4-B).

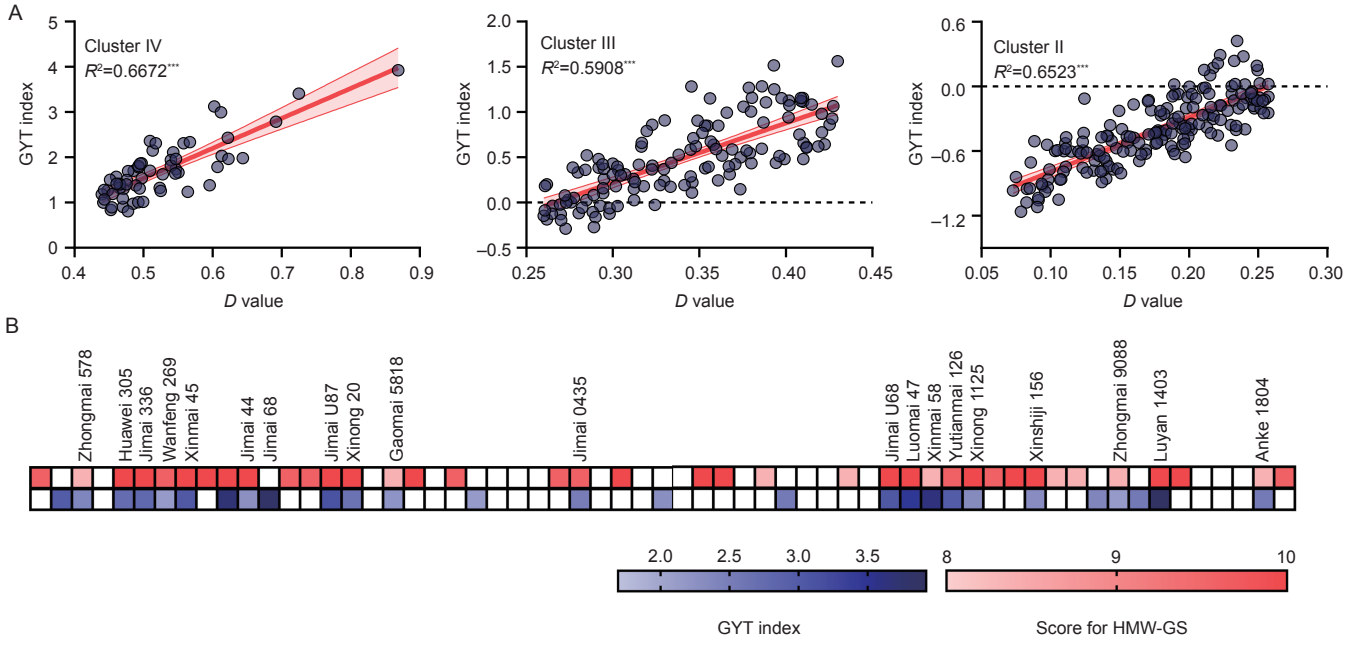


Fig. 7 Influence of wheat yield on the comprehensive evaluation of wheat quality traits. A, correlation analysis between comprehensive evaluation value *D* and genotype by yield×trait (GYT). The data were all standardized. The red band represents the 95% confidence interval for the correlation between the *D* value and the GYT index. ***, $P<0.001$. B, GYT index and high-molecular-weight glutenin subunits (HMW-GS) score of wheat cultivars in Cluster IV. Each grid represents a cultivar, and the white grids in the GYT index and HMW-GS scores indicate that the GYT index did not reach the average value and the HMW-GS score was below 8 points; cultivars marked with the name indicate that the GYT index was above the average and the HMW-GS score was above 8 points.

Table 3 The 20 high-quality and high yielding wheat cultivars from Cluster IV[1)]

Cultivar	CPC	WGC	WA	ST	MAXR	SA	BD	*D* value	GYT index	HMW-GS score
Zhongmai 578	15.4	33.6	60.5	18.8	656.0	143.0	806.5	0.4972	1.8669	8
Huawei 305	14.9	32.5	60.6	14.7	654.5	136.5	840.0	0.5430	2.1097	10
Jimai 336	14.5	31.2	60.0	18.1	716.5	137.0	842.0	0.5131	2.1491	10
Wanfeng 269	15.0	34.8	59.5	14.9	574.5	131.5	816.5	0.4858	1.7001	9
Xinmai 45	16.6	33.5	63.0	19.9	625.0	153.0	795.5	0.5672	2.3341	10
Jimai 44	16.8	32.0	62.8	40.0	745.2	142.4	794.0	0.6023	3.1231	10
Jimai 68	16.3	33.7	60.3	15.5	583.5	145.0	801.0	0.4930	1.7786	10
Jimai U87	16.2	33.6	64.9	23.8	511.0	102.0	815.5	0.6221	2.4311	10
Xinong 20	16.0	35.9	63.9	11.0	513.0	126.0	814.5	0.6132	2.0323	10
Gaomai 5818	14.9	31.9	67.6	9.5	402.0	98.0	816.0	0.5468	1.7368	8
Jimai 0435	16.2	35.7	62.9	13.9	541.5	94.9	799.3	0.5395	1.9402	9
Jimai U68	15.7	30.9	60.5	20.3	780.5	153.5	816.5	0.5092	2.3594	10
Luomai 47	16.6	35.2	65.8	14.3	586.5	108.5	822.0	0.6917	2.7873	10
Xinmai 58	16.2	35.1	61.0	29.9	689.5	155.5	806.5	0.6120	2.9918	8
Yutianmai 126	16.0	32.7	59.0	20.3	658.0	165.5	817.0	0.5177	2.3121	9
Xinong 1125	14.8	32.9	63.0	12.2	479.0	98.5	837.0	0.5396	1.8155	10
Xinshiji 156	14.4	32.7	63.5	12.2	565.5	110.5	817.5	0.4926	1.8060	10
Zhongmai 9088	15.1	31.8	64.2	13.8	412.5	78.5	827.0	0.5092	1.7012	8
Luyan 1403	17.9	39.9	66.5	25.4	591.0	122.0	815.0	0.8688	3.9222	10
Anke 1804	15.3	33.2	62.1	11.5	564.5	111.0	833.0	0.5468	1.9646	8

[1)] CPC, crude protein content; WGC, wet gluten content; WA, water absorption; ST, stability time; MAXR, maximum resistance; SA, stretch area; BD, bulk density; *D* value, comprehensive evaluation value of quality traits; GYT, genotype by yield×trait; HMW-GS, high-molecular-weight glutenin subunits.

Wheat cultivars with different gluten strengths have different quality index requirements (Ma *et al.* 2021). In this study, 35.1, 43.6, and 69.3% of the 436 tested wheat cultivars failed to meet the medium-gluten standards of MAXR, SA, and ST, respectively (Fig. 3-C). According to previous reports, these three traits play interconnected and critical roles in dough performance and the formation of final quality. ST reflects the stability of dough during mixing, indicating the duration that the gluten network can maintain its structure, which is foundational to dough strength and durability (Hu *et al.* 2021). As an indicator of dough extensibility, SA reflects the flexibility of the gluten network during stretching, which directly impacts moldability in processing (Hu *et al.* 2021). MAXR represents the dough's resistance to deformation, which is closely linked to gluten strength and elasticity (Hu *et al.* 2021). Together, these factors determine the structural stability and processing suitability of the dough, thereby influencing wheat quality (Veraverbeke and Delcour 2002; Hu *et al.* 2021). Therefore, the precise enhancement of several important quality traits, including MAXR, SA and ST, is critical for breeding high-quality wheat.

4.2. HMW-GS and 1RS translocation significantly influence wheat quality in the Huang-Huai wheat region

In this study, the HMW-GS scores of 436 wheat cultivars were analyzed using a modified HMW-GS score scale (Payne *et al.* 1987). In clusters I-IV, both the original and adjusted scores of HMW-GS ranged from high to low in the order of IV>III>II>I. This was consistent with the phenotypic results (Figs. 3-B and 5-E–H), which highlighted the crucial role played by the HMW-GS composition in determining wheat quality.

The *Dx5*+*Dy10* allele on the *Glu-D1* locus has been identified as an elite allele for improving bread-making quality (Jiang *et al.* 2019; Morris 2021). The combination of phenotypic results and molecular marker detection of the 436 wheat cultivars showed that wheat cultivars carrying *Dx5*+*Dy10* exhibited a significantly higher comprehensive evaluation value *D* than those carrying *Dx2*+*Dy12* (Fig. 6-A–C). Further analysis revealed significantly greater ratings for ST, SA, and MAXR among wheat cultivars carrying *Dx5*+*Dy10* (Fig. 6-C), which was consistent with the findings of Amritpal *et al.* (2013) and Kiszonas *et al.* (2021). Therefore, this indicates that *Dx5*+*Dy10* may improve wheat quality by influencing ST, SA, and MAXR. The influence of the *Glu-D1* subunit is reflected in several key aspects. The high-molecular-weight protein chains of *Glu-D1* are long and highly elastic, enabling effective cross-linking with LMW-GS to form a stable gluten network, thereby significantly enhancing dough SA (Lafiandra *et al.* 2022). These subunits exhibit strong resistance to deformation during dough mixing and stretching, allowing the dough to maintain structural stability and extend ST during processing (Weegels *et al.* 1996). In addition, the high tensile strength of *Glu-D1* aggregates helps to maintain gluten network integrity under substantial stress, thus improving MAXR (Gao *et al.* 2016).

Despite an increasing trend in the selection frequency of *Dx5*+*Dy10* in the Huang-Huai wheat region in recent years (Fig. 6-D), potential for further improvement remains. This could explain the significant variations observed in ST, SA, and MAXR among different wheat cultivars in the Huang-Huai wheat region in this study. Thus, strengthening positive selection for the *Dx5*+*Dy10* subunit will be required for the genetic improvement of high-quality wheat cultivars.

Given the significant negative impact of chromosome 1RS on wheat quality (Zhou *et al.* 2021), the distribution of the *Sec-1* locus on 1RS among the 436 wheat cultivars was analyzed. The results revealed a gradual decline in the

proportion of wheat cultivars with *Sec-1* from 2016 to 2023, with a final total proportion of 48.8% (Fig. 6-D). There was a successive reduction in the proportion of *Sec-1* along with a corresponding increase in the average HMW-GS scores for wheat cultivars from clusters I to IV (Figs. 5-E–H and 6-F). This demonstrated that *Sec-1* had negatively affected the comprehensive evaluation value *D* by reducing ST, SA, and MAXR. The presence of *Sec-1* likely impacts those three traits through its interference with gluten structure. First, *Sec-1* may reduce the cross-linking between HMW-GS and LMW-GS, weakening the gluten network's strength and leading to lower MAXR (Wieser *et al.* 2000). In addition, the disrupted continuity of the gluten network will result in reduced dough SA, making the dough more prone to breakage during stretching. Furthermore, the instability of the gluten network affects the ST of the dough, causing it to lose strength more readily during processing (Veraverbeke and Delcour 2002; Hu *et al.* 2021). Finally, the effect of *Sec-1* on the quality of wheat cultivars carrying *Dx5+Dy10* was greater than cultivars carrying *Dx2+Dy12*. These results indicate that negative selection against *Sec-1* has promoted the improvement of wheat quality in the Huang-Huai wheat region, and *Sec-1* can be an important indicator in the comprehensive evaluation and classification of wheat quality. Therefore, the subunit types of *Glu-D1* and *Sec-1* are important factors in determining the quality classification of wheat cultivars. During the process of wheat high-quality breeding, more attention should be paid to the development of cultivars that carry the *Dx5+Dy10* subunit, but do not carry the *Sec-1* locus.

4.3. Comprehensive method for evaluating wheat quality and its application

Evaluating a complex trait determined by multiple constituent factors is often challenging, and requires a systematic and comprehensive approach that considers the interactions between those traits (Ma *et al.* 2021). Fuzzy mathematics provides an appropriate framework for realizing that goal (Xu *et al.* 2021). In this study, by applying FCE to the principal component values and trait weights obtained from PCA, a comprehensive evaluation value *D* for wheat cultivars was calculated, enabling a rational, quantitative assessment of wheat quality from a phenotypic perspective. Moreover, the combined use of PCA and FCE mitigates the inherent subjectivity of weighting in FCE, thereby enhancing the precision of the results. Notably, cultivars in Cluster IV exhibited superior performance in terms of gluten strength, with the highest average score for the *D* value (Table 2), HMW-GS score (Fig. 5-F), and other quality attributes (Fig. 3-B). The proportion of *Dx5+Dy10* in Cluster IV significantly surpassed those observed in other clusters (Fig. 6-F). Consequently, cultivars within Cluster IV have great potential as high-quality parents with strong-gluten properties for wheat breeding.

During the process of evaluating and screening germplasm resources, breeders often face the challenge of dealing with multiple traits. In addition to the target breeding traits, a cultivar must meet the minimum requirements for other key traits (i.e., yield) (Cooper *et al.* 2009; Yan *et al.* 2021). Considering the significance of yield in crop production, achieving a balance between yield-related traits and target traits poses a major challenge in crop breeding. The GYT biplot is a well-established method for selecting multiple breeding traits based on selection indexes (Yan and Frégeau-Reid 2018; Yan *et al.* 2021), and it has been successfully applied in multi-trait breeding practices for wheat (Mohammadi *et al.* 2019; Tsenov *et al.* 2021). In this study, by combining the phenotypic data of quality-related traits, average yield data, and HMW-GS scores based on molecular marker detection, a multi-dimensional comprehensive evaluation method was developed for screening germplasm resources for elite target traits, which can precisely consider the relationships between the "target trait-main genetic locus-yield". Given the diverse breeding goals across ecological regions, each with unique trait preferences, this study outlines a streamlined method for evaluating wheat cultivars based on region-specific target traits. By applying dimensionality reduction to key trait components and integrating allele genotyping at important loci, this approach enables a comprehensive, multi-dimensional assessment of cultivar performance. This provides a practical framework for selecting wheat cultivars with desirable traits tailored to specific ecological conditions, which enhances the applicability and effectiveness of this method. Using this method, a significant positive correlation was observed between the *D* value and GYT index in clusters II to IV, which identified 20 high-quality and high yielding cultivars from Cluster IV (Fig. 7; Table 3). This assessment was based on analyzing the impact of favorable *Glu-1* allele combinations on wheat quality, and the fact that the HMW-GS score should not be lower than 8 when using this method to select high-quality and high-yield wheat cultivars. This study demonstrated that the HMW-GS score and GYT index could be readily utilized for breeding high-quality wheat in the Huang-Huai wheat region.

5. Conclusion

ST, SA and MAXR were identified as the key factors influencing wheat quality in the Huang-Huai wheat region. HMW-GS and *Sec-1* primarily impacted these three traits to subsequently influence wheat quality, with more significant impacts on the comprehensive evaluation value *D*, PC1–PC3, and the main component traits (ST, SA and MAXR) of PC1. A multi-dimensional comprehensive evaluation method combining the *D* value, HMW-GS score and GYT index provided an effective approach for identifying high-quality and high-yield wheat cultivars. Wheat cultivars without *Sec-1* have a higher GYT index. Therefore, when selecting high-quality and high-yield wheat cultivars based on the GYT index, the HMW-GS score should be no less than 8 points. Following this criterion, 20 elite wheat cultivars were identified as suitable parents for wheat quality breeding.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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