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GENETIC ANALYSIS OF THE GRAIN PROTEIN CONTENT IN SOFT RED WINTER WHEAT (*Triticum aestivum* L.)

Jinbao YAO, Hongxiang MA, Xueming YANG, Miaoping ZHOU, Dan YANG*

Provincial Key Laboratory of Agrobiology, Jiangsu Academy of Agricultural Sciences, Nanjing, CHINA
**Corresponding author: yaojb@jaas.ac.cn*

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ABSTRACT

Improvement of grain protein content is the main objective in soft red wheat breeding programs. The main objective of this study was to investigate the mode of inheritance and combining ability of grain protein content in wheat. Seven genetically diverse soft red wheat cultivars were crossed in an incomplete 7×7 diallel fashion. F1 and F2 progenies along with their parents were evaluated in two separate experiments to do F1 and F2 diallel analysis. The results indicated significant differences among the parents for general combining ability and crosses for specific combining ability. Among the parents Ningmai 9 was the best combiner and could be utilized for developing soft wheat cultivars with low protein content. The specific crosses for grain protein content were Ningmai 8×Ningmai 9 and Ningmai 8×Yangmai 5. The additive-dominance model was adequate for grain protein content in F1, while showed partially adequate in F2. Greater value of additive (D) over dominance (H1 and H2) demonstrated additive nature of genes for grain protein content in both generations. Grain protein content exhibited high value of narrow sense heritability. The genetic analysis suggested that grain protein content could be improved through pedigree and progeny selection.

Key words: Combining ability, Diallel cross, Grain protein content, Triticum aestivum L.

INTRODUCTION

Soft wheat flours are most suitable for making cakes and biscuits. Good quality soft wheat flour produces large spread cookies with large diameter, low thickness, and tender texture (Moiraghi et al., 2011). Cookie quality is associated with soft wheat flour of low protein content (Leno et al., 1996). Significant negative correlation between grain protein content and cookie diameter has been reported (Ram and Singh, 2004; Guttieri et al., 2004). Moreover, the significant negative correlation of wet gluten content, solvent retention capacities (SRCs), water soluble pentosan, with cookie diameter has also been observed (Guttieri and Souza, 2003; Zhang et al., 2007; Geng et al., 2012). To develop the wheat cultivars with low protein content is one of the main breeding objectives in the Yangtze River basin, where it is the largest area of soft wheat production in China.

Genetic differences and environmental effects on grain protein content have been reported previously (Miezan et al., 1977; Kramer, 1979; Baenziger et al., 1985). In most of the diallel studies of wheat, grain protein content seemed to be controlled by the partial dominance with additive gene effects (Huo et al., 1996; Akram et al., 2007). However, over dominance type of gene action was also noted for grain protein content (Hsu and Sosulski, 1969; Halloran, 1975). Rahman et al. (2003) reported that grain protein content could result from additive and dominant genes with the possibility of epistatic genetic effects. Heritability estimate is a valuable parameter for determining the magnitude of genetic gain from selection. Low, medium, and high narrow sense heritability estimates were reported for grain protein content (Mckendry et al., 1988; Wang et al., 1991; Ekiz et al., 1998; Rong et al., 2001; Bnejdi et al., 2010).

The development of the unique, low grain protein content, high grain yield genotype in the Yangtze River basin soft wheat breeding program afforded the authors with an excellent opportunity to study the inheritance of grain protein content using diallel crosses. Accordingly, the objectives of this study were: (i) to estimate GCA, SCA and other genetic parameters by using F1 and F2 progenies in two sets of diallel crosses, (ii) identify the best general and specific combiners among different cultivars and crosses, (iii) perform graphical analysis of gene actions for grain protein content. The result of this study can be used in the selection of desirable parents for an effective breeding program to develop the new soft wheat varieties with low grain protein content.

MATERIALS AND METHODS

Plant material and experimental design

The research work comprised of parents, F1 and F2 population experiments of wheat was conducted during the crop seasons of 2010-2012 at the Jiangsu Academy of

Agricultural Sciences, Nanjing, China. Seven diverse soft red wheat cultivars viz. Ningmai 8, Ningmai 9, Yangmai 5, Yangmai 9, Yangmai 11, Sumai 3 and Wangshuibai varied by pedigree, morphological characters, yield potential and quality traits were sown in Oct. 2010. Plots consisting of 3 rows, each 2 m in length, with a plant and row spacing of 5 cm and 30 cm, respectively were used to facilitate hand emasculation and crossing. All the cultivars were crossed following incomplete 7×7 diallel fashion. The F1 and F2 population having 21 hybrids along with 7 parents were sown in a Randomized Complete Block Design with three replications during Oct. 2011 and 2012, respectively. In F1's, each genotype occupied a plot of two 2-m rows spaced 30 cm apart, while in F2's, each genotype consisted of seven rows spaced 30 cm apart. Enough seeds were planted, and then plants thinned to have 20 plants per meter of row for harvesting. For proper growth and development of the plants, agronomic practices and plant protection measures recommended for wheat crop were adopted during the growing season. The experimental field was fertilized with 210 kg ha-1 of N, 105 kg ha-1 of P2O5, and 105 kg ha-1 of K2O. Both the phosphorus and potassium were totally applied as base fertilizer during land reparation. N was applied at preplant, the five-leaf stage, and booting stage at the ratio of 6:2:2. Harvesting was performed after the grain was mature and the plants were dried, at which time grain moisture was determined.

Trait measurement and statistical analysis

The data were recorded for grain protein content, tested by near infrared reflectance (NIR) after one month of harvesting. The data were subjected to analysis of variance using the SAS software (SAS Institute Inc. version 9.1). The general and specific combining ability values were estimated using Method II, Model I of Griffing's (1956). Two scaling tests (Mather and Jinks, 1982) were applied to test the validity of the additive-dominance model. Further, the Hayman (1954) method was used for estimation of gene actions.

RESULTS

Combining ability analysis

Analysis of variance revealed highly significant differences among the genotypes in both F1 and F2 diallel experiments for grain protein content (Table 1). These results permitted further analysis of combining abilities. The mean squares of general combining ability (GCA) and specific combining ability (SCA) in F1 and F2 diallel experiments were highly significant (Table 1), indicating the importance of both additive and non-additive gene effects. However, the magnitudes of GCA variances were several times than SCA (9.10 in F1 and 11.75 in F2). This indicates the preponderance of additive gene effects in the genetic control of grain protein content.

Table 1. Analysis of variance for combining ability of grain protein content in the F_1 and F_2 generations of wheat

Source of variation	df	F_1			F_2		
		SS	MS	F	SS	MS	F
Replications	2	0.052	0.026	0.28	0.222	0.111	1.00
Genotypes	27	27.185	1.007	10.61**	24.970	0.925	8.33**
Error	54	5.125	0.095		6.009	0.111	
GCA	6	6.552	1.092	34.52**	6.416	1.069	28.89**
SCA	21	2.509	0.120	3.78**	1.908	0.091	2.46**
Error	54	1.708	0.032		2.003	0.037	

**, Significant at 1% probability level.

Table 2. Mean values and general combining ability (GCA) effect for grain protein content in F_1 and F_2 generations

Parents	F_1		F_2	
	Protein content (%)	GCA	Protein content (%)	GCA
Wangshuibai	13.55 aA	0.508 aA	13.66 aA	0.430 aA
Sumai 3	13.08 bAB	0.314 bAB	13.40 aAB	0.241 bAB
Yangmai 11	12.71 bcBC	0.110 cBC	12.77 bcBC	0.022 cBC
Ningmai 8	12.34 cdC	− 0.147 deDE	12.75 bcBC	− 0.094 cdC
Yangmai 5	12.22 dC	− 0.250 eE	12.44 cC	− 0.200 dC
Yangmai 9	12.20 dC	− 0.011 cdCD	13.31 abAB	0.214 bAB
Ningmai 9	11.46 eD	− 0.524 fF	11.63 dD	− 0.613 eD
Correlation coefficient [a]	0.975**		0.977**	

The values followed by different capital or small letters within the same column are significantly different at 1% and 5% probability levels, respectively.

*, **, Significant at 5% and 1% probability level, respectively

a, correlation coefficient (*r*) between the mean value for grain protein content and the value for GCA of seven genotypes

Performance of parents and combining ability

Mean value and GCA effects of the seven parents for grain protein content in both F1 and F2 generations were given in Table 2. Significant differences were found among parents. Grain protein content ranged from 11.46% and 11.63% for Ningmai 9 to 13.55% and 13.66% for Wangshuibai, with an overall mean of 12.51% and 12.85% in F1 and F2 generations, respectively (Table 2).

Estimates for GCA effects varied between 0.524 (Ningmai 9) and 0.508 (Wangshuibai) in F1, and between 0.613 (Ningmai 9) and 0.430 (Wangshuibai) in F2 diallel analysis for grain protein content. The greatest negative GCA effects, i.e. contribution to lower grain protein, were exhibited by Ningmai 9 in both F1 and F2. This result indicated that Ningmai 9 was the best combiner for decreasing grain protein content in its progeny. Yangmai 5 and Ningmai 8 showed negative GCA in both F1 and F2, and they may also be recommended as superior parents for breeding programs aimed at reducing the grain protein content. Yangmai 9 showed negative GCA effects in F1 but positive GCA effects in F2, suggesting that Yangmai 9 was not stable in performance over generation. The parents that consistently showed high and positive GCA effects in both F1 and F2 were Wangshuibai, Sumai 3 and Yangmai 11.

The correlations between GCA and parental performance were positive and significant with values of 0.975** and 0.977** in F1 and F2, respectively. The result suggested that GCA could be predicted from parental performance in different generations.

Unlike GCA-effects, the SCA-effects (Table 3) are the result of non-additive gene action. Number of crosses showing negative SCA-effects was a little high in F2 than F1. Crosses, such as Ningmai 8 × Ningmai 9, Ningmai 8 × Yangmai 5, Ningmai 9 × Wangshuibai, and Yangmai 9 × Yangmai 11 exhibited strong negative SCA effects for grain protein content in both F1 and F2 generations. These crosses were lower grain protein content (data not shown) and could be utilized as low grain protein content hybrids.

Table 3. Effects of specific combining ability for grain protein content in 21 crosses

Cross	**F_1**	**F_2**
Ningmai 8×Ningmai 9	- 0.366	- 0.265
Ningmai 8×Yangmai 5	- 0.356	- 0.508
Ningmai 8×Yangmai 9	0.018	0.035
Ningmai 8×Yangmai 11	- 0.213	0.113
Ningmai 8×Sumai 3	0.329	- 0.072
Ningmai 8×Wangshuibai	- 0.408	- 0.114
Ningmai 9×Yangmai 5	0.157	- 0.169
Ningmai 9×Yangmai 9	0.089	0.251
Ningmai 9×Yangmai 11	0.161	- 0.237
Ningmai 9×Sumai 3	- 0.573	- 0.056
Ningmai 9×Wangshuibai	- 0.224	- 0.165
Yangmai 5×Yangmai 9	- 0.278	- 0.075
Yangmai 5×Yangmai 11	- 0.220	0.003
Yangmai 5×Sumai 3	- 0.204	- 0.152
Yangmai 5×Wangshuibai	- 0.282	0.292
Yangmai 9×Yangmai 11	- 0.172	- 0.277
Yangmai 9×Sumai 3	0.037	- 0.089
Yangmai 9×Wangshuibai	0.127	- 0.548
Yangmai 11×Sumai 3	- 0.238	- 0.194
Yangmai 11×Wangshuibai	- 0.032	0.210
Sumai 3×Wangshuibai	0.011	- 0.212
$SE(S_{ij}\text{-}S_{ik})$	0.474	0.514
$SE(S_{ij}\text{-}S_{kl})$	0.444	0.480

Adequacy tests for additive-dominance model

The adequacy of data to additive dominance (AD) model was tested by two scaling tests i.e. joint regression analysis and analysis of variance for Wr+ Vr and Wr− Vr (Table 4). The regression analysis revealed that regression coefficient (b) departed significantly from zero but not from unity in both generations, suggesting the absence of non-allelic interactions in genetic behavior of grain protein content which attested grain protein content valid for AD model in both generations. The suitability of the model data analysis was also tested with the analysis of variance of (Wr+ Vr) and (Wr− Vr) (Table 4). The lack of significant variation in the (Wr− Vr) arrays for grain protein content in both generations suggested that any kind of epistasis was not involved in the phenotypic expression of the trait. Although the value of regression coefficient (b) proved the fitness of the data of grain protein content (0.901) in F2 generation for AD model, mean square values of (Wr+ Vr) for grain protein content in F2 generation indicated no significant deviation, thus emphasizing partial adequacy of AD model for grain protein content in F2. However, grain protein content exhibited full adequacy for AD model in F1.

Table 4. Adequacy test of additive-dominance model for grain protein content

Parameters	Grain Protein Content (%)	
	F_1	F_2
Joint regression (b)	0.901±0.134	0.784±0.170
Test for b=0	6.724**	4.612**
Test for b=1	0.739 NS	1.271 NS
Mean squares of Wr+ Vr between arrays	0.399 **	0.056 NS
Mean squares of Wr− Vr between arrays	0.012 NS	0.003 NS
Fitness of the data to Additive-Dominance model	Full	Partial

**, Significant at 1% probability level, NS, Non-significant.

Components of genetic variation

Additive (D) and non-additive (H1 and H2) components were all highly significant in F1 and F2, indicating that both additive and dominance effects were important components of genetic variation for grain protein content (Table 5). However, additive (D) effects were greater than dominance (H1 and H2) in both generations, suggesting that additive gene action played a predominant role in controlling the genetic mechanism of the trait. This advocated that selection can be helpful for the improvement of the trait. The magnitudes of H2/4H were closer to 0.25 in both generations, indicating a symmetrical distribution of positive and negative alleles among the parents demonstrated by non-significant F value determining the relative frequency of dominant and recessive alleles. Degree of dominance (H1/D)0.5 was less than unity in both generations, thus confirming the presence of partial dominance with additive effects. The mean dominance effect of the heterozygote locus (h2) was significant, suggesting that high heterotic effect values would be expected for grain protein content among crosses. Significant environmental component (E) indicated that the grain protein content was highly affected by environmental factors. Narrow sense heritability (h2N) was estimated to be 70.76% and 71.70% in F1 and F2, respectively.

Table 5. Components of genetic variation for grain protein content in wheat

Components of variation	Grain Protein Content (%)	
	F_1	F_2
D	0.429**±0.027	0.439**±0.021
F	− 0.044±0.064	− 0.010±0.051
H_1	0.308**±0.065	0.185**±0.052
H_2	0.286**±0.057	0.197**±0.045
h^2	0.729**±0.038	0.479**±0.031
E	0.031**±0.009	0.037**±0.008
$(H_1/D)^{1/2}$	0.847	0.649
$H_2/4H_1$	0.232	0.266
h^2_N (%)	70.76	71.70
r[(Wr+Vr), Yr]	0.869*	0.101

*, **, Significant at 5% and 1% probability level, respectively

Graphical Analysis

The Vr/Wr graph (Fig.1 and Fig.2) showed that the regression line cut the Wr-axis above the point of origin in both generations which indicated the presence of partial dominance in the inheritance of grain protein content. The distribution of array points along the regression line (Fig.1) showed that Ningmai 9 and Yangmai 5 contained maximum dominant genes as they were located nearer to the point of origin. Wangshuibai and Sumai 3 were furthest away from the origin and thus they possessed maximum recessive genes. The Vr/Wr graph (Fig. 2) exhibited that Yangmai 9 was located near the origin, indicating that it carried maximum dominant genes. In contrast, Ningmai 8 and Yangmai 5 were located further away from the origin, indicating a relative abundance of recessive genes in these two parents.

Positive r-value between parental values (Pr) with (Wr + Vr) in F1 and F2 (Table 5) indicated a tendency for low grain protein content to be associated with dominance and high grain protein content with recessive genes.

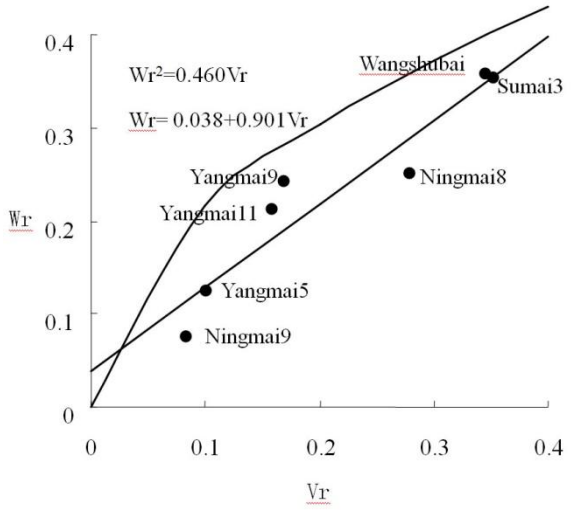

Fig 1. Vr versus Wr graph for grain protein content in F_1

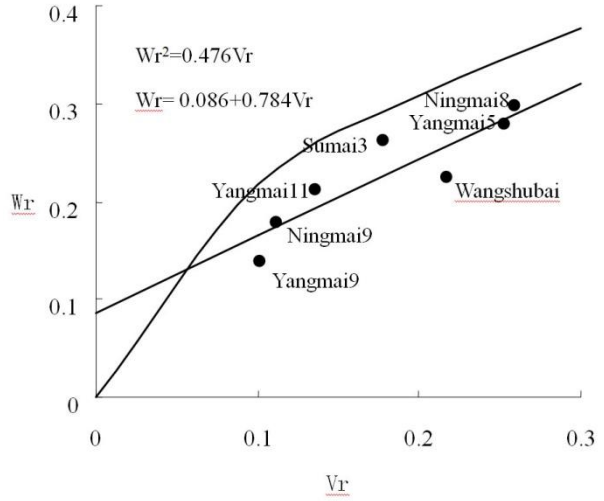

Fig 2. Vr versus Wr graph for grain protein content in F_2

DISCUSSION

In the present investigation grain protein content was found to be controlled by additive and non-additive gene effects, however, additive effects were more important in the genetic control of grain protein content. The present findings thus supported the results of Wang and Lu (1991), Rong et al. (2001), Joshi et al. (2004), Lysa (2009) and Akram et al. (2011), which also showed that additive genetic variance as the main component of genetic variance of grain protein content in wheat. However, preponderance of non-additive gene effect was reported by Kraljevic-Balalic et al. (1982). In this study, due to presence of additive effects, the estimates of narrow sense heritability were higher for grain protein content. Such higher heritable value for grain protein content was also reported by other researchers (Ekiz et al., 1998; Bnejdi et al., 2010). Saranga et al. (1992) stated that higher magnitude of heritability in F2 may have been due to greater recombination of genes or low environmental component. However, Falconer (1989) stated that the estimates of heritability were subjected to environmental variation, and therefore these must be reported and used with great care while making selection from segregating material. Nonetheless, the study offers a lot of scope for improvement of grain protein content in soft wheat breeding program through individual plant selection in early generations.

Based on GCA of parental lines (Table 2), it can be found that Ningmai 9 was the best combiner parents for improvement of grain protein content in soft wheat breeding program, as with the highest negative and significant GCA effects for grain protein content in both F1 and F2 diallels. In addition, the lower mean grain protein content in both F1 and F2 diallels was obtained for Ningmai 8×Ningmai 9 and Ningmai 9×Yangmai 5, respectively (data not shown). Accordingly, to improve grain protein content in soft red wheat, parents like Ningmai 9 can be used in breeding programs as the sources of desirable genes. In fact, the parent Ningmai 9 has been proven to be a highly useful genetic source of low protein content for soft wheat breeding in the Mid-lower reaches of the Yangtze River, China. The five soft red wheat cultivars, namely, Ningmai 13, Ningmai 18, Shengxuan 6, Yangmai 18 and Yangmai 21 with low protein content, high yield potential and nine wheat lines with larger cookie diameter than Ningmai 9 have been developed, using Ningmai 9 as a direct crossing parent since 2006 (Yao et al., 2010; Yao et al., 2012). Therefore, the use of the cultivar Ningmai 9 as a parent in the crosses is recommended by which one selects segregates for lower grain protein content.

In general, there was considerable consistency for the results obtained from analysis of F1 and F2 progenies in terms of GCA, SCA, H2N (Joshi et al., 2004; Golkar et al., 2011). It is expected that the results of analysis for F1 and F2 progenies in a diallel set of crosses should not be different in terms of theoretical aspects (Mather and Jinks, 1982). The results of this study and the others in safflower (Pahlavani et al., 2007; Golkar et al. 2011) and in cotton (Khan et al., 2009) indicated that there are some consistencies between results of F1 and F2 diallel analyses. Therefore, it seems that F2 diallels may provide similar results as F1 diallels in other crops. Verhalen and Murray (1969) used F2 data in cotton. Cho and Scott (2000) used F2 data in soybean. Amiri-Oghana et al. (2009) used F2 data in oilseed rape. These studied all reported that F2 analysis provided reliable and better information than F1 generation. One of the most important advantages of the F2 diallel is to have sufficient seeds to overcome the difficulties regarding artificial crossing and F1 seed production in many hermaphroditic plants such as wheat. Also, sufficient F2 seeds provide the opportunity to have more replication or environments in the experiments.

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