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ARTICLE

Segregation ratios of colored grains in F_1 hybrid wheat

Zifeng Guo[1], Ping Xu[1], Zhengbin Zhang[1*] and Yunna Guo[1]

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Abstract - *Nutritious and functional foods from wheat have received great attention in recent years. Colored-grain wheat contains a large number of nutrients such as anthocyanins and hence the breeding is interesting. In this work, colored-grained wheat lines of mixed pollination of einkorn wheat (*Triticum boeoticum*, AA) and French rye (French* Secale cereale*, RR) were used as male parents and wheat line Y1642 (derived from common wheat and* Agropyron elongatum*, AABBDD) was used as the female parent. These colored wheat were used for diallel cross to study the segregation ratios of F_1 colored grains. Results show that the color inheritance of purple-grained wheat follows a maternal inheritance pattern and that the blue-grained wheat expresses xenia in most cases. In some circumstances, the grains with different color shades appear in the same spike.*

Key words: *Blue-grained wheat, Purple-grained wheat, Inheritance, Segregation ratios.*

INTRODUCTION

Nutritious and functional foods from wheat have received great attention in recent years. Since lots of human diseases are related to micronutrition (Kapur et al. 2002, Uauy et al. 2006), improving the micronutrients in foods has become an important field of the Second Green Revolution. Bio-enhanced breeding such as genetic breeding method was used to improve the nutrients of wheat and other food crops (Li et al. 2006, Reuters 2006, Fan 2007). Researches show that colored-grain wheat contains a large number of valuable nutrients (Li et al. 2003, Li et al. 2006, Mazza 2007). Particularly, it is rich in anthocyanins (Abdel-Aal et al. 2006, Knievel et al. 2009), that have many functions such as antioxidant, antibacterial, anticancer, and reduction of the incidence of cardiovascular disease (Mazza 2007). Therefore, colored-grain wheat breeding has become an important aspect of bio-enhanced breeding.

Colored-grain wheat varieties with good genetic stability, excellent stress resistance and high yield are required. To this end, it is needed to fully understand the inheritance of colored-grain wheat and hence genetic researches on colored-grain wheat has attracted great attention. Some researches about colored-grain wheat inheritance have been reported but the results are inconsistent because the used experimental material is different. For example, Caporn (1918) reported that the purple-grained wheat deriving from tetraploid wheat was controlled by two dominant genes. Sharman (1958) crossed Ethiopian tetraploid wheat with white wheat and purple wheat and found that the color of purple-grained wheat fitted a dominant gene model. Piech and Evans (1979) studied purple-grained hexaploid wheat and found that two complementary genes located in the 3A and 7B chromosomes were related to the color of purple-grained wheat. Gilchrist and Sorrells (1982) studied 'Charcoal' wheat and found that the color of purple pericarp was controlled by two incompletely dominant genes. Suneson (1964), Piech and Evans (1979), Li (1982), Kuspira (1989) and Keppenne (1990) found that the color of blue-grained wheat was controlled by one gene. The difference is that Suneson (1964) and Piech and Evans (1979) called the blue-grained gene *Bl*, whereas Keppenne and Baenziger (1990) defined the blue-grained gene as *Ba*. *Bl* and *Ba* both derive from *Agropyron*, and hence the two genes may be the same. Kuspira et al. (1989) called the blue-grained gene *Bk*. Lan et al. (2008) found that two blue-grained lines D87065 and D87089 were derived from *Thinopyrum* and one line 92-1 derived from rye, which were all controlled by two dominant complementary genes. The blue-grained line 7083L-16 fitted one gene model.

Generally, there is no grain color segregation in F1 hybrid from white or red-grained wheat cross. However, because the purple-grained wheat follows a maternal inheritance pattern, the blue-grained wheat expresses xenia, and hence there are many kinds of colored grain segregations in F1 hybrid generation derived from cross between different colored grain wheat. In

[1] Center for Agricultural Resources Research, Institute of Genetics and Developmental Biology, CAS, Shijiazhuang 050021, China. *E-mail: zzb@sjziam.ac.cn

addition, because of the instability of some hybrid parents' genetic background, especially in some out-cross wheat lines, F_1 hybrid may also appear segregation. However, this segregation has been scarcely reported. In this work, inheritance of colored-grain wheat was investigated through grain color segregation ratios of wheat with different color grains in the F_1 generation of hybrid wheat. This contribution may provide useful information for color grain wheat breeding.

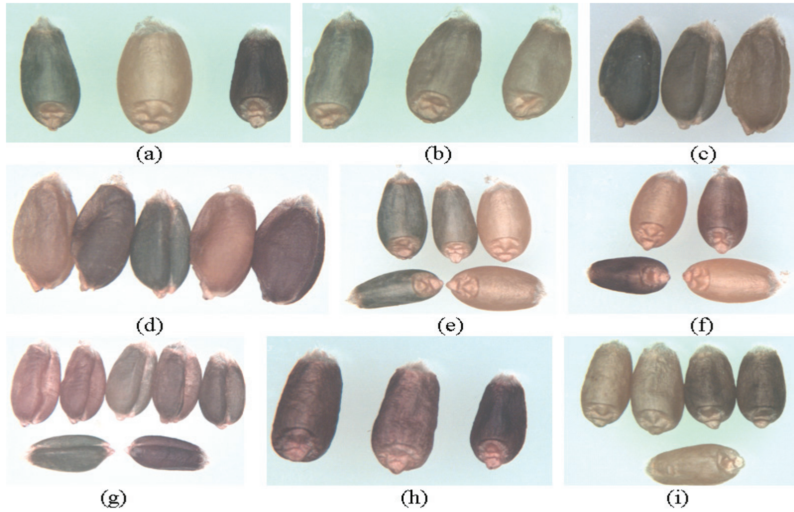

Figure 1. a) Blue, white and purple grains (from left to right); b) deep, medium and light blue grains (from left to right); c) deep, medium and light purple grains (from left to right); d) different colored grains in the same spike; e) blue and white parents (down) and F_1 generation grains (up); f) purple and white parents (down) and F_1 generation grains (up); g) blue and purple parents (down) and F_1 generation grains (up); h) two purple parents (left) and F_1 generation grains (right); i) W1 white parent (down) and grain color segregation of the self-cross (up).

MATERIAL AND METHODS

The colored-grain wheat lines used in this work were bred and selected by Dr. Zhengbin Zhang at the Center for Agricultural Resources Research, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences. The lines were F_7 generations derived from the outcross by mixed pollination of einkorn wheat (*Triticum boeoticum*, AA) and French rye (*French Secale cereale*, RR) as male parents with the high-quality bread wheat line Y1642 (derived from common wheat and *Agropyron elongatum*, AABBDD) as the female parent. These lines have independent genetic background compared with other colored-grain wheat lines used in previous studies.

Diallel cross was performed using five kinds of wheat, including two kinds of purple-grain wheat, two kinds of white-grained wheat, and one kind of blue-grained wheat (Table 1). When the F_1 hybrid was planted, the five parents were also planted at the same time. After harvested, analysis and statistics were made as soon as possible. To analyze the grain color segregation ratios of various genetic phenomena according to the theoretical segregation ratios, the chi-square test was analyzed by SPSS16.0 software.

Table 1. Cross between different color grain wheat lines

Number	Cross combination
1	B1 ×P1
2	B1 ×P2
3	B1 ×W1
4	B1 ×W2
5	W2 ×W1
6	W2 ×P2
7	W2 ×B1
8	W2 ×P1
9	P2 ×B1
10	P2 ×P1
11	P2 ×W2
12	P2 ×W1

B: blue; W: white; P: purple

RESULTS

Grain color of hybrid parents and the segregation of F_1 hybrid

We found a wide variety of grain color segregation among different colored-grain wheat hybrids, as shown in Figure 1. Figure 1a shows blue grain, white grain and purple grain from left to right. These three typical grains are selected as standard for other grains. Figure 1b and c show the blue and purple grains with different shades, which can be divided into deep, medium and light. These transitional colors may be related to genes dose effect of grain color, modifier gene and other factors such as environmental conditions and the stages of seed development. Figure 1d shows different colored grains in the same spike. Similar phenomenon has scarcely been reported in previous studies. In this work, white and blue grains, and white and purple grains are found in the same spikes. Figure 1e, f and g show the hybrid parents and grain color segregation of the F_1 generation. It can be noticed that the grains' shades of F_1 are between the two parents' grain colors, neither lighter nor darker. Figure 1h indicates that the grain color of F_1 generation is deeper than that of the two purple parents. Therefore, there are transgressive inheritances or heterosis in grain colors among different color grain wheat lines. A white-grained wheat line (W1) and the grain color segregation of its self-cross are shown in Figure 1i. This white-grained wheat line has been developed to F_7 generation, but there are 7 spikes of white-grained wheat and 8 spikes of purple-grained wheat derived from its self-cross progenies. Therefore, it was concluded that the purple-grain may be controlled by a recessive gene in this white-grained wheat line.

Analysis of color-grain spike numbers in F_1 hybrid

As shown in Table 2, in the F_1 generation, when using blue-grained wheat (B1) as female parent and purple-grained wheat (P2, P1) as male parent, it is obtained 229 spikes with blue and purple grains, and 22 spikes with blue and yellow grains. The large proportion of wheat with blue and purple grains suggests that the blue-grained wheat expresses a strong xenia effect. The occurrence of wheat with blue and yellow grains may be related to the grain color genes interactions between blue-grained and purple-grained wheat parents.

When purple-grained wheat (P2, P1) as female parent was crossed with blue-grained wheat (B1), it was obtained 71 spikes with blue and purple grains and 27 spikes with purple grains in the F_1 generation. It shows that some spikes with blue and purple grains express xenia, whereas some purple grain spikes follow a maternal inheritance pattern.

For the F_1 generation of cross using white-grained wheat (W2) as female parent and blue-grained wheat (B1) as male parent, it was obtained 28 spikes with blue and yellow grains and 31 spikes with yellow grains. These results indicate that some spikes express xenia, and the color gene interaction between blue-grained and white-grained wheat may be responsible for the appearance of yellow grains.

When blue-grained wheat (B1) was used as female parent and white-grained wheat (W1) as male parent, it was obtained, in the F_1 generation, 89 spikes with blue and purple grains, and 18 spikes with blue and yellow grains. However, all the 7 samples are the spikes with blue and yellow grains for blue-grained wheat (B1)/white-grained wheat (W2) system. These results suggest that the color gene interaction between blue-grained and white-grained wheat may be responsible for the appearance of yellow grains.

When purple-grained wheat (P2, P1) was used as female parent to cross with white-grained wheat (W2) and white-grained wheat (W1), respectively, grains of the F_1 generation were all purple. It suggests that the color inheritance of purple-grained wheat follows a maternal inheritance pattern.

Using white-grained wheat (W2) as female parent to cross with white-grained wheat (W1), it was obtained 51 spikes with purple grains and 68 spikes with yellow grains in the F_1 generation. The possible explanation is that the white wheat line is an unstable line, which separates into two lines like as purple-grained line and white-grained line. Yellow grains are caused by the color gene interaction between white grains and purple grains.

Based on the above-mentioned results, it was found that the color inheritance of purple-grained wheat follows a maternal inheritance pattern and blue-grained wheat expresses a strong xenia in most cases. The appearances of other colored grains such as yellow grains are related to color genes interaction. The genetic mechanism requires further investigation.

Analysis of grain color segregation ratios in the F_1 hybrid

Grain color segregation ratios of spikes with blue and purple grains

As shown in Table 3, 195 spikes exhibit a segregation ratio of 11:5 (purple: blue), which accounts for 50.13% of all samples. This result suggests that purple grains are controlled by two dominant genes compared with blue grains. Ninety two spikes (23.65%) exhibit a segregation ratio of 13:3, which means that purple grains express inhibiting effect compared with blue grains. Sixty five spikes (16.71%) exhibit a segregation ratio of 9:7, which also indicates that

Table 2. Number of color grain spikes in the F_1 hybrid

Female parent	Male parent	Spikes with colored grains			
		blue/yellow	blue/purple	purple	yellow
Blue (B1)	Purple (P2, P1)	22	229		
Purple (P2, P1)	Blue (B1)		71	27	
White (W2)	Blue (B1)	28			31
Blue (B1)	White (W2)	7			
Blue (B1)	White (W1)	18	89		
White (W2)	Blue (B1)	28			31
White (W2)	Purple (P2, P1)			205	16
Purple (P2, P1)	White (W2)			139	
Purple (P2, P1)	White (W1)			240	
White (W2)	White (W1)			51	68
Purple (P2, P1)	Purple (P2, P1)			148	

Table 3. Segregation ratios of spikes with blue and purple grains in the F_1 hybrid

Segregation ratio (purple: blue)	Numbers of spikes	Percentage	χ^{2*}
11:5	195	50.13	0.000-1.404
13:3	92	23.65	0.000-0.960
9:7	65	16.71	0.000-1.099
15:1	26	6.68	0.000-2.068
1:3	4	1.03	0.000-0.177
7:9	3	0.78	0.025-0.310
63:1	1	0.20	0.000
33 (36, 51): 0	3	0.78	0.000

*$\chi^2_{0.05,1}$ =3.84; $\chi^2_{0.01,1}$=6.63

Table 4. Segregation ratios of spikes with blue and white grains in the F_1 generation

Segregation ratio (blue: white)	Numbers of spikes	Percentage	χ^{2*}
9:7	45	60.81	0.106-0.989
11:5	15	20.27	0.006-0.784
13:3	2	2.70	0.132-1.231
1:3	6	8.10	0.053-0.207
7:9	5	6.75	0.087-2.249
0:40	1	1.35	0.000

*$\chi^2_{0.05,1}$ =3.84; $\chi^2_{0.01,1}$=6.63

purple grains are controlled by two dominant complementary genes compared with blue grains. Twenty six spikes (6.68%) exhibit a segregation ratio of 15:1, which shows that purple grains express duplicate effect on blue grains.

The segregation ratios of 11:5, 13:3, 9:7 and 15:1, together, correspond for 97.17% of the all samples, which indicates purple grains are controlled by two dominant genes that interact with each other. The segregation ratios of 7:9 and 1:3 show that purple grains are controlled by two and one recessive genes, respectively.

There are some special segregation ratios such as 33 (36, 51): 0. These ratios indicate that the purple-grained spikes completely follow a maternal inheritance pattern. The segregation ratios of 63:1 may be caused by xenia or the recessive gene segregation of blue-grained wheat.

Grain color segregation ratios of spikes with blue and white grains

Table 4 summarizes the segregation ratios of spikes with blue and white grains and the chi-square test results. Forty five spikes (60.81%) exhibit a segregation ratio of 9:7 (blue: white). It can be concluded that blue grains are controlled by two dominant complementary genes, comparing with white-grain. Fifteen spikes (20.27%) exhibit a segregation ratio of 11:5, which shows blue grains are controlled by two dominant genes when compared with white grains. Two spikes (60.81%) show a segregation ratio of 13:3, which indicates that blue grains express inhibiting effect. The segregation ratios of 9:7, 11:5 and 13:3, together, account for 83.78% of all samples, indicating that blue grains are controlled by two dominant genes which interact with each other. The segregation ratios of 7:9 and 1:3 mean blue grains are controlled by two and one recessive genes, respectively. The segregation ratio of 0:40 indicates that xenia and the recessive gene segregation of blue-grain do not work in this spike.

DISCUSSION

The results show that the color inheritance of purple-grained wheat follows a maternal inheritance pattern and that the blue-grained wheat expresses xenia. It was found that the grain color of purple-grain is controlled by two dominant genes, compared with blue-grain, whereas blue-grain is controlled by two dominant genes, compared with white-grain.

Various studies confirmed that purple-grain is controlled by dominant gene. For example, Sharman (1958) reported that the grain color of purple-grain from Ethiopia was controlled by one dominant gene. McIntosh and Baker (1967) detected two duplicate dominant genes with a possible complementary effect. Gilchrist and Sorrells (1982) found that the purple pericarp of 'Charcoal' wheat was controlled by two incompletely dominant genes. Recently, Knievel et al. (2009) reported that the purple pericarp of *Triticum aestivum L.* fits two dominant genes model.

Piech and Evans (1979), Li et al. (1982), Kuspira et al. (1989) and Keppenne and Baenziger (1990) proposed that blue-grain was controlled by one gene. Morrison et al. (2004) reported that the blue-grain gene Ba(a) didn't express xenia. In the present case, however, a small portion of the experimental samples showed that the purple or the blue grain is controlled by two or one recessive gene. These results have scarcely been reported in previous experiments. In this study, wheat with purple and white grains in the same spike wasn't found. However, Pal'mova and Nikolaenko (1931) reported that this kind of wheat was found in purple-grain tetraploid wheat. This may be caused by the difference in tetraploid wheat and hexaploid wheat.

It is generally accepted that there are four main factors that cause the fluctuation of segregation ratios and grain colors. The first is the gene dose effect; the second is the gene interaction; the third is the genetic background; and the fourth is the grain development and environmental conditions. Figure 1b and c show some transitional colors and these phenomena may be caused by dose effect of grain color gene. Knott (1958) also reported that the genes for blue aleurone express a distinct dose effect. Li et al. (1983), Li et al. (1986) and Lan et al. (2008) proved the gene dose effect in blue-grain wheat. Gilchrist and Sorrells (1982) and Knievel et al. (2009) reported that there are gene dose effects in purple-grain wheat.

As shown in Figure 1d-h, some grain colors of the F_1 generation are different from the parents'. It was concluded that the gene interaction may be responsible for the changes. The gene interaction has been reported in previous studies. For example, Kattermann (1932) reported that the grain color of blue-grain wheat was influenced by *F/f* and *H/h*. The *F* gene comes from rye, which controls the grain color, and the *H* gene can hinder the expression of the *F* gene. *FFHH* and *ffHH* express white grain, whereas *Ffhh* expresses blue grain. Piech and Evans (1979) proposed that the purple-grain gene *R* can influence the expression of blue-grain gene *Bk*. Gilchrist and Sorrells (1982) found that the purple-grain gene was affected by non-purple-grain wheat. It is expected that the gene interaction also plays an important role in this study.

The fluctuations of segregation ratios and grain color shades and the segregation of the white-grain wheat line (W1) show that purple and blue grain wheat lines are both of genetic instability because of random xenia phenomenon. This is consistent with the results previously reported. Neuman et al. (1989a, b) found that purple and blue-grain wheat are both unstable after hybridization. Tesfaye et al. (1991) studied a tetraploid wheat from Ethiopia and found there was a considerable fluctuation in the numbers of purple-grain, red-grain and white-grain. They ascribed the fluctuation into that these colored-grain lines were unstable. Moreover, Li et al. (1982) reported that the low transfer efficiency of gamete could lead to the distortion of segregation ratios in blue-grain wheat. Zeven (1991) concluded that certation was another factor of these fluctuations.

In addition, it should be noted that the experimental results are inevitably affected by environmental factors. Gilchrist and Sorrells (1982) found that temperature affected the color of purple pericarp. Hurd (1959) and Matus-Cádiz et al. (2003) reported that the grain color of blue-grain wheat was affected by environmental conditions. Zeven (1991) reported that light intensity and temperature can affect the production of anthocyanin, and the anthocyanin is the most important factor of grain color. Morrison and Rajhathy (1957) found that environmental conditions affected the expression of blue-grain gene.

CONCLUSIONS

In summary, two purple-grain wheat, two white-grain wheat, and one blue-grain wheat was used for diallel cross to study the segregation ratios of F_1 colored grains. The color inheritance of purple-grain wheat follows a maternal inheritance pattern and that of blue-grain wheat expresses xenia in most cases. In the collections of wheat with blue and purple grains, it was obtained four segregation ratios of 11:5, 13:3, 9:7 and 15:1 (purple: blue), accounting for 97.17% of the total samples. For wheat with blue and white grains, three segregation ratios of 9:7, 11:5 and 13:3 (blue: white), together, account for 83.78% of the total samples. In some circumstances, the grains with different color shades appear in the same spike. The genetics of colored-grains wheat may be affected by various factors such as the interaction between different genes, genes dosage effect, and environmental conditions, which requires further investigations.

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Segregações em grãos coloridos em híbridos F_1 de trigo

Resumo – *Alimentos nutritivos e funcionais de trigo têm recebido grande atenção atualmente. Trigos de grãos coloridos contêm um grande número de nutrientes tais como antocianinas, e isso é interessante para melhoramento. Nesse trabalho, linhagens de trigo de grãos coloridos polinizadas com trigo ??? (Triticum boeoticum, AA) e centeio francês (French Secale cereale, RR) foram usadas como machos e a linhagem Y1642 (derivada de trigo comume??? Agropyron elongatum, AABBDD) como fêmea. Esses trigos coloridos foram usados em cruzamentos dialélicos para estudar segregação de grãos coloridos* F_1*. A herança da cor púrpura de grãos seguiu um padrão materno e trigos de grãos azuis expressaram efeito de xênia, em muitos casos. Grãos com diferentes cores sombreadas apareceram na mesma espigueta.*

Palavras-chave: *Trigos de grãos azuis, trigos de grãos púrpura, herança, segregação.*

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