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Genetic analysis for anthocyanin and chlorophyll contents in rapeseed

Análise genética para antocianinas e de clorofila em sementes de colza

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ABSTRACT

*Rapeseed (**Brassica napus** L.) with purple-red leaf is a valuable resource for plant breeder. It was utilized in breeding program as a morphological marker, and the source of resistance gene to biotic or abiotic stress due to its anthocyanin content (AC). However, the inheritance of AC and the correlation with chlorophyll content (CC) in rapeseed leaf are still unknown. This study aimed to investigate the gene action and heritability of AC and CC in a 10-Zi006 × 10-4438 rapeseed cross using generation mean analysis. The results indicated that AC and CC were controlled by main gene effect and non-allelic interactions. The AC was mainly controlled by genetic effect. However, the genetic effect and non-genetic effect were both important for CC. In addition, the total fixable gene effects was higher than unfixable gene effects for AC, but opposite results was found for CC. Both negative and positive correlations between AC and CC were obtained in different generations.*

Key words: *generation mean analysis, gene effect, genetic model, heritability.*

RESUMO

*Colza (**Brassica napus** L.) de folhas vermelho-púrpura é um recurso valioso para os produtores. Foi utilizada em programas de melhoramento como um marcador morfológico ao gene de resistência a estresses abióticos, bióticos ou devido ao seu teor de antocianinas (AC). No entanto, a herança da AC e a correlação com o teor de clorofila (CC) na folha de colza ainda são desconhecidos. Este estudo teve como objetivo investigar a ação dos genes e hereditariedade da CA e CC em 10 Zi006 × 10-4438 colza, usando geração de análise. Os resultados indicaram que CA e CC foram controladas por efeito do gene principal e interacções não-alélicas. O AC foi controlado principalmente por efeito genético. No entanto, os efeitos genético e não genético foram ambos importantes para CC. Além disso, o total de efeitos gênicos solucionáveis foi maior do que os efeitos de genes para AC, mas os resultados opostos foram encontrados para CC. Correlações negativas e positivas entre CA e CC foram obtidas em diferentes gerações.*

Palavras-chave: *análise de geração, gene, modelo genético, herdabilidade.*

INTRODUCTION

Anthocyanin, a type of flavonoid pigments, is commonly responsible for orange red to violet blue color in plant tissues (TANAKA et al., 2008). It was mainly studied in horticultural crops due to some health benefits (SHIN et al., 2006; WILLIAMS et al., 2008; SINGH et al., 2011; LIANG et al., 2012; SABOLU et al., 2014). In addition, anthocyanin plays an important role as a morphological marker in hybrid rapeseed (WANG et al., 2007). In China, hybrid breeding is one of the most effective ways to increase seed yield. However, the false hybrid were often produced due to pollens contamination. Three-line GMS and CMS + SI (self-incompatibility) systems were suggested as an effective methods to cope this problem (SHEN et al., 2008). In addition, selection of restorer or temporary maintainer line with purple-red leaf for developing rapeseed hybrid have been recommended to identify the false F_1 hybrid (WANG et al., 2007; WU et al., 2007). The rapeseed line 10-Zi006 with purple-red leaf had been successfully

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developed by interspecific hybridization. This obvious color started at seedling stage, and the leaf will change to green color at bolting stage or full-blossom stage differed from line to line (WANG et al., 2007).

Moreover, anthocyanin was an important pigment in response to cold stress in winter rapeseed (SOLECKA et al., 1999), and in ameliorating environmental stresses induced by visible and UV-B radiation and drought conditions (CHALKER-SCOTT, 1999). Therefore, development of rapeseed cultivars with high AC is very important role in increasing plant resistance to drought and cold stress which are the main limiting factors in rapeseed production. However, the possible effects of AC were confounded by the decrease of photochemical efficiency when CC loss in senescing leaves of ***Cornus sanguinea*** and ***Parthenocissus quinquefolia*** (MANETAS et al., 2011). In addition, a significant decrease of photosynthetic pigments simultaneous with an increase of AC was measured in poinsettia bract development (SLATNAR et al., 2013). Due to limited information available on gene action for AC and CC in rapeseed leaf, the objective of this research were to define the gene action for AC and CC, and investigate the correlation between them for further hybrid breeding of rapeseed.

MATERIALS AND METHODS

Two inbred lines, 10-Zi006 with purple-red leaf and 10-4438 with green leaf were crossed to generate the F_1 generation in 2010/2011. In 2011/2012, F_1 were selfed to develop F_2 generation and backcrossed to each parent to obtain B_1 and B_2 generations, respectively. Six generations were evaluated using a randomized complete block design with 3 replications at GAAS (Guizhou Academy of Agriculture Sciences, Guiyang, China) in 2012/2013 and 2013/2014. All six generations were sowed in nursery plots and then transplanted into individual plot after 35 days. Each plot consisted of different numbers of row with 240cm in length. Seelings were transplanted at an inter-row spacing of 45cm and an intra-row spacing of 33.3cm with two plants per hill. P_1, P_2 and F_1 were grown in six rows for both years. F_2, B_1 and B_2 were represented by 27, 21 and 12 rows in 2012/2013, and represented by 21, 12 and 12 rows in 2013/2014, respectively.

The top fully expanded leaf of each plant in six generations were measured for AC and CC at seedling stage. The measurement of total AC was performed by using photometric method (MEHRTENS et al., 2005). Total CC was determined by SPAD Chlorophyll Meter Reading (Minolta SPAD-502 plus, Osaka, Japan) and each leaf was measured five times in different parts to monitor the chlorophyll status.

A, B and C scaling test according to MATHER (1949) and HAYMAN & MATHER (1955) were used for determination of absence or presence of non-allelic interactions. Joint scaling test proposed by CAVALLI (1952) was used to estimate the parameters of m, d and h, and test the goodness of fit of the additive-dominance model by χ^2 testing. Estimation of six parameters were performed according to HAYMAN (1958). Broad sense and narrow sense heritability were estimated using the method outlined by WARNER (1952). R software was used for data analysis (R DEVELOPMENT CORE TEAM, 2015).

RESULTS AND DISCUSSION

The analysis of variance (Table 1) showed that AC was significant and CC was highly significant between years. The results indicated that both studied traits were significantly affected by the environment. This might be due to the environmental factors such as UV-A, UV-B, temperature, light intensity, nutrition and moisture regulated the synthesis of anthocyanin in leaves (LEE et al., 2003; SCHABERG et al., 2003; TOSSI et al., 2011; WANG et al., 2012). In addition, highly significant difference between generations on the traits were detected, especially between parental lines (Figure 1). Moreover, the environment (year) × generations interaction was significant for AC but not for CC.

The scaling test and estimation of six parameters were presented in table 2. The *t*-test between parents for both traits indicated that the data was suitable for genetic analysis. The scaling

Table 1 - Analysis of variance for anthocyanin and chlorophyll contents of P_1, P_2, F_1, F_2, B_1 and B_2 generations evaluated in 2012/13 and 2013/14 at Guiyang, Southwest of China.

Source of variation	df	----------Mean square----------	
		AC	CC
Replications	2	0.002	0.711
Years	1	0.232*	203.633**
Generations	5	3.634**	60.871**
Years × Generations	5	0.024*	0.322
Error	22	0.006	0.919
Total	35		

AC = Anthocyanin content; CC = Chlorophyll content; *P<0.05; **P<0.01;

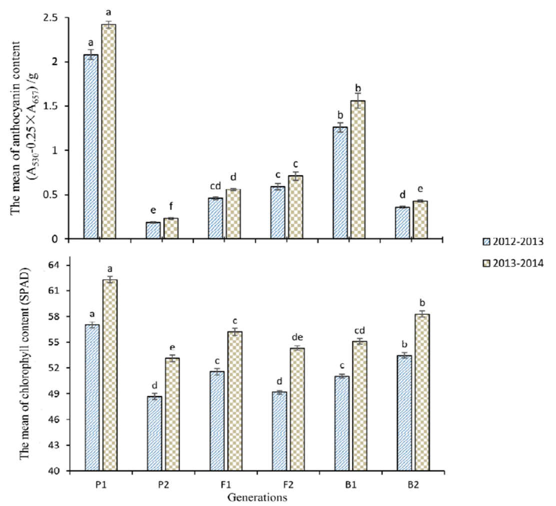

Figure 1 - Generation means and standard errors of anthocyanin and chlorophyll content in 2012/2013 and 2013/2014. a, b, c, d, e and f indicate the significance sign of "Duncan" multiple comparisons for the mean of generations.

test indicated that additive-dominance model were inadequate for AC and CC and revealed of non-allelic interaction. Joint scaling test confirmed absolutely the results with highly significant of χ^2 vales in the three parameter models. Positive additive effect [d] was highly significant for AC. Contrarily, negative additive effect for CC was also significant in both seasons. Dominance effect [h] was not significant for AC but positive effect was highly significant for CC in both 2013 and 2014. High significant additive × additive epistatic effects [i] were detected for AC and CC in both years. Additive × dominance effect [j] was found to be negative and high significant for CC but was not significant for AC in both years. Dominance × dominance effect [l] were negative and significant for AC and highly negative significant for CC in both years. The previous studies showed that additive gene effect was significant for AC in grape and eggplant, and additive gene action as main genetic effect for inheritance of AC were supported by higher heritability (SINGH et al., 2011; LIANG et al., 2012; SABOLU et al., 2014). However, SABOLU et al. (2014) reported a dominance gene effect for AC. In contrast, dominance effect was the main genetic effect for CC (SONG et al., 2014). In addition, a simple additive-dominance genetic model was adequate both for AC and CC in pepper fruit (LIANG et al., 2012). Our results showed that additive gene effect was the mainly genetic effect for AC and CC, and additive-dominance genetic model was inadequate both for AC and CC.

The decomposition of gene effects and estimation of heritability for AC and CC were listed in table 3. Total fixable gene effects was higher than non-fixable gene effects on genetic control of AC, but the contrast result was found for CC in both seasons. In addition, the higher broad sense heritability and moderate narrow sense heritability for AC indicated that the trait was controlled mainly by genetic effect, and both additive and non-additive gene effects were important. However, moderate broad sense heritability and lower narrow sense heritability were detected for CC indicating the trait was affected by both genetic and non-genetic effect,

Table 2 - The *t*-test, scaling tests and six parameter model in a 10-Zi006 × 10-4438 cross for anthocyanin and chlorophyll contents.

Parameter	---AC---		---CC---	
	2012/13	2013/14	2012/13	2013/14
t-value	34.04**	32.77**	16.84**	16.80**
---Scaling test---				
A	-0.02±0.115	0.14±0.176	-6.51***±0.679	-8.34***±0.890
B	0.07**±0.027	0.07*±0.029	6.70***±0.849	7.23***±0.938
C	-0.83***±0.157	-0.93***±0.195	-12.15***±1.275	-10.63***±1.530
χ^2	39.25***	31.54***	305.62***	243.30***
---Six-parameter model---				
m	0.590***±0.036	0.710***±0.047	49.170***±0.218	54.29***±0.7812
[d]	0.900***±0.051	1.130***±0.086	-2.430**±0.396	-3.20**±0.6491
[h]	0.205±0.179	0.375±0.257	11.065***±1.266	8.11***±3.4279
[i]	0.880**±0.176	1.140**±0.255	12.340***±1.178	9.60*** ±3.3838
[j]	-0.045±0.058	0.035±0.089	6.605***±0.467	-7.78***±0.7630
[l]	-0.903*±0.258	-1.35*±0.396	12.530**±2.033	-8.49**±4.2080

AC = Anthocyanin content; CC = Chlorophyll content; t-valu e= t test for parents; *P<0.05; **P<0.01; ***P<0.001; m = mean of the generation; [d] = additive effect; [h] = dominance effect; [i] = additive × additive effect; [j] = additive × dominance effect; [l] = dominance × dominance effect.

Table 3 - The decomposition of gene effects and heritability in a 10-Zi006 × 10-4438 cross for anthocyanin and chlorophyll contents.

Characters	Year	Main effects		Epistatic effects	Total gene effects		Heritability	
		[d]	[h]		Fixable	Non-fixable	h_B^2	H_N^2
AC	2012/13	0.900	0.205	1.828	1.78	1.153	83.79	50.59
	2013/14	1.130	0.375	2.525	2.27	1.76	83.19	35.56
CC	2012/13	2.430	11.065	31.475	14.77	30.2	52.75	34.92
	2013/14	3.200	8.110	25.87	12.8	24.38	54.37	36.46

AC = Anthocyanin content; CC = Chlorophylls content; Epistatic effects = [i] + [j] + [l]; Fixable components = [d] + [i]; Non-fixable components= [h] + [j] + [l] (ignoring signs); h_B^2= Broad sense heritability; h_N^2= Narrow sense heritability.

and the additive effect and non-additive effect as well as environmental effect were important.

Analysis for twelve parameters models (Table 4) indicated additive effect [d], additive × additive effect [i], dominance × dominance effect [l], environmental effect (el) and environmental × additive effect (gdl) were significant or highly significant for genetic control of AC. the additive effect, dominance effect [d], additive × additive effect, additive × dominance effect [j], dominance × dominance effect and environmental effect were highly significant for CC. However, the m+ [d] + [h] + [i] + [l] + el + gdl + gil and m+ [d] + [h] + [i] + [j] + [l] + el were the perfect model for the genetic control of AC and CC in rapeseed.

The relationships between AC and CC were calculated in P_1, P_2, F_1, F_2, B_1 and B_2 populations with 80, 78, 75, 418, 318, 156 plants in 2012/2013 and 75, 66, 69, 301, 160 and 156 plants in 2013/2014. The negative correlations between AC and CC were obtained in P_1, F_2 and B_1 generations in two years. B_1 and F_2 generations was significantly negatively correlated in both years. However, no significant positive correlation were detected in P_2, F_1 and B_2 generations (Table 5). In accordance with this studies, the same relationship was detected between black and violet pepper groups (STOMMEL et al., 2014), indicating that decreasing of CC was due to the high concentration of anthocyanin. Fortunately, positive correlation was also observed between AC and CC in F_1 generation. This result reveal that breeding of rapeseed hybrid with purple-red leaf for drought and cold stress resistance could be achieved, while CC in leaves is maintained.

Table 4 - The genotype × environment interactions for anthocyanin and chlorophyll contents in six generations of a 10-Zi006 × 10-4438 cross grown in two years.

	AC		CC	
	Full model	Fitness of model	Full model	Fitness of model
m	0.650**±0.030	0.650**±0.029	51.740**±0.178	51.691**±0.174
[d]	1.015**±0.050	1.017**±0.016	-2.815**±0.318	-2.672**±0.307
[h]	0.290±0.157	0.291*±0.120	9.545**±1.016	10.029**±0.985
[i]	1.010**±0.155	1.009**±0.122	10.930**±0.954	11.396**±0.922
[j]	-0.005±0.053	-	-7.195**±0.367	-7.03**±0.358
[l]	-1.140**±0.236	-1.144**±0.135	-10.470**±1.614	-11.22**±1.568
e1	0.060*±0.030	0.058**±0.007	2.570**±0.178	2.373**±0.094
gd1	0.115*±0.050	0.075**±0.015	-0.385±0.318	-
gh1	0.085±0.157	-	-1.520±1.016	-
gi1	0.130±0.155	0.038*±0.016	-1.410±0.954	-
gj1	0.040±0.053	-	-0.590±0.367	-
gl1	--0.210±0.236	-	2.060±1.614	-
χ^2(df)	-	2.17 (4)^{ns}	-	5.66 (5)^{ns}

AC = Anthocyanin content; CC = Chlorophyll content; ^{ns}No significant at P=0.05; *P<0.05; **P<0.01; m = mean of the generation; [d] = additive effect; [h] = dominance effect; [i] = additive × additive effect; [j] = additive × dominance effect; [l] = dominance × dominance effect; el = environmental effect; gdl = environmental × additive effect; ghl = environmental × dominance effect; gil = environmental × additive × additive effect; gjl = environmental × additive × dominance effect; gll; environmental × dominance × dominance effect.

Table 5 - Pearson correlation coefficients for anthocyanin and chlorophyll contents in P_1, P_2, F_1, F_2, B_1 and B_2 generations.

Generations	2012/2013	2013/2014
P_1	-0.15	-0.19
P_2	0.16	0.15
F_1	0.07	0.08
F_2	-0.18**	-0.12*
B_1	-0.26**	-0.26**
B_2	-0.08	-0.01

*P<0.05; **P<0.01.

CONCLUSION

Inheritance of AC and CC in rapeseed leaf were not follow the simple additive-dominance genetic model, but the non-allelic interactions played an important role. In addition, AC was controlled mainly by genetic effect and CC was affected both by genetic effect and non-genetic effect. This result indicated that selection for AC in early generations would be more effective. However, selection in later generation with SSD/pedigree breeding methods is a tool for the improvement of CC.

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