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GENETIC ANALYSIS OF SEED COAT COLOR AND ANTHOCYANIN CONTENT IN MUNGBEAN

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SUMMARY

Mungbean (*Vigna radiata*) is a nutritionally rich leguminous crop widely consumed in both its whole and processed forms. Seed coat color affects consumer preference and nutritional value. The objective of this study sought to investigate the genetic inheritance of seed coat color and anthocyanin content in mungbean. Qualitative and quantitative genetic analyses for the traits succeeded in using parental and populations derived from crosses between Kamphaeng Saen 2 (KPS2; green seed) × Jessore (yellow seed) and KPS2 × LD2016-002 (black seed). The χ^2 analysis showed seed coat color behaves as a simple Mendelian trait, with yellow being recessive to green and black dominant over green. The generation mean analysis suggested the primary influences for anthocyanin concentration in the green × yellow cross come from a single major gene, while the green × black cross involves additional genes. Estimates of the number of effective factors in both crosses also pointed to the presence of a major gene with a strong effect. However, the continuous distribution of anthocyanin content in segregating populations in both crosses indicates the trait is quantitative in nature, implying the involvement of multiple genes aside from the major gene primarily controlling pigment accumulation. These findings are useful for breeding for mungbean seed quality.

Keywords: Mungbean, seed coat color, anthocyanin, generation mean analysis, genetic inheritance

Key findings: Chi-square analysis indicated the yellow seed coat color is recessive to green and has the control from a single gene, whereas the black seed coat color is dominant over green and also has a single gene governing it. Generation mean analysis of the green × yellow cross demonstrated monogenic control of anthocyanin content, while analysis of the green × black cross suggested the involvement of two or more genes in controlling this trait.

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INTRODUCTION

Mungbean (*Vigna radiata* [L.] Wilczek) is a leguminous crop of significant economic importance in South and Southeast Asia. It has a worldwide cultivation on more than 7 million hectares (Somta *et al*., 2022). Mungbean seed is popular for its high nutritional value, with about 20%–25% protein and 60%–65% carbohydrates (Somta *et al*., 2022). Furthermore, mungbean is rich in vitamins, minerals, antioxidants, and various phenolic compounds (Ganesan and Xu, 2018; Hou *et al*., 2019; Somta *et al*., 2022) and low in cholesterol (Zhu *et al*., 2018). These nutritional qualities make mungbean one of the healthiest legume crops.

Most mungbean production usage is for direct consumption in various savory and sweet dishes or processed into products, such as bean sprouts, vermicelli, split beans, and mungbean flour (Nair and Schreinemachers, 2020). Mungbean is also gaining attention as a plant-based protein alternative to animal-derived proteins (Somta *et al*., 2022). Its increasing popularity as a health food among health-conscious consumers and individuals with dietary restrictions—such as gluten intolerance—has led to the development of many mungbean flour-based alternative food products.

Seed coat color has emerged as an important trait influencing both the nutritional value and marketability of mungbean products (Thakur *et al*., 2019). Mungbean seeds exhibit various seed coat colors, such as yellow, glossy green, green, and black-green being the most common, albeit most commercial mungbean cultivars have green seed coats. These seed coat colors show a close association with nutritional properties. For instance, black-seeded mungbeans are typically rich in anthocyanin content (Hou *et al*., 2019; Ma *et al*., 2021; Mau *et al*., 2023).

Anthocyanin is an antioxidant providing health benefits by scavenging free radicals, activating antioxidant enzymes, and chelating metal ions (Mattioli *et al*., 2020; Tena *et al*., 2020). Consumer preferences on mungbean seed color vary by region: glossy green mungbeans are desirable in countries like Australia and India, while yellow-seeded mungbeans are a preference in certain parts of India—especially in West Bengal—as well as in Bangladesh and Sri Lanka (Oladejo *et al*., 2021).

Seed coat color is an influential characteristic that affects mungbean quality, consumer demand, and nutritional benefits. Understanding the genetic basis controlling seed coat color is essential for breeding programs aiming to develop mungbean varieties that meet market preferences and nutritional standards. Therefore, the objective of this study sought to investigate the inheritance pattern of genes controlling seed coat color and the genetic basis associated with anthocyanin content in mungbean seeds.

MATERIALS AND METHODS

Plant material

This study used three mungbean accessions, Kamphaeng Saen 2 (KPS2), Jessore, and LD2016-002. These accessions are cultivated mungbeans from Thailand, Bangladesh, and China, which have green, yellow, and black seed coats, respectively. Six basic populations developed: P_1 (female parent), P_2 (male parent), F_1, F_2, BC_1P_1, and BC_1P_2, which came from the crosses KPS2 × Jessore and KPS2 × LD2016-002. In each cross, growing P_1, P_2, and F_1 plants of each population occurred. Further on, self-pollinating an F_1 plant continued to produce F_2 populations and backcrossed with 20 plants of each P_1 and P_2 to produce BC_1P_1 and BC_1P_2 populations, respectively, in a crossing block. The P_1 (female parent), P_2 (male parent), F_1, F_2, BC_1P_1, and BC_1P_2 of each cross succeeded in their growing in an experimental field of Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom, Thailand. At maturity, dry seeds and pods of each plant in the populations reached harvest, followed by recording the seed color of each plant.

Anthocyanin content

Anthocyanin content, as determined, followed procedures described by Mastropasqua *et al*. (2020) with minor modifications. Briefly, mungbean seeds sustained incubation at 65 °C for 4 h with 1 ml of a solution containing 98% methanol and 0.24 M HCl before centrifugation at 12,000 rpm for 10 min at room temperature. The anthocyanin content measurement utilized spectrophotometer at both 530 and 657 nm wavelength. Subsequently, the anthocyanin content calculation used the following equations.

$$\text{Anthocyanin content} = A_{530} - (0.25 \times A_{657})$$

Data analysis

Genetic inheritance of seed coat color in F_2, BC_1P_1, and BC_1P_2 populations of each cross entailed determination by the χ^2 goodness-of-fit test using the R program 2.14.0 (R Development Core Team, 2013). Genetic inheritance detection of anthocyanin content in each cross engaged the generation mean analysis by Mather and Jinks (1982). The means, standard error, and variance calculations for anthocyanin content of the P_1, P_2, F_1, F_2, BC_1P_1, and BC_1P_2 populations were successful using the Excel program. The mean and standard error of all the populations received testing for the adequacy of the additive-dominance model using a joint scaling test (Cavalli, 1952). Genetic effects with a six-parameter model involving mean (*m*), additive (*d*), dominance (*h*), additive × additive (*i*), additive × dominance (*j*), and dominance × dominance (*l*) attained their estimates using weighted least squares following Mather and Jinks (1982). Testing the significance of the scales and gene effects employed the *t*-test (Singh and Chaudhury, 1985). The adequacy of the additive (*m*, *d*, and *h* effects) model and non-additive (*m*, *d*, *h*, *i*, *j*, and *l* effects) model succeeded in their determination by the χ^2 test. All performed analyses used the *R* program 2.14.0 (R Development Core Team, 2013).

Broad-sense heritability calculation followed the formula described by Warner (1952) and Wright (1968) as follows:

$$H^2 = \frac{\sigma^2_G}{\sigma^2_P}$$

Where σ^2_G and σ^2_P are the variances of genotype and phenotype, respectively.

The variation due to phenotypes (P), environments (E), and genotypes (G) reached estimates as follows:

$$\sigma^2_P = \sigma^2_{F2}$$

$$\sigma^2_E = (\sigma^2_{P1} + \sigma^2_{P2} + 2\sigma^2_{F1})/3$$

$$\sigma^2_G = \sigma^2_P - \sigma^2_E$$

Where σ^2_{P1}, σ^2_{P2}, σ^2_{F1}, and σ^2_{F2} are the variances of the P_1, P_2, F_1, and F_2 generations, respectively.

The number of effective factors (EF) controlling anthocyanin content employed two methods of calculation—Method I (Wright, 1968):

$$EF_1 = \frac{(P_1 - P_2)^2[1.5 - 2h(1 - h)]}{8[\sigma^2_{F2} - 0.25(\sigma^2_{P1} + \sigma^2_{P2} + 2\sigma^2_{F1})]}$$

Where F_1, P_1, and P_2 are generation means, while σ^2_{P1}, σ^2_{P2}, σ^2_{F1}, and σ^2_{F2} are variances of anthocyanin in the respective generations, $h = (F_1 - P_1)/(P_2 - P_1)$ and Method II (Lande, 1981):

$$EF_2 = \frac{(P_1 - P_2)^2}{8[\sigma^2_{F2} - 0.25(\sigma^2_{P1} + \sigma^2_{P2} + 2\sigma^2_{F1})]}$$

Where "generation means" and "variances" have the same meaning as in EF_1 above.

Table 1. Segregation analysis of seed coat color in six populations derived from the cross between KPS2 (P_1) × Jessore (P_2).

Generation	Observed number		Ratio		Expected number		χ2	*P* value
	Green (G)	Yellow (Y)	G	: Y	Green	Yellow		
P_1	67	0	1	: 0	67	0	-	-
P_2	0	78	0	: 1	0	78	-	-
F_1	72	0	1	: 0	72	0	-	-
F_2	1,083	362	3	: 1	1,083.75	361.25	0.0021	0.9637
BC_1P_1	202	0	1	: 0	202	0	-	-
BC_1P_2	103	88	1	: 1	95.5	95.5	1.1780	0.2778

RESULTS

Inheritance of seed coat color

In the cross where KPS2 (green seed coat) was the maternal parent (P_1) and Jessore (yellow seed coat) was the paternal parent (P_2), all plants in the F_1 and BC_1P_1 populations exhibited green seed coats (Table 1 and Figure 1a). This indicates the yellow seed color is a recessive trait. Segregation of seed coat color in the F_2 and BC_1P_2 populations fits the expected 3:1 (1,083 plants with green seeds: 362 plants with yellow seeds) and 1:1 (103 plants with green seeds and 88 plants with yellow seeds) ratio, respectively (Table 1), indicating the yellow seed coat color has the control of a single recessive gene.

In the cross between KPS2 (green seed coat) as the maternal parent (P_1) and LD2016-002 (black seed coat) as the paternal parent (P_2), the seed coat color of all the F_1 and BC_1P_2 populations was black (Table 2 and Figure 1b). This signifies the black seed was dominant over the green seed. In the F_2 population, segregation of the seed coat color fits a 3:1 (1,227 plants with black seeds: 392 plants with green seeds) ratio (Table 2). However, segregation of the seed coat color in the BC_1P_1 did not fit the 1:1 (plants with black seeds: plants with green seeds) ratio (Table 2). Nonetheless, results of segregation analysis in F_2 and BC_1P_2 suggested the black seed coat color has the control of a single dominant gene.

Anthocyanin content

Results of anthocyanin content measurement in seeds of parents and six basic populations of the cross KPS2 × Jessore and KPS2 × LD2016-002 have summaries in Table 3. Among the three parental mungbean accessions, LD2016-002 had the highest anthocyanin content, followed by KPS2 and Jessore, with mean values of 2.63, 0.70, and 0.24, respectively. In the cross KPS2 × Jessore, the F_1 generation showed a similar anthocyanin content to KPS2 (Figure 2). The F_2 population exhibited transgressive segregation of the anthocyanin content with ranges of 0.16 to 1.53 and a mean of 0.63 (Figure 2). The BC_1P_1 population showed similar segregation of anthocyanin content to that in the F_2 population, ranging from 0.13 to 1.60, with a mean of 0.67, while the BC_1P_2 population showed anthocyanin content ranging from 0.29 to 1.32, with a mean of 0.53 (Figure 2). Frequency distribution of the anthocyanin in the F_2, BC_1P_1, and BC_1P_2 populations all showed continuous distribution (Figure 2).

In the cross KPS2 × LD2016-002, the F_1 population revealed an intermediate anthocyanin content between the parents with a mean of 1.68. The F_2 population displayed a strong transgressive segregation of anthocyanin content (Figure 3), with a range of 0.33 to 5.22 and a mean of 1.94. The BC_1P_1 population exhibited anthocyanin content, ranging from 0.27 to 3.23 with a mean of 0.98. Most of the BC_1P_1 plants had anthocyanin

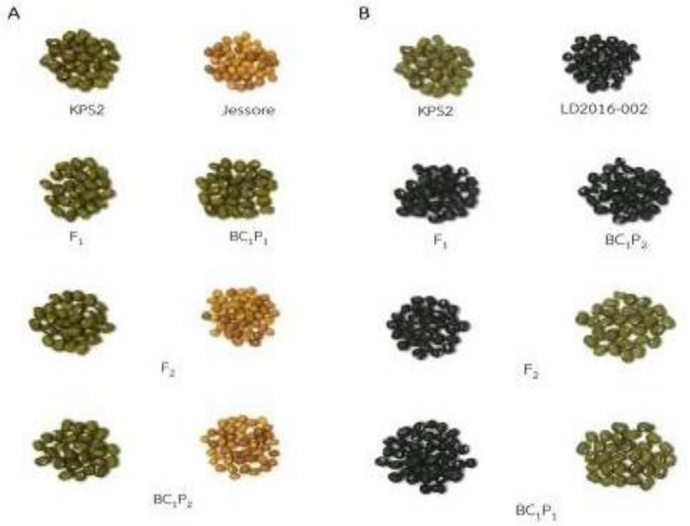

Figure 1. Seed coat color segregation in six populations derived from the crosses KPS2 (P_1) × Jessore (P_2) demonstrated that yellow seed coat color is recessive to green (A) and KPS2 (P_1) × LD2016-002 (P_2) showed that black seed coat color is dominant over green (B), where F_1 represents the first filial generation from P_1 × P_2, F_2 represents the generation obtained by self-pollination of F_1, BC_1P_1 represents the first backcross generation produced by crossing F_1 with P_1, and BC_1P_2 represents the first backcross generation produced by crossing F_1 with P_2.

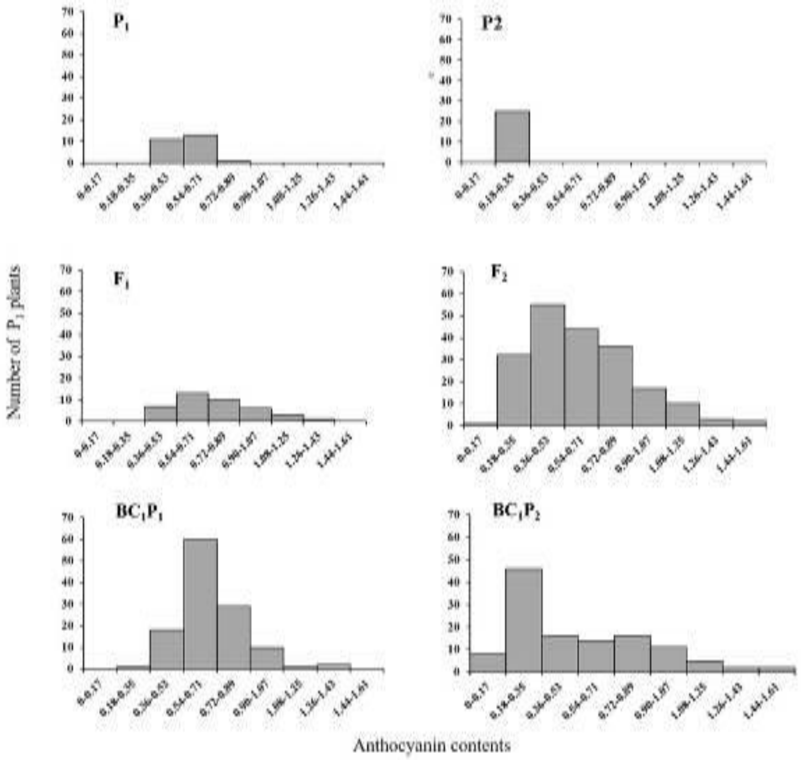

Figure 2. Distribution of anthocyanin content in six generations derived from the cross between KPS2 (green seed coat) and Jessore (yellow seed coat).

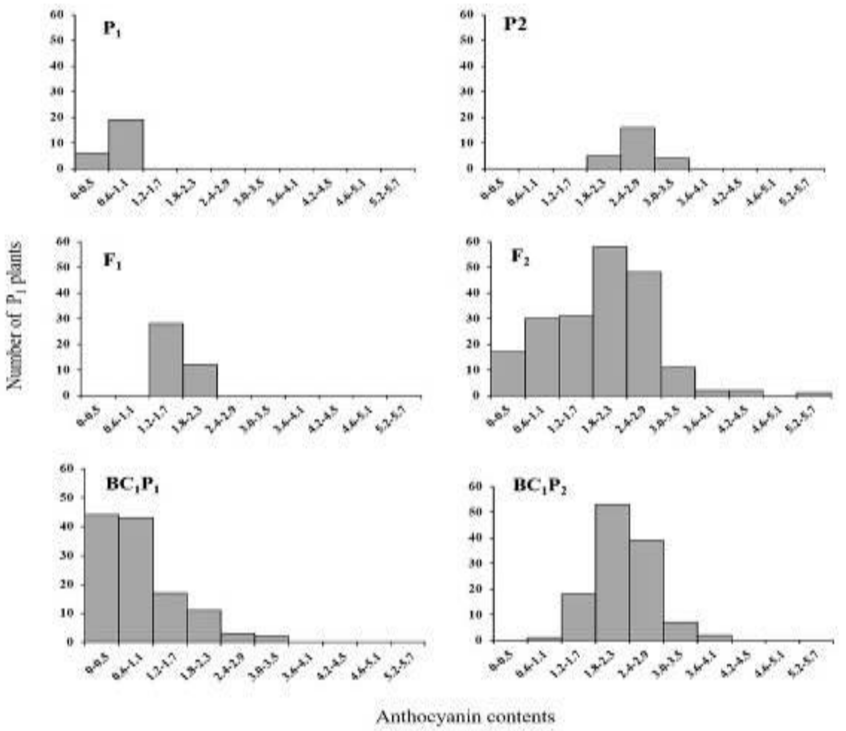

Figure 3. Distribution of anthocyanin content in six generations derived from the cross between KPS2 (green seed coat) and LD2016-002 (black seed coat).

Table 2. Segregation analysis of seed coat color in six populations derived from the cross between KPS2 (P_1) × LD2016-002 (P_2).

Generation	Observed number		Ratio		Expected number		χ2	*P* value
	Green (G)	Black (B)	G	: B	Green	Black		
P_1	67	0	1	: 0	67	0	-	-
P_2	0	75	0	: 1	0	75	-	-
F_1	0	71	0	: 1	72	0	-	-
F_2	392	1,227	1	: 3	361.25	1,083.75	0.0021	0.9637
BC_1P_1	139	87	1	: 1	113	113	11.9650	0.0005
BC_1P_2	0	227	0	: 1	0	227	-	-

content similar to that of the KPS2. The BC_1P_2 population exhibited anthocyanin content ranging from 1.14 to 4.12, with a mean of 2.29 (Figure 3). Most of the BC_1P_2 plants had anthocyanin content similar to that of the LD2016-002. Similar to the cross KPS2 × Jessore, frequency distribution of the anthocyanin in all the F_2, BC_1P_1, and BC_1P_2 populations of the cross KPS2 × LD2016-002 showed continuous distribution (Figure 3). This suggests that the anthocyanin content is a quantitative trait.

Heritability and generation mean analysis

Broad-sense heritability (H^2) values calculated for anthocyanin content in the crosses KPS2 × Jessore and KPS2 × LD2016-002 were moderate and nearly the same, being 0.75 and 0.78, respectively (Table 3). This suggests the anthocyanin content mainly has the control of genetic factor(s).

Generation mean analysis in the cross KPS2 × Jessore revealed a simple additive-dominance model was statistically able to

Table 3. Mean, standard error (SE), and variance of anthocyanin content in six generations derived from the cross KPS2 × Jessore and KPS2 × LD2016-002.

Generation	KPS2 × Jessore			KPS2 × LD2016-002		
	Mean	SE	Variance	Mean	SE	Variance
P_1	0.70	0.02	0.01	0.70	0.02	0.01
P_2	0.24	0.00	0.00	2.63	0.07	0.13
F_1	0.77	0.04	0.05	1.68	0.04	0.06
F_2	0.63	0.02	0.08	1.94	0.07	0.32
BC_1P_1	0.67	0.01	0.03	0.98	0.06	0.43
BC_1P_2	0.53	0.03	0.11	2.29	0.05	0.28
Heritability	0.75			0.78		

Table 4. Joint scaling test for anthocyanin content in six generations derived from the cross KPS2 × Jessore and KPS2 × LD2016-002.

Generations	Scaling test	Degree of freedom	Variance	SE	t-value	P-value
KPS2 × Jessore						
A	0.02	182	0	0.05	0.43	0.33^{ns}
B	0.06	182	0.01	0.07	0.8	0.21^{ns}
C	0.18	286	0.01	0.11	1.67	0.05^{ns}
KPS2 × LD2016-002						
A	-0.42	182	0.02	0.13	-3.27	0.0006**
B	0.57	182	0.02	0.13	2.15	0.0164*
C	1.10	286	0.09	0.3	3.78	0.000**

Table 5. Estimated gene effects for anthocyanin content in six generations derived from the cross KPS2 × Jessore and KPS2 × LD2016-002.

Genetic parameters	Cross combination	
	KPS2 × Jessore	KPS2 × LD2016-002
Mean (*m*)	0.60	1.94
Additive gene effect (*d*)	0.16	-1.31
Dominant gene effect (*h*)	0.40	-1.21
Additive x additive gene effect (*i*)	-	-1.22
Additive x dominance gene effect (*j*)	-	-0.35
Dominance x dominance gene effect (*l*)	-	1.37
χ^2	3.24	0.00

adequately explain the variation in anthocyanin content among the generations (Table 4). This indicates a single gene with additive and dominance gene effects controls anthocyanin content in this cross combination. The values of *m*, *d,* and *h* calculated for anthocyanin content of this cross were 0.60, 0.16, and 0.4, respectively (Table 5). Nonetheless, generation mean analysis in the cross between KPS2 × LD2016-002 revealed the non-additive dominance model was able to adequately explain the variation among the generations (Table 4). This result signifies the anthocyanin content in this cross has at least two genes controlling it. The values of *m*, *d*, *h*, *i*, *j,* and *l* calculated for anthocyanin content in this cross were 1.94, -1.31, -1.21, -1.22, -0.35, and 1.37, respectively (Table 5).

Anthocyanin content factors

The number of effective factors for anthocyanin content in the cross KPS2 × Jessore by methods I and II was 0.89 and 0.48, respectively, while that in the cross KPS2 × LD2016-002 was 0.6 and 0.6, respectively (Table 6).

Table 6. The number of effective factors method I and II for anthocyanin content in the crosses KPS2 × Jessore and KPS2 × LD2016-002.

Effective factors	KPS2 × Jessore	KPS2 × LD2016-002
EF1	0.89	0.60
EF2	0.48	0.60
Mean	0.69	0.60

DISCUSSION

Mungbean seed coat color revealed an association with anthocyanin contents. This study investigated genetic control for the seed coat color in the mungbean. We found the yellow seed coat color is recessive to green seed coat color and has the control of a single gene (Table 1). This finding agrees with previous results reported by Wang *et al*. (2013) and Dhare *et al*. (2023). However, because yellow seed color is recessive, backcross breeding requires an additional self-pollination generation to select progenies expressing this trait.

Researchers also found the black seed coat color is dominant over the green seed coat and is very likely being governed by a single gene (Table 2). Although the segregation of seed color in the BC_1P_1 generation deviated from the expectation of the monogenic trait. Wang *et al*. (2013) and Wang *et al*. (2024) reported the black seed coat color in mungbean is a monogenic trait.

In addition to seed coat color, the study also investigated genetic inheritance of anthocyanin content in the seed coat. Continuous distribution of the anthocyanin content in the seed coat in various populations derived from the cross green seed × yellow seed (Figure 2) and green seed × black seed (Figure 3) suggested this trait is quantitative in nature, thus having the control of several genes. Although gene mapping and transformation demonstrated that the gene *VrMYB90* controls the presence of black color and anthocyanin biosynthesis in the seed coat of mungbean, *VrMYB3* also emerged to play important roles in black seed coat and anthocyanin biosynthesis (Ma *et al*., 2023; Wang *et al*., 2024). In fact, various regulatory and structural genes contribute to the pathway of anthocyanin biosynthesis (Liu *et al*., 2018). Quantitative genetic studies by generation mean analysis and estimation of the number of effective factors analysis showed a single gene controls quantitative variation of anthocyanin content in the cross of green seed × yellow seed (Tables 5 and 6). These results agree with results of segregation analysis of the yellow seed coat color (Table 1). Thus far, the molecular identity of the gene responsible for yellow seed coat color in mungbean has not been explicit.

Generation mean analysis revealed two or more genes control anthocyanin content in the cross of green seed × black seed (Table 5), while the number of effective factors analysis disclosed a single gene controls the trait in the same cross (Table 6). Nonetheless, the result of the number of effective factors analysis in this cross is in line with the result of segregation analysis that a single gene controls the black seed coat color. Recently, the molecular basis of the gene controlling black seed coat succeeded in its identification by Ma *et al*. (2023) and Wang *et al*. (2024). These studies demonstrated that the *VrMYB90* gene-encoding transcription factor MYB90 has an association with the black seed coat color by regulating structural genes for anthocyanin biosynthesis in the seed coat.

CONCLUSIONS

Genetic analyses demonstrated that while seed coat color in mungbean follows simple Mendelian inheritance, yellow being recessive to green and black dominant over green, the underlying anthocyanin content shows a more complex pattern. Although a single major gene primarily regulates anthocyanin levels in the green × yellow cross, additional genes contribute in the green × black cross, reflecting the polygenic nature of pigment accumulation. This apparent contrast is because anthocyanin is only one component of a broader pigment system; a major regulatory gene can switch the pigment pathway on or off to produce distinct color classes. Meanwhile, the amount of pigment synthesized is under the control of multiple structural and regulatory genes in the flavonoid pathway. Therefore, despite the simple inheritance of visible seed color, anthocyanin accumulation remains quantitatively inherited, generating continuous variation in pigment concentration and color intensity. These insights refine our understanding of seed coat pigmentation and offer valuable guidance for breeding strategies and molecular research aimed at improving seed quality in mungbeans.

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