

Full Length Research Paper

Genetics of seed coat color in sesame (*Sesamum indicum* L.)

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Seed coat colour of sesame is commercially an important trait. Developing white seeded varieties with long lasting luster has received momentous attention in most of the major sesame producing countries including India. The present investigation centered on the genetic control of seed coat colour in sesame. No genetic nomenclature is available in sesame to describe seed coat colour. This is the first attempt to designate genes engendering specific seed coat colour. The findings are based on five different crosses with seed coat colour belonging to white, beige and various shades of brown colour. In general, tetragenic model corroborated with the colour combinations. The colour beige seemed to be fixable as well as suppressive over other colors. In white seeded seeds, several genes co-existed and those genes produced colored segregants in F_2 generation. Two loci, *Gr* and *I*, regulated suppression or intensification of pigment production. Two major genes *V* and *B* were accountable for basic colour production. The recessive allele '*b*' tightly linked with '*r*', resulted into beige colour which suppressed the effect either of the loci *V* and *B*. The study of inheritance pattern of seed coat would aid to evolve varieties with specific desired seed coat color.

Key words: Genes, inheritance, seed coat colour, nomenclature and *Sesamum indicum* L.

INTRODUCTION

Sesame, an ancient oilseed crop, is termed as a 'queen of oilseeds' by Bedigian and Harlan (1986) as it is rich in polyunsaturated fatty acid, proteins, vitamins, niacin, minerals and lignans (Budowski and Markley, 1951; Moazzami and Kamal-Eldin, 2006; Nakimi 1995; Yamashita et al., 1992) and is popularly used as a food and medicine (Mochizuki et al., 2010; Liao et al., 2010; Jan et al., 2009; Jan et al. 2011; Coulman et al., 2009). The seed coat color of healthy sesame seed ranges from black to white through different intermediates like, dark brown, brown, light brown, beige, and cream. White sesame seeds, have higher oil, protein and moisture ratios as compared to black seeded sesame (Kanu, 2011). Seed

coat color in sesame seems to be associated with seed biochemical properties, antioxidant content and activity, level of disease resistance among sesame accessions, in addition to being a marker of evolution within the *Sesamum* genus (Budowski and Markley, 1951; Nakimi, 1995; Kanu, 2011; Shahidi et al., 2006; El-Bramawy et al., 2008; Zhang et al., 2012, 2013). Pathak and Dixit (1992) reported that the preference for colour in sesame differs from region to region. In spite of ameliorating demand of white seeded sesame, high yielding white seeded sesame varieties with good oil content are quite limited in India. The lack of knowledge about genetic complexity of the trait might be responsible for less

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progress in evolving varieties of desired colour (Tiwari and Campbell, 1996).

The physical appearance of seed colour is a key marketing factor and acceptability of sesame type varies greatly with cultural preference. Japanese prefer black seeded sesame and Sudanese favor white seeded ones (Hossain et al., 2010). In particular, a larger seed size, coupled with a light-colored seed coat like white often command price premiums in a market-dependent manner (Graham et al., 2001). Darkening or segregation of desirable color in the seed coat due to genetic recombination results in a less-marketable product (Cassells and Caddick, 2000). In Eastern India, white seeded sesame is sold at a price at least 30% higher than that of brown seeded or black seeded varieties because of consumer's preference and greater culinary utility (Chakraborty et al., 1984).

Considerable strides over the last few years at the National and International level have resulted into up-grading agronomic traits including yield in sesame. But the issue of inheritance of seed coat colour remained unattended. All earlier researchers in sesame, outlined seed coat colour to be under digenic control with several confounding segregants beyond plausible explanation (Nohara et al., 1933; Gutierrez et al., 1994; Baydar and Turgut, 2000; Falusi, 2007). Recently, Zhang et al. (2013), using a high-density linkage map analyzed the genetic segregation and quantitative trait loci (QTL) for sesame seed coat color and showed that two major genes with additive-dominant-epistatic effects along with polygenes were responsible for controlling the seed coat color trait. Keeping in view, complicated picture of inheritance, the present investigation was undertaken to unravel genetics of seed coat colour under different genetic background.

MATERIALS AND METHODS

Seed colour classification and evaluation

Genotypes belonging to different seed coat colour were selected as experimental materials (Table 1 and Figures 1-6). Seed coat colour accession number was assigned for each colour according to norms of the International Plant Genetic Resources Institute (IPGRI and NBPGR, 2004). Seeds were classified phenotypically as soon as possible after harvest to minimize misclassification resulting from seed darkening, immaturity, weathering, or disease.

Sesame, a self-pollinating crop with epipetalous flowers has the advantage of easy emasculation and pollination. To carry out crossing program flowers were hand-emasculated the previous afternoon and covered with waxy pollination bags. Next day cross pollination was made by dusting the pollen grains of the desired flower directly onto the stigmas of emasculated flowers. Total 41 crossings were done among the parental materials for inheritance study. The F_1 plants were self-pollinated to produce the F_2 . The parents, F_1 , reciprocals, F_2 and F_3 progenies were grown in the Agricultural experimental station, Calcutta University at Baruipur, West Bengal, India (22.35°N, 88.44°E.). Normal recommended agronomical practices were followed for cultivation. The selfed seeds of individual plants were harvested and scored for seed colour to determine the inheritance pattern of the trait. Out of 41 crosses, 5 crosses are being reported here: OSC-593 X Amrit, Rama X VRI-1, Tillotama X NIC-8316, Tillotama X Gujarat Til-2, Uma X TKG-352.

RESULTS AND DISCUSSION

The F_1 seeds of any cross involving two parents and their reciprocals were similar in colour to that of the maternal parent of the specific cross and hence depicted seed colour was under control of maternal tissue, Wilson and Hudson (1979), earlier reported similar findings. Chen and Heneen, (1992) were of the opinion that interaction between maternal and embryonic component determined seed coat colour in Brassica. Van-Deynze and Pauls (1994) reported more conclusively that seed coat colour albeit, is primarily determined by maternal genotype, but genetic constitution of parents finally determine expression of character.

The genetic control of seed colour in the investigated crosses seemed to fit the tetragenic ratio. In sesame, nomenclature is unavailable to describe the genes controlling seed coat colour. This is the first attempt where genes of seed coat colour have been designated. The investigation confirmed that four genes namely *Gr*, *B*/*R*], *V* and *I* were involved in the determination of seed coat colour. The recessive genes, *gr* and *i* prevented production of colour pigment that is, they acted as inhibitors. The white seeded sesame transpired when both the locus *Gr* and *I* were in recessive homozygous state. The locus *I* in dominant state was responsible for engendering more intensified colour.

Seed coat colour would be black when one dominant allele was present at these three loci namely *Gr*, *V* and *R*, with either dominant or recessive gene at *I* locus Dominant *I* gene produced bright black, whereas, recessive *i* generated dull black. In general, colored seeds were dominant over non-colour seed. Coloured light brown was dominant over white seeded coat colour. The gene, *B*, responsible for colour production was very closely linked to *R* locus and did not produce any recombinant. The gene products of *I* and *[BR]* produced brown colour which was dominant over white colour. Interestingly, the dominance relations of the four genes were in the order *[BR]*, *I*, *V*, *Gr*, where the presence of colour was due to dominant genotype in each case. Most cultivated sesame varieties homozygous for a dominant form of the *I* gene resulting in varieties with colored seed coat.

On the basis of above description, the total explanation of genetic ratio for colour inheritance was attempted.

Cross 1: OSC-593 X Amrit

The parent OSC-593(♀), a white seeded variety was crossed to Amrit (♂), a light brown seeded variety, the F_1 progenies engendered white seeded hybrid (F_1) with colour like that of OSC-593 and the F_2 progenies segregated into brown, light brown and white seeded plants in 9:6:1 ratio (Table 2). The reciprocal cross involving Amrit as female and OSC-593 as male parent produced F_1 progenies of light brown colour.

Table 1. Seed coat colour and parentage of the genotypes used in this study.

Genotype	Parentage	Source	Seed coat colour	Score for Seed-coat colour
GT-2	Gujarat Til-1x TC-25	ICAR Sesame Project, Jabalpur	White	1
OSC-593	Not available	ICAR Sesame Project, Jabalpur	White	1
RAMA	Selection from 'Khosla' local	Calcutta University	Medium brown	5
UMA	Mutant of Kanak	ICAR Sesame Project, Jabalpur	Beige	3
NIC-8316	Indigenous collection	ICAR Sesame Project, Jabalpur	Beige	3
TILLOTAMA	Selection from local germplasm Jinardi Ducca-2	Calcutta University	Medium brown	5
VRI-1	pureline selection from thirukattupalli local of TN	Calcutta University	Dark brown	6
Amrit	Selection from XU-2 X Krishna	ICAR Sesame Project, Jabalpur	Light brown	4
TKG-352	Not available	ICAR Sesame Project, Jabalpur	White	1

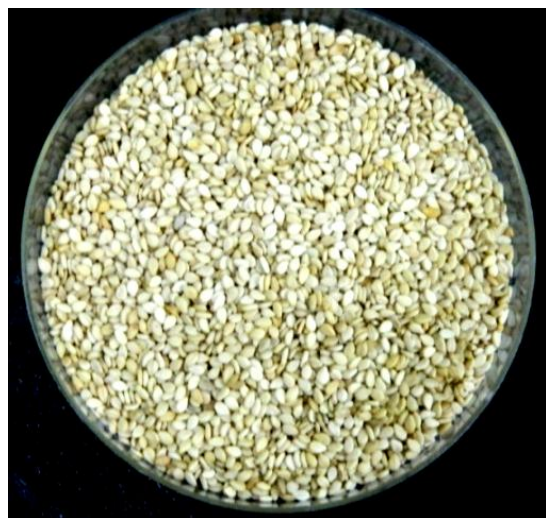


Figure 1. White colored seed, code-1.



Figure 3. Light brown colored seed, code-4.



Figure 2. Beige colored seed, code-3.



Figure 4. Medium brown colored seed, code-5.



Figure 5. Dark brown colored seed, code-6.



Figure 6. Bright black coloured seed, code-12.

Cross 2: Rama X VRI-1

The 2nd cross combination was involved with Rama, a medium brown seeded variety, as a female parent and VRI-1, a dark brown seeded variety, as a male parent. The hybrid (F_1) seed coat colour corroborated with female parent that is, Rama and reciprocal cross between varieties VRI-1 and Rama confirmed similar earlier observation of maternal tissue inheritance (Table 3). A segregation pattern of 9:3:3:1 ratio belonging to black, dark brown, medium brown and light brown seeded plant respectively, was found in F_2 generation. The segregation

nature confirmed simple digenic control but the present explanation is not based on two genes only.

Cross 3: Tilottama X NIC-8316

A popular variety, Tilottama characterized by medium brown seed coat, when was hybridized with a beige colored seed, NIC-8316, the F_1 progenies were like to that of female parent (Table 4). The reciprocal cross also affirmed similar findings. The F_2 progenies produced three groups of different seed coat colour namely brown, light brown and beige colored seed coat having 9:6:1 ratio, respectively. Surprisingly, such ratio was obtained only when the variety Tillotama was acted as a female parent. The F_2 progenies of the reciprocal cross did not exhibit further segregation and only beige colored seeds were obtained. In other words, beige colored seeds were fixable in nature. The recessive gene, *bb*, in association with tightly linked gene, *rr*, generated beige colour and an inhibitory effect over other genes was responsible to produce beige colour of fixable nature. It is a unique observation of this inheritance study.

Cross 4: Tilottama X Gujarat Til-2

The medium brown seed coated variety Tilottama, when combined with Gujarat Til-2, a white seeded variety, generated F_1 progenies, belonging to medium brown colored seed. The reciprocal cross of Gujarat Til-2, as female, and Tilottama, as male, engendered F_1 seeds, like that of maternal tissue (Table 5). The F_2 progenies segregated into 15 brown: 1 white colored seeded plants.

Cross 5: Uma X TKG-352

The cross combination consisted of variety Uma, a beige colored type of seed and TKG-352, a white seeded variety. The beige colored variety, Uma, when was hybridized with TKG-352, all F_1 progenies expressed seed coat colour like that of Uma (Table 6). The F_2 progenies, on the other hand, did not exhibit further segregation and produced only beige colored seeds. Interestingly, the beige colored seed did not segregate further after F_2 . The reciprocal cross combination that is, TKG-352 X Uma produced F_1 progenies having white seeded sesame.

Since, the seed coats consisted of maternal tissue; seed coat colour is determined by the genotype of the plant in which the seeds develop, rather than by the genotype of the embryo within that seed. The ovule is the progenitor of the seed and embryonic development proceeds within the protective maternal tissue of the ovule, which turns into the seed coat encircling the developing embryo along with endosperm (West and Harada, 1993). Thus, testa is a maternally determined tissue, whilst the endosperm and the embryo development are the result of fertilization (Albert et al., 1997). A maternal effect on seed

Table 2. Observed segregation ratio of plants in different generation of cross OSC-593 X Amrit.

Possible genotype of light brown-seeded parents	Number of lines	Generation	Seed color			Ratio	x ²	P value
			Brown	Light brown	White			
<i>grgr[B_R_]vvii/ grgr[B_r_]vvii/ grgr[bbrr]vvii</i>	90	P1	-	-	90			
<i>GrGr[bbrr]vvII/ GrGr[bbR_]VVii/GrGr[B_R_]vvii</i>	90	P2	90	-	-			
F ₁	94	F ₁	-	-	94			
F ₁ (Reciprocal)	92	RF ₁	-	92	-			
F ₂	210	F ₂	120	74	16	9:6:1	0.94	5.991

Table 3. Observed segregation ratio of plants in different generation of cross Rama X VRI-1.

Possible genotype of light brown-seeded parents	Number of lines	Generation	Seed color				Ratio	x ²	P value
			Black	Dark Brown	Medium Brown	Light Brown			
<i>GrGr[B_R_]vvII/ GrGr[b_R_]V_II</i>	90	P1	-	-	90	-			
<i>GrGr[B_r_]VVii/ GrGr[B_r_]VVII</i>	90	P2	-	90	-	-			
F ₁	81	F ₁	-	-	81	-			
F ₁ (Reciprocal)	78	RF ₁	-	78	-	-			
F ₂	232	F ₂	132	39	45	16	9:3:3:1	0.68 7.815	

Table 4. Observed segregation ratio of plants in different generation of cross Tilottama X NIC-8316.

Possible genotype of light brown-seeded parents	Number of lines	Generation	Seed color			Ratio	x ²	P value
			Medium Brown	light Brown	Beige			
<i>GrGr[B_R_]vvII/ GrGr[b_R_]V_II</i>	90	P1	90	-	-			
<i>GrGr[bbrr]vvii</i>	90	P2	-	-	90			
F ₁	68	F ₁	68	-	-			
F ₁ (Reciprocal)	60	RF ₁	-	-	60			
F ₂	199	F ₂	106	78	15	9:6:1	0.99	5.991

Table 5. Observed segregation ratio of plants in different generation of cross Tilottama X Gujarat Til-2.

Possible genotype of light brown-seeded parents	No. of lines	Generation	Seed color		Ratio	x ²	P value
			Brown	White			
<i>GrGr[B_R_]vvII/ GrGr[b_R_]V_II</i>	90	P1	90	-			
<i>grgr[B_r_]vvii/ grgr[B_R_]vvii/ grgr[bbrr]vvii</i>	90	P2	-	90			
F ₁	89	F ₁	89	-			
F ₁ (Reciprocal)	74	RF ₁	-	74			
F ₂	237	F ₂	218	19	15:1	1.75	3.841

is not surprising since the supply of carbohydrates, nutrients and water provided by the plant to the developing seeds as well as the structure of the seed coat could affect seed development and deposition of reserve (Bewley and Black, 1994). Segregation for seed coat can be determined only by advancing the progenies an

additional generation (Liu et al., 2005). Reciprocal crosses was performed in order to confirm the pigment accumulation in maternal tissue. The present study did not deviate from earlier observation of crosses and so, irrespective of the crosses, seed coat colour of F₁ was determined by the seed colour of the female parent.

Table 6. Observed segregation ratio of plants in different generation of cross Uma X TKG-352.

Possible genotype of light brown-seeded parents	Number of lines	Generation	Seed color		Ratio	χ^2	P value
			Beige	White			
<i>GrGr[bbrr]jvii</i>	90	P1	90	-			
<i>grgr[bbrr]jvii/ grgr[B_r_]jvii/ grgr[B_R_]jvii</i>	90	P2	-	90			
F ₁	93	F ₁	93	-			
F ₁ (Reciprocal)	96	RF ₁	-	96			
F ₂	443	F ₂	443	0	-	-	-

It is pertinent to discuss some of the genesis of variation of seed coat colour in crops. Flavonoids including anthocyanin play an important role in emending discernible colour variation (Mol et al., 1998). A similar finding has been reported in seed colour in sweet clover where, pigment of seed coat and the embryo interact for generating seed colour (Gorz. et al., 1975). Seed coat colour variation in bean is broadly controlled by production of flavonoids (Beninger et al., 1998). Modifying genes also interact with colour producing genes to express different colour combination and sometimes make hindrance for a definite conclusion (Beninger and Hosfield, 1999; Beninger et al., 1999). The study carried out by Ono et al. (2006), hinted that the lignan formation was developmentally regulated keeping with same pace with seed development and this also interfered in seed coat colour development. Sesamin, a major shareholder of lignan, is widely distributed in vascular plants, of *Sesamum* spp., but its biosynthesis and physiological roles are yet to be established. The recent findings of Zhang et al. (2013) have further confirmed the presence of two major genes in seed coat colour inheritance, though all seed colors were not included in the study. The present investigation disclosed the involvement of two genes in the production of pigments and two other additional genes as modifier genes. A number of genotypes may give rise to the same phenotypes by following the present genetic model. Bedigian (2010) and Falusi (2007) reported earlier similar kind of observation.

Presently, somewhat unique finding was obtained so far as beige colored seed was concerned, as the colour has inhibitory effect on other colors, whatever the genetic constitution may be. Genetic structure of seed coat colour and identification of candidate gene through QTL or association mapping may not lead to precise definition of genes unless functional genomics studies are also not involved (Zhang et al., 2013). However, Plant breeders would like to get benefit of developing new varieties of commercially important seed coat colour by utilizing the information of genetics and desired goal is expected to be achieved through conventional breeding program.

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