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RESEARCH ARTICLE

Development and genetic analysis of conspicuous purple coloured corolla lip flower with multicapsules genotype in sesame (*Sesamum indicum* L.)

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Abstract. The present investigation was framed to understand the genetics and development of conspicuous purple coloured corolla tip flower and multicapsules at axil in sesame (*Sesamum indicum* L.) from the cross between genotypes IC-205776 (♀) × EC-118591 (♂). The conspicuous corolla lip colour is recessive in expression and under digenic control, differing from the earlier reports. The ratio at F_2 generation was best fit for 13:3 indicating inhibitory gene action for purple corolla lip colour. Among two genes, one acts as an inhibitory gene at recessive condition to produce conspicuous purple corolla lip colour. Multicapsules/axil is dominant in expression, controlled by more than one gene. The ratio of multiple capsules/axil and single capsules/axil at F_2 generation was the best fit for the ratio 11:5 indicating dominance modification of duplicate genes for a number of capsules per axil. Single capsule/axil results due to dominance modification of duplicate genes where the homozygous condition of one gene reverses the dominance relation of another gene in heterozygous condition. Joint segregation analysis indicated independent segregation of corolla lip colour and capsule number per axil.

Keywords. inheritance; conspicuous; flower lip; colour; multicapsules; sesame.

Introduction

Sesame (*Sesamum indicum* L.) is an Indian origin oilseed crop cultivated in tropical and sub-tropical regions which belong to the genus *Sesamum* and the family Pedaliaceae. Sesame is being cultivated and consumed in India since time immemorial for its nutrition rich seed as well as high quality edible oil. India has a rich diversity housed in six wild species, namely *S. malabaricum*, *S. mulayanum*, *S. alatum*, *S. latiniatum*, *S. prostratum* and *S. radiatum*, along with cultivated sesame (Joshi 1961; Bhat *et al*. 1999). It is evident from several studies (Bedigian 2003, 2014) that domestication of *S. indicum* occurred on the Indian subcontinent. The broad spectrum of genetic diversity in sesame crop found in the country can be attributed to its genome plasticity to adopt in any given environment. As a result, a wide range of morphological variants is found in specific ecological region of cultivation. The morphological characters like branching pattern, flower colour, corolla lip colour, pubescence (on a stem, leaves, flowers and capsules), capsule number per axil, seed coat colour were found to be stable across the environment (Bedigian *et al*. 1986; Pandey *et al*. 2015; Ramya *et al*. 2020). Therefore, these characters serve as morphological markers for breeders who help in the selection process. Understanding the inheritance pattern of these characters is necessary to utilize these traits as morphological markers. Genetics of morphological characters like stem and capsule pubescence (Yol and Uzunn 2011), lobed basal leaves were studied (Venkataramana Rao *et al*. 2012) which indicates monogenic inheritance. Agronomic traits like branching pattern, capsules number per plant, seeds per capsules, test weight, capsule length and oil content indicate that these characters are controlled

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by more than two genes (Sumathi and Muralidharan 2010).

The sesame flowers develop in the leaf axil with small pedicels; they are bisexual, zygomorphic, with tubular and campanulate corolla with five petals. The lower petal is longer than other petals which are known as lip. The colour of the lip is different from interior or exterior corolla tube and other petal colour. The colour of the lip varies from white to different shades of purple. According to Bedigian (2014), *S. malabaricum* a progenitor of *S. indicum* possess the characteristic feature of a pink flower with a conspicuous dark purple in the lower lip of the corolla. Pink flower with a conspicuous purple colour in the lower lip of the corolla as per the descriptors of IPGRI and NBPGR 2004 is one of the distinct characteristic found in wild species and traditional cultivars in India (Loknathan *et al*. 1993). This attractive trait with the purple lower lip of the corolla can serve as a morphological marker during developing elite cultivars.

Capsule number per plant is an important character that has a direct and positive effect on increased seed yield. Therefore, an increasing number of capsules per plant is one of the main objectives of the breeding programme. One of the approaches to increase the number of capsules is through promoting additional capsules at each axil. The number of capsules at each axil may vary from two to six (Bedigian *et al*. 1986; Morris 2009). Genotypes bearing more number of capsules at each axil have a yield advantage (Baydar 2005) compared to genotypes with single capsules. Cultivated varieties in China, Korea and elsewhere are predominated with multicapsules at each leaf axils on single stem plants (Morris 2009). An increasing number of capsules per plant is one of the important ways for increasing production as the trait has a direct effect on seed yield (Ranganatha *et al*. 2012; Monpara *et al*. 2019). Genotypes with additional capsules per leaf axil are needed, since theoretically, plants bearing more than one capsules at each axil will add to more number of capsules per plant than one capsule in each leaf axil, which consequently would result in more seed yield. Multiple flowers at axil with attractive conspicuous purple-lipped corolla flowers manifesting to multiple capsules at axils are not available among Indian germplasm. To develop a distinct elite genotype having multiple flowers at axil with an attractive purple colour in the lower lip of the corolla giving multicapsules, a cross between two diverse genotypes were attempted. A landrace IC-205776 from Rajasthan state was crossed with an exotic line EC-118591 was made. In this article, genetics of a conspicuous purple lip of corolla and multicapsules at axil is presented. A sound understanding of the characters and their genetic behaviour helps in practicing an appropriate breeding method, which helps in developing elite genotypes with desired traits.

Materials and methods

Development and evaluation of genetic material

In the present study, the female parent, a landrace from Rajasthan IC-205776 of *S. indicum* is characterized by pink colour flowers with conspicuous purple colour lip (similar to those present in wild-type *S. mulayanum)*, single flowers at each axil and produced single capsules per node with brown seed (figure 1, a&b). The male parent is an exotic line EC-118591, characterized by white flowers with white lip and multiple flowers at each axil (three flowers) resulting in multicapsules with brown seed (figure 1, c&d). Parents were raised during summer 2018 at the experimental farm of ICAR-Indian Institute of Oilseeds Research, Hyderabad (situated at 17°15' N latitude and 78°18' E longitude at an altitude of 542 m above mean sea level) characterized with red sandy loam type of soil. Mature flower buds of IC-205776 (♀) were tagged with threads and anthers were removed by pulling out the corolla tube to which anthers are attached; a small piece of plastic straw was placed carefully to cover the stigma during the previous evening. Following morning (7–9 am IST) freshly dehisced pollen from EC-118591 (♂) were collected and dusted on the stigmatic surface of emasculated flowers of IC-205776 (♀) by removing the piece of plastic straw which was placed to cover the stigma. Mature capsules were harvested to collect F_1 seeds and sown during summer 2019, artificial selfing using glue method (Ramya *et al*. 2019) was taken up to ensure self-pollination. F_2 seeds were collected separately from each F_1 plant. Parents, F_1 and F_2s were raised during kharif 2019. The recommended package of practices with fertilizer applications (30 kg nitrogen, 20 kg phosphorus and 20 kg potash), timely weeding, irrigation, pest and disease management were taken up.

Statistical analysis

A total set of 528 F_2 plants were scored for corolla lip colour, number of flowers and capsules at each axil. A chi-square (χ^2) goodness of fit test was performed on the F_2 populations against theoretical segregation ratio using the formula: $\chi^2 = \Sigma(O - E)^2/E$, where O and E are the observed and expected values, respectively (Steel and Torrie 1980). Joint segregation analysis was performed to test the independent segregation of two characters under study.

Results and discussion

F_1 hybrid

All the F_1 plants derived from the cross between IC-205776 and EC-118591 produced white lip corolla with multiple capsules per axil (three to six capsules at each axil). The

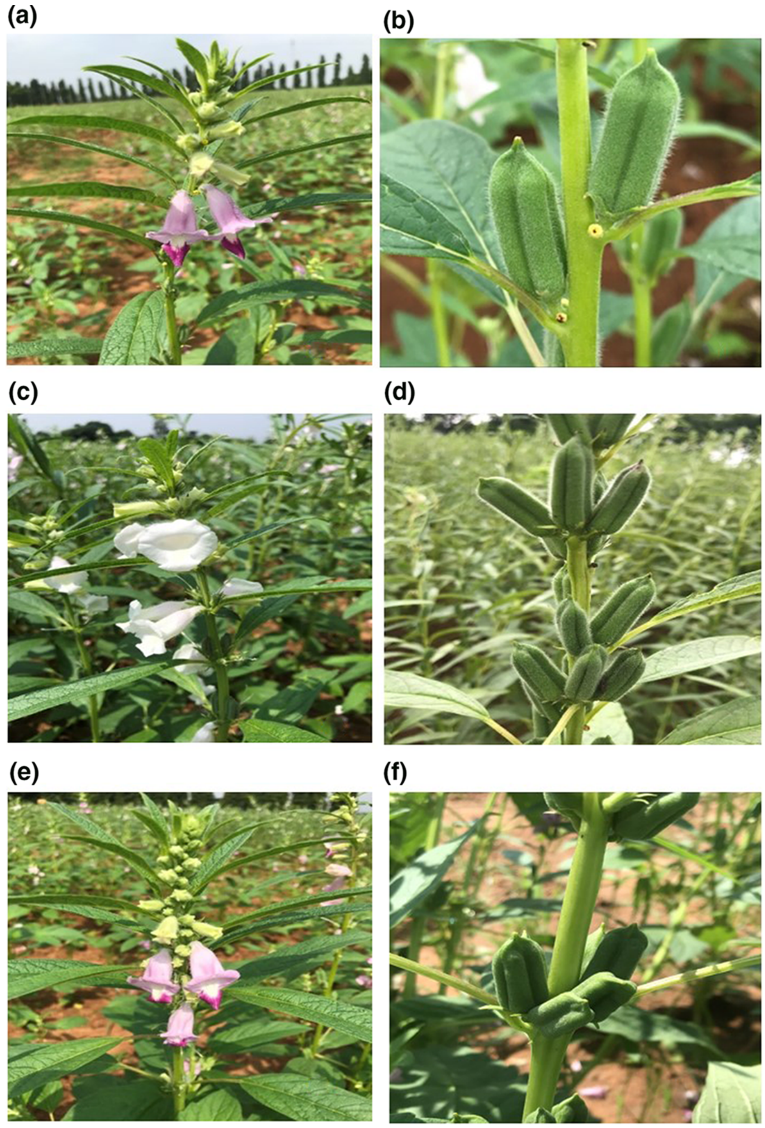

Figure 1. (a) Female parent IC-205776 single flower at axil with pink corolla and conspicuous purple colour on lower lip of corolla, (b) single capsule at axil (c) male parent (EC-118591) multiple flower at axil with colourless corolla and colourless lower lip of corolla, (d) multiple capsule at axil, (e) segregant plant in F_2 with multiple flower at axil having conspicuous purple colour on lower lip of corolla (f) multiple capsule/axil.

white lip of corolla is the typical character of any cultivated sesame and its expression in F_1 hybrid indicates that the character may be under the influence of dominant genes from the parent EC-118591. Pink flower with conspicuous purple colour in the lower lip of the corolla is one of the distinct characteristic of a wild species *S. malabaricum* progenitor of *S. indicum* (Bedigian 2014). Interspecific crosses with *S. malabaricum*; with *S. indicum* has resulted in hybrids with purple colour in the lower lip of the corolla (Prabakaran *et al*. 1995; Dasharath *et al*. 2007; Annapurna Kishore Kumar and Hiremath 2008). Dominant expression of the purple lip of corolla was observed in an interspecific cross between *S. mulayanum* Nair (syn. *S. malabaricum* Burm. or syn. *S. orientale* var. *malabaricum* Nar.) (Biswas and Mitra 1990; Tanaseka *et al*. 2012).

In the present study, the female parent IC-205776 is *S. indicum* having all the characteristics of cultivated type but with an exception of pink flower with the conspicuous purple lip of the corolla. The absence of purple colour in F_1 hybrids indicated that the parent does not carry dominant genes for the expression of purple colour. Expression of multiple capsules per axil in the F_1 hybrids indicated that this trait could be governed by dominant genes from the parent EC-118591.

F_2 generation

A total of 528 F_2 plants were scored for the lip colour of corolla and capsule number per plant. Independent segregation with a perfect classification of F_2 plants into four

Table 1. Segregation of purple lip colour of corolla in F_2 population.

Traits	Observed	Expected	Goodness of fit for 13:3
White lip of corolla	439	429	χ^2 =1.24; P=0.26 at 1 df
Purple lip of corolla	89	99	

Table 2. Segregation of capsule number per axil in F_2 population.

Traits	Observed	Expected	Goodness of fit for 11:5
Single capsule/axil	178	165	χ^2 =1.49; p=0.23 at 1 df
Multicapsule/axil	350	363	

classes, namely white lip corolla, multiple capsule/axil; white lip corolla, single capsule/axil; purple lip corolla, multiple capsule/axil; purple lip corolla, single capsule/axil gave an indication that the two characters under the study are independent to each other which may follow the digenic pattern of inheritance. The hypothesis was that the two characters may be governed by single set of genes segregating independently. Therefore, the data was tested for goodness of fit for a typical 9:3:3:1 ratio of F_2 plants. The significant chi-square value (χ^2 = 18.67 at P = 0.00002), indicated an absence of goodness of fit for the expected ratio and hence the hypothesis was rejected. The probable reason could be that multiple genes may govern the two characters with the possibility of interactions. Therefore, character wise analysis of inheritance is being presented under the study (tables 1 & 2).

Inheritance of purple lip colour of corolla

The conspicuous purple pigmentation on corolla lip in F_2 plants was found in 89 plants of 528 F_2 plants. A segregation ratio of 13:3 gave the best fit (table 1) indicating that the trait could be under the influence of multiple genes with inhibitory effect. There was no goodness of fit for the typical 3:1 ratio (χ^2 = 18.67, $P < 0.0002$). The dominant gene will produce purple pigmentation on corolla lip but another dominant inhibitory gene prevents the production of anthocyanin leading to a white corolla lip. Purple lip colour is expressed due to the synthesis of anthocyanin by a dominant gene when the other inhibitory gene is in a homozygous recessive state. Anthocyanins, which are a chemically diverse class of secondary metabolites, are responsible for colours in flowers and fruits. Studies (Freyre *et al*. 2015) on genetics and anthocyanin analysis of purple flower colour in *Ruellia simplex* (Mexican Petunia) shows that the purple colour is dominant over pink colour expressing at 3:1 F_2 ratio. The high performance liquid chromatography (HPLC) analyses of anthocyanin detected delphinidin derivatives are responsible for purple corolla colour, whereas pelargonidin derivatives are responsible for the pink corolla colour. Various studies have demonstrated that the pollinators rely strongly on flower colour to make their foraging decisions (Ômura and Honda 2005; Dötterl *et al*. 2014). Honey bee, which are the most common visitors of sesame flowers are mostly attracted to purple, violet and blue floral colours (Faegri and Van der Pijl 1979; Giurfa *et al*. 1995; Reverte *et al*. 2016). The conspicuous purple pigmentation on the corolla lip is a prominent descriptive trait of the wild species *S. malabaricum* and *S. mulayanum*. The accession IC-205776 is a landrace from Rajasthan, India, also has the characteristic conspicuous purple pigmentation on the corolla lip. Loknathan *et al*. (1993) has documented that some accessions of *S. indicum* in India were characterized with purple pigmentation on the lower lip of the corolla. These accessions were not utilized extensively in breeding and therefore, the genetics of purple pigmentation on corolla lip was not studied by many sesame workers. Monogenic inheritance with dominant expression (3:1) of the purple lip of corolla has been reported in an interspecific cross between *S. mulayanum* Nair and *S. indicum* (Biswas and Mitra 1990; Tanaseka *et al*. 2012). Hybridization between wild and cultivated species to transfer purple pigmentation of corolla lip may have disadvantageous due to deleterious linkages like dormancy (Tanaseka *et al*. 2012), low oil content, seed shattering etc. Exploiting the various accessions of *S. indicum* to transfer the trait of interest have the least or nil linkage effect and improvement of the trait of interest would be faster and effective. As the plants with conspicuous purple lip colour in the F_2 generation (figure 1, e&f) carry inhibitory recessive genes in homozygous condition, it is easy to fix this trait by selfing. This trait can serve as a morphological marker for identification and selection in segregating population. Also, sesame genotypes with the conspicuous purple lip colour will attract more honey bees that results in better seed set and therefore high yields (Sajjanar and Easwarappa 2015; Stein *et al*. 2017). An elite, high yielding variety with the conspicuous purple corolla lip colour is lacking in the list of available released varieties in India (Bisen *et al*. 2020). The population available from the cross IC-205776 x EC-118591 will be useful in developing elite lines with the unique trait of conspicuous purple colour corolla lip. The anthocyanin biosynthetic pathway is well studied in petunia, snapdragon, maize, rice etc. The variation in gene expression patterns, loss of function mutations, substrate specificities alterations contributed to the structural diversity of anthocyanins (Provenzano *et al*. 2014). Until date, no reports are available for studies on anthocyanins and genes involved in governing them in sesame crop. Nevertheless, the knowledge of genes and genetics of floral colour and the advantages of dark flowers are documented in other crops (Faegri and Van der Pijl 1979; Giurfa *et al*. 1995; Reverte *et al*. 2016). Therefore, the information generated and population developed from the present study can be used for further studies to understand the anthocyanin biosynthesis pathways and genes involved in sesame.

Inheritance of capsule number per axil

A total of 528 F_2 population derived from the cross between genotypes, IC-205776 (single capsule/axil) and EC-118591 (multicapsule/axil) were phenotyped for the number of capsules per axil. It was observed that the multiple capsules/axil are not found uniformly in all the axils due to flower drop even though multiple flowers were observed at all the axils. Similar observations were recorded by Rheenen (1981), where soil type and nutrition plays a crucial role in the development of multiple capsules/axil at the axil as the efficiency of the source (leaves) need to be more to support more number of sinks (capsules). Scoring for number of flowers/axil is appropriate in elucidating the genetics of capsule number per axil. In the F_2 generation, there were 350 plants with multiple capsules per axil and 178 single capsules per axil. The segregation ratio 11:5 gave the best fit (table 2) indicating that the trait is under the influence of two genes having dominance modification of duplicate genes. The observed numbers failed to fit the typical monogenic ratio 3:1 ($\chi^2 = 21.374$; $P < 0.00001$). In general, the dominant relationship between two alleles at a locus does not change, under the influence of a certain environment and in specific genetic background; the dominance relationship at some loci is affected by alleles at other loci (Singh 2007). Single capsules per node are produced due to interaction between two genes reciprocally may modify the dominance relationship at the other locus. The recessive homozygous condition of one gene reverses the dominance relationship at the other locus so that the genotypes Ca1ca1ca2ca2 and ca1ca1Ca2ca2 produces single capsule/axil similar to phenotype of the homozygous double recessive genotype (ca1ca1ca2ca2). Thus, the typical 15:1 ratio for duplicate gene action is modified as 11:5 due to the reciprocal dominance modification of ca1 and ca2. Fuchs *et al*. (1972) gave the genetic basis for an 11:5 dihybrid ratio, which was observed in *Gossypium hirsutum*. Aleurone layer colour in rice also follows 11:5 ratio for dark red and light yellow colour (Singh *et al*. 2017). Radial fruit cracking resistance in tomato is controlled by two genes, which segregate in 11:5 ratios in F_2 population (Mustafa *et al*. 2019). Studies by Yol and Uzun (2011) indicated monogenic dominance of a single capsule at an axil was dominant over multiple capsules per axil and a 3:1 segregation ratio in the F_2 in a cross between a cultivar from Turkey and exotic accession. Since the genetics of traits depends on the genetic architecture of the parents, contrasting results from different studies could be expected.

Multiple capsules (three to six capsules/axil) are reported in many genotypes and germplasm accession. Indian sesame cultivars GT-4, GTJ-5, RT-351 etc. are popular cultivars exhibiting multicapsules/axil. Baydar (2005) proposed breeding for additional capsules per axil, will increase the number of capsules/plant, which is advantageous to increase seed yield per plant. High yield potential in multicapsules genotypes should be assessed because they appear to be ideal for improving seed yield nonetheless trait is highly sensitive to the environment. Multicapsule at axil is a result of dominance modification of duplicate genes. Multicapsules will certainly have a yield advantage under favourable environmental conditions over single capsules.

Independent segregation of corolla lip colour and capsule number per axil

In this study, the hypothesis of independent assortment of the Mendelian ratio of 9:3:3:1 was rejected, since the characters studied were governed by different genes with interaction. Conspicuous purple corolla lip colour is a recessive character controlled by two genes, with an inhibitory gene interaction following the ratio of 13:3 (white lip: purple lip colour). Multicapsule/axil is a dominant character and segregates in 11:5 (multiple capsules: single capsules) ratio which indicated dominance modification of duplicate genes. In this study, to test the independent segregation of two characters under study, joint segregation analysis was performed for corolla lip colour and capsule number per axil (table 3). In joint

Table 3. Joint segregation analysis of corolla lip colour and capsule number per axil in IC-205776 × EC-118591 F_2 population.

Phenotype	White lip corolla with multicapsules /axil	White lip corolla with single capsule/axil	Purple lip corolla with multicapsules /axil	Purple lip corolla with single capsule/axil	χ^2 Value
Observed number of plants	290	149	60	29	2.82 (*P*-value = 0.42)
Expected number of plants	294.94	134.06	68.06	30.94	
Expected ratio	143	65	33	15	
Expected genotypic combinations	ppIIC1C1C2C2 (parent) $P\_I\_C_1\_C_2\_$ $ppI\_C_1\_C_2\_$ $ppiiC_1\_C_2\_$	$P\_I\_C_1c_1c_2c_2/c_1C_1c_2c_2$ $ppI\_c_1c_1C_2c_2/c_1c_1c_2C_2$ $ppiic_1c_1c_2c_2$	$P\_ii\ C_1\_C_2\_$ $P\_iiC_1C_1c_2c_2$ $P\_iic_1c_1C_2C_2$	$PPiic_1c_1c_2c_2$ (parent) $P\_iiC_1c_1c_2c_2/c_1C_1c_2c_2$ $P\_iic_1c_1C_2c_2/c_1c_1c_2C_2$ $P\_iic_1c_1c_2c_2$	

segregation analysis, the observed phenotypic ratio for four phenotypes, namely white corolla lip with multiple capsules, white corolla lip with single capsules, purple corolla lip with multiple capsules and purple corolla lip with single capsules was in fit with expected phenotypic ratio (143:65:33:15), (χ^2 =2.83, *P*=0.42), which indicated that corolla lip colour and capsule number per axil segregate independently. Considering independent segregation of two traits under study and their inheritance pattern probable genotypes for four classes of phenotypes were worked out. The Punnett square table for all possible genotypic combinations worked out for four phenotypes, namely white corolla lip with multiple capsules, white corolla lip with single capsules, purple corolla lip with multiple capsules and purple corolla lip with single capsules is provided in table 1 in electronic supplementary at http://www.ias.ac.in/jgenet/. The probable genotypes worked out for the four classes of phenotypes are given in table 3. The above ratio may vary depending on allelic configurations at the loci of the parents selected. The selection of parents with homozygous loci for the trait studied is crucial to work out the inheritance pattern. In this study, the parents were homozygous for the contrasting characters for obtaining the given results (table 3).

Multiple flowers at axil with attractive conspicuous purple-lipped corolla flowers are not available among Indian germplasm (Bisht *et al*. 1998, 2004). In the present population of 528 plants developed from cross IC-205776 x EC-118591, 60 plants were isolated for multiple flowers at axil with conspicuous purple colour corolla lip flowers producing multiple capsules/axil (figure 1, e&f). Identifying and selecting plant types with synchronous flower maturity at axil is necessary to manifest into multicapsules at every axil for higher productivity. The knowledge of gene actions of characters help in a thorough understanding of the inheritance of the characters. Further, genes linked with these traits can be identified through advance molecular mapping strategy using the population developed in this study.

In conclusion, a distinct genotype bearing pink coloured multiple flowers at axil with an attractive conspicuous purple-lipped corolla and yielding multiple capsules per axil were developed. The genetics of the purple colour of corolla and multiple capsules per axil indicated that the two characters are controlled by two sets of genes, which are independent in expression and genetic control. The results of the study showed that the conspicuous corolla lip colour and multicapsules at axil is a recessive character deviating from the earlier reports since different parents were used in the studies. Corolla lip colour is controlled by two genes, an inhibitory gene interaction resulting in the production of conspicuous purple corolla lip colour. Multicapsule/axil is a dominant character and segregates in an 11:5 ratio which indicated dominance modification of duplicate genes. Joint segregation analysis indicated that there is no linkage between corolla lip colour and capsule number per axil. The novel lines developed in this study with pigmented corolla and multiple capsules would serve as indicators for selection and improved yield in sesame.

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