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Research article

Inheritance, heritability and association of agronomic traits and sesamin and sesamolin contents in sesame (*Sesamum indicum* L.)

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Abstract

Although many research reports provide information on the gene action of agronomic traits, such basic information is still inadequate for the sesamin and sesamolin contents. The current study determined the gene effects that control agronomic traits and the sesamin and sesamolin contents, estimated the heritability of those traits and investigated the correlations and path analysis among the traits studied. Two crosses, MKS-I-84001 × White UB2 and White UB2 × Kanchanaburi, were made among three parents to generate six populations. All generations were planted in a randomized complete block design with three replications at Kalasin University, Thailand. Genetic analysis showed that the dominance gene effect significantly controlled the inheritance of sesamin. The additive × dominance interaction effects provided a major contribution to the inheritance of the sesamolin content while grain yield/plant was mainly controlled by dominance × dominance interaction effects. The sesamin and sesamolin contents showed low and moderate heritability, respectively. The sesamin and sesamolin contents had significant negative correlations with capsules/plant (correlation coefficient [r] = -0.55 [$p < 0.01$] and -0.41[$p < 0.05$], respectively), 1,000 grain weight (r = -0.54 [$p < 0.01$] and -0.59 [$p < 0.01$], respectively) and grain yield/plant (r = -0.51[$p < 0.01$] and -0.35 [$p < 0.05$], respectively). Path analysis showed that the 1,000 grain weight had the highest negative direct effect on the sesamin (-0.42) and sesamolin (-0.60) contents followed by capsules/plant. Information on the gene action and heritability of sesamin and sesamolin can be used for choosing a suitable breeding method, and information on the correlation can be utilized as a criterion to select those traits through agronomic traits.

Introduction

Sesame (*Sesamum indicum* L.) is traditional, high value health food in Asian and African countries (Dossa et al., 2018). The genus *Sesamum* comprises 35 recognized species of which *S. indicum* L. is cultivated extensively (Pathak et al., 2014). During the last 20 years, the world production of sesame seeds had substantially increased from 2.82 million t in 1996 to 6.11 million t in 2016 (FAOSTAT, 2018). Sesame is mostly grown in Africa and Asia; in 2016, the world top sesame producer was Tanzania with 0.94 million t, followed by Myanmar (0.81 million t) and India (0.79 million t) (FAOSTAT, 2018). Sesame seeds are rich in oil (57−63%), which contains high levels of unsaturated fatty acids mainly oleic and linoleic, rich in protein (23−25%) containing large amounts of methionine and tryptophan, and the seeds are also rich in micronutrients (Hassan et al., 2018). Sesame seeds contain a class of unusual compounds known as lignans, which comprise sesamin and sesamolin (Wu, 2007). They have multiple physiological functions, such as anti-carcinogenic activity

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(Yokota et al., 2007), anti-inflammatory and immunomodulatory functions (Hsu et al., 2005; Nonaka et al., 1997), anti-hypertensive activity (Nakano et al., 2008) and neuroprotective effects against hypoxia or brain damage (Cheng et al., 2006). Due to these desirable properties, there is growing interest in the use of sesame seeds and products in many food and pharmaceutical applications (Hassan et al., 2018).

Nowadays, people have become increasingly interested in healthy foods, so plant breeding for higher nutrient value is necessary to satisfy the consumer need. Generally, sesame breeding programs have mostly focused on crop production capacity and high oil content, but the functional activities of lignan in sesame have become a major interest (Rangkadilok et al., 2010). Therefore, sesame breeding to increase the sesamin and sesamolin contents in sesame seed should be undertaken because it will be beneficial to both consumers and various industries such as food and cosmetics. Generation mean analysis provides information on the relative importance of average effect of the genes (additive effects), dominance deviations and effects due to non-allelic genetic interactions in determining genotypic values of the individuals and consequently, mean genotypic values of families and generations (Said, 2014). This information can be utilized for choosing a suitable breeding method, which allows plant breeders to achieve their goals (Kumar and Genesan, 2004). Sharmila et al. (2007) reported that the yield of sesame is mainly controlled by dominance and epistatic gene effects. Although many research studied have reported on knowledge of the gene action of the agronomic traits of sesame, there is still a lack of basic information on the gene action of sesamin and sesamolin in sesame seed.

The heritability of interested traits is an important factor in plant breeding because it reflects possible genetic contributions to a population's phenotypic variance. Ogata and Kato (2016) reported that sesamin and sesamolin exhibited high heritability. However, the heritability of lignans estimated based on the formula of Burton (1951) has never been reported, and this information depends on the population and environment that have been used. Understanding the association between interested traits is crucial for the selection process and this association can be described using correlation and path coefficient analysis. Path analysis provides more information than a simple correlation matrix because it illustrates the partitioning of the direct effects and the indirect effects from the total effect, providing a more realistic relationship of the traits, and helps in effective selection (Sumathi and Muralidharan, 2007). Very few reports have provided information on correlation and the path coefficient of agronomic traits with sesamin and sesamolin contents in sesame.

Therefore, this study estimated the gene effect in controlling the inheritance of agronomic traits, sesamin and sesamolin contents, estimated the heritability of those traits and examined the association between agronomic traits with the sesamin and sesamolin contents in sesame.

Materials and Methods

Plant materials

Three pure lines (MKS-I-84001, White UB2 and Kanchanaburi) with differences in yield components, seed size and color were used as genetic materials in this study. White UB2 is a pure line with a large grain size, white grain color, good adaptability and high yield. MKS-I-84001 and Kanchanaburi are pure lines with a small grain size and a black grain color. The F_1 hybrids were generated by crossing between MKS-I-84001 × White UB2 and White UB2 × Kanchanaburi in a field of the Division of Plant Production Technology, Kalasin University in the early rainy season (March–July 2016). The F_1 generation plants were self-pollinated to produce F_2 seeds and were back-crossed to both parental lines to generate backcross populations (BC_1P_1 and BC_1P_2) in the late rainy season (October 2016 – January 2017).

Field management

The six populations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) for each cross were planted in a randomized complete block design with three replications in the early rainy season (March–July 2017) in a field of the Division of Plant Production Technology, Kalasin University. The experimental units had varying number of rows, depending on the genetic uniformity of each generation. For the non-segregating generations including P_1 (MKS-I-84001 and White UB2), P_2 (White UB2 and Kanchanaburi) and F_1 each plot contained three rows/plot while the F_2 generations were planted with six rows/plot and the backcross generations were planted with five rows/plot. Each row was 3 m long, with 10 cm spacing between plants and 50 cm between rows. Recommended practices for production of sesame were followed and plant protection was performed uniformly for all generations during the experiment. Branches/plant, length of capsule, capsules/plant, 1,000 grain weight and grain yield/plant were recorded. The sesamin and sesamolin contents were analyzed. Data on agronomic traits was collected from 12 plants/plot for the non-segregating populations (P_1, P_2 and F_1) and the backcross and F_2 populations consisted of 30 and 40 plants/plot, respectively. For sesamin and sesamolin contents, we collected data from 10 plants/plot for the non-segregating population while backcrosses and F_2 consisted of 20 and 30 plants/plot, respectively.

Sample extraction for sesamin and sesamolin determination

Seed samples were extracted according to the method described by Rangkadilok et al. (2010) with slight modifications. Briefly, 10 g of each sample was ground into powder and weighed (0.4 g) into 15 mL plastic tubes. Then 80% methanol (5.0 mL) was added and the whole sample was extracted for 30 min. Each sample was then centrifuged at 2,000×g, for 3 min at 25°C. The supernatant was transferred into a 10 mL volumetric flask and the residue was re-extracted with 4.0 mL of 80% methanol. All extracted solutions were combined and volume adjusted using 80% methanol before filtering through a 0.45 µm nylon membrane followed by analysis using high-performance liquid chromatography (HPLC).

High-performance liquid chromatography analysis for sesamin and sesamolin

The HPLC analysis of the sesamin and sesamolin contents was performed using a Shimadzu SPD-M20A with a diode array detector. A reversed-phase column, Inertsil ODS-3 C_{18} 5 µm, 4.6 × 250 mm (GL Sciences Inc.; Japan) was used in this study. The solvent and gradient elution conditions used were as described by Rangkadilok et al. (2010) with slight modifications. The mobile phase consisted of water (solvent A) and methanol (Merck, KGaA; Germany) (solvent B) at a flow rate of 1 ml/min. Gradient elution was performed as: 0−5 min, 5−18% solvent B; 5−10 min, 18−35% solvent B; 10−15 min, 35−62% solvent B; 15−20 min, 80% solvent B; 20−25 min, 80% solvent B; and 25−30 min, 80−5% solvent B. Operating conditions were as: column temperature 25°C, injection volume 20 µL and detection at 280 nm. The standards for sesamin and sesamolin used in this study were purchased from Sigma-Aldrich. Sesamin and sesamolin in samples were identified by comparing their relative retention times with those of standard compounds.

Statistical analysis

Analysis of variance was carried out for agronomic traits and the sesamin and sesamolin contents based on a randomized complete block design. Duncan's new multiple range test was used to compare means at the 0.05 probability level. The presence of non-allelic interactions was tested using the joint scaling test (Cavalli, 1952) and a t-test was used to detect whether A, B and C were significantly different from zero. Genetic effects were estimated using a model suggested by Mather and Jinks (1982). Broad sense heritability was computed according to Burton (1951). Correlation and path coefficient analysis were computed according to Dewey and Lu (1959).

Results

Differences among parental lines and crosses

Analysis of variance revealed significant differences among parental lines and crosses for almost all traits except for capsules/plant in the MKS-I-84001 × White UB2 cross (Table 1). There were significant differences in branches/plant, length of capsule, 1,000 grain weight and grain yield/plant between parental lines in the MKS-I-84001 × White UB2 cross while capsules/plant, sesamin and sesamolin contents were not significantly different between parental lines. The White UB2 had significantly greater length of capsule, 1,000 grain weight and grain yield/plant than the MKS-I-84001. For the White UB2 × Kanchanaburi cross, significant differences were detected among the parental lines for almost all traits studied except capsules/plant. The agronomic traits of this cross seemed like previous crosses, for which the yield components of the White UB2 were significantly higher than for the Kanchanaburi parents. The highest sesamin (2.32 mg/g grain) and sesamolin (1.30 mg/g grain) contents were recorded for the Kanchanaburi sample, which had significantly more sesamin and sesamolin contents than the White UB2.

Length of capsule, capsules/plant, 1,000 grain weight and grain yield/plant of the F_1 generation in both crosses seemed higher than for the mid-parent, but the sesamin and sesamolin contents of the F_1 generation plants in both crosses were lower than for the mid-parent. The F_1 generation had the lowest content for sesamin in both crosses (1.69 and 1.63 mg/g grain, respectively). The sesamin content of the F_1 generation of the MKS-I-84001 × White UB2 cross was significantly different from the MKS-I-84001 parent, but not significantly different from the White UB2. The sesamolin content of the F_1 generation of the MKS-I-84001 × White UB2 cross was not significantly different from its parents. The sesamolin content of the BC_1P_2 generation was significantly greater than for the BC_1P_1 generation for this cross. In addition, the sesamin and sesamolin contents of the F_1 generation of the White UB2 × Kanchanaburi cross were significantly lower than for the Kanchanaburi parent, but not significantly different from the White UB2.

The segregation pattern of the F_2 population did not fit either a single or two gene model, but instead had a continuous distribution of the sesamin and sesamolin contents in sesame seed (Fig. 1 and 2). Therefore, these traits were assumed to be controlled polygenically.

Gene action

The scaling test (A, B and C) was significant for almost all traits studied except the sesamin content in both crosses, and the branches/plant and capsules/plant in the MKS-I-84001 × White UB2 cross (Table 2). The additive gene effect was significant for length of capsule in both crosses, but dominance and epitasis effects were more important. Therefore, the selection of this trait in an early generation using a pedigree method may not be effective although there is an additive gene effect. The dominance gene effect was significant for capsules/plant in both crosses. For the 1,000 grain weight, both crosses showed significant dominance and additive × dominance interaction effects, but only the MKS-I-84001 × White UB2 cross had significant additive × additive interaction effects. This may have indicated transgressive segregation that produced some genotypes that have never appeared in the parent generation. Dominance × dominance interaction effects were significant for grain yield/plant in both crosses. The results obtained for sesamin content from the three-parameter model revealed that the dominance gene effect was significant in both crosses. The sesamolin content of both crosses showed significant additive × dominance interaction effects, but only the MKS-I-84001 × White UB2 cross showed significant additive gene effect and the White UB2 × Kanchanaburi cross showed significant additive × additive interaction effects (Table 2). These results showed clearly that the important yield components and lignan are mainly controlled by dominance or epitasis gene effects. The selection of these traits in the early generation may not be effective because traits controlled by those are unstable and the traits that have been selected in the early generation may disappear in a later generation.

Table 1 Mean values of agronomic traits and sesamin and sesamolin contents in six populations of two sesame crosses

Population	Branches/plant	Length of capsule (cm)	Capsules/plant	1,000 grain weight (g)	Grain yield/plant (g)	Sesamin (mg/g grain)	Sesamolin (mg/g grain)
C-I							
P_1 (MKS-I-84001)	3.08 ± 0.21^{a}	2.43 ± 0.05^{c}	49.79 ± 3.77	2.82 ± 0.06^{c}	3.03 ± 0.26^{c}	2.06 ± 0.12^{a}	0.72 ± 0.03^{ab}
P_2 (White UB2)	1.49 ± 0.30^{b}	2.88 ± 0.05^{a}	63.25 ± 5.05	3.34 ± 0.04^{a}	5.88 ± 0.49^{ab}	1.89 ± 0.14^{abc}	0.60 ± 0.02^{ab}
F_1	2.11 ± 0.27^{ab}	2.89 ± 0.03^{a}	72.08 ± 5.12	3.18 ± 0.04^{ab}	7.98 ± 0.57^{a}	1.69 ± 0.12^{c}	0.60 ± 0.02^{ab}
F_2	2.25 ± 0.15^{ab}	2.51 ± 0.03^{bc}	65.11 ± 3.45	2.96 ± 0.04^{bc}	4.95 ± 0.35^{bc}	1.79 ± 0.10^{bc}	0.62 ± 0.02^{ab}
BC_1P_1	2.48 ± 0.16^{ab}	2.45 ± 0.03^{bc}	61.66 ± 3.44	3.05 ± 0.03^{bc}	4.66 ± 0.32^{bc}	1.80 ± 0.08^{bc}	0.58 ± 0.03^{b}
BC_1P_2	1.56 ± 0.16^{b}	2.59 ± 0.02^{b}	59.77 ± 3.20	3.06 ± 0.03^{bc}	4.79 ± 0.28^{bc}	2.01 ± 0.11^{ab}	0.74 ± 0.03^{a}
Mid-parent	2.29	2.66	56.52	3.08	4.46	1.98	0.66
C-II							
P_1 (White UB2)	1.57 ± 0.31^{c}	2.90 ± 0.03^{a}	60.17 ± 4.20^{b}	3.30 ± 0.05^{a}	6.53 ± 0.52^{ab}	1.86 ± 0.14^{b}	0.63 ± 0.04^{c}
P_2 (Kanchanaburi)	3.29 ± 0.30^{a}	2.54 ± 0.04^{c}	42.00 ± 3.76^{b}	2.66 ± 0.02^{b}	3.56 ± 0.44^{c}	2.32 ± 0.21^{a}	1.30 ± 0.05^{a}
F_1	2.97 ± 0.27^{ab}	2.81 ± 0.04^{ab}	85.33 ± 6.45^{a}	3.21 ± 0.03^{a}	7.84 ± 0.38^{a}	1.63 ± 0.14^{b}	0.76 ± 0.04^{bc}
F_2	2.21 ± 0.17^{bc}	2.63 ± 0.03^{bc}	52.12 ± 2.79^{b}	3.07 ± 0.04^{a}	4.14 ± 0.28^{bc}	1.69 ± 0.10^{b}	0.75 ± 0.04^{bc}
BC_1P_1	1.65 ± 0.16^{c}	2.73 ± 0.03^{abc}	57.83 ± 2.62^{b}	3.15 ± 0.05^{a}	5.42 ± 0.32^{abc}	1.90 ± 0.11^{b}	0.84 ± 0.03^{bc}
BC_1P_2	1.88 ± 0.15^{c}	2.65 ± 0.03^{bc}	50.72 ± 2.38^{b}	3.08 ± 0.04^{a}	4.05 ± 0.24^{bc}	1.97 ± 0.14^{ab}	0.90 ± 0.03^{b}
Mid-parent	2.43	2.72	51.08	2.98	5.05	2.09	0.97

C-I = MKS-I-84001 × White UB2; C-II = White UB2 × Kanchanaburi; $BC_1P_1 = F_1 \times P_1$; $BC_1P_2 = F_1 \times P_2$
mean ± SD in the same column with different lowercase superscripts are significantly different ($p < 0.05$).

Table 2 Joint scaling test and estimates of gene effects of agronomic traits and sesamin and sesamolin contents in two crosses of sesame

Trait	Cross	A	B	C	*m*	[*d*]	[*h*]	[*i*]	[*j*]	[*l*]
BP	C-I	-0.24 ± 0.47	-0.49 ± 0.52	0.21 ± 0.88	$2.23 \pm 0.16^{**}$	$0.85 \pm 0.14^{**}$	-0.21 ± 0.31	–	–	–
	C-II	$-1.23 \pm 0.53^{*}$	$-2.51 \pm 0.50^{**}$	$-1.97 \pm 0.97^{*}$	$2.02 \pm 0.11^{**}$	-0.22 ± 0.22	-1.23 ± 0.88	-0.61 ± 0.33	$0.86 \pm 0.22^{**}$	$4.01 \pm 0.97^{**}$
LC	C-I	$-0.41 \pm 0.08^{**}$	$-0.57 \pm 0.07^{**}$	$-1.06 \pm 0.15^{**}$	$2.52 \pm 0.02^{**}$	$-0.20 \pm 0.03^{**}$	$0.23 \pm 0.05^{**}$	0.07 ± 0.14	0.08 ± 0.05	$1.01 \pm 0.11^{**}$
	C-II	$-0.25 \pm 0.08^{**}$	-0.05 ± 0.08	$0.55 \pm 0.17^{**}$	$2.72 \pm 0.01^{**}$	$0.08 \pm 0.04^{*}$	0.06 ± 0.05	0.25 ± 0.16	$-0.10 \pm 0.05^{*}$	0.05 ± 0.23
CP	C-I	1.44 ± 9.38	-15.78 ± 9.62	3.22 ± 18.32	$54.99 \pm 2.79^{**}$	-3.82 ± 2.60	$15.07 \pm 5.53^{**}$	–	–	–
	C-II	$-29.84 \pm 9.31^{**}$	$-25.89 \pm 8.85^{**}$	$-64.37 \pm 17.96^{**}$	$53.55 \pm 1.50^{**}$	$8.68 \pm 2.36^{**}$	$34.24 \pm 7.03^{**}$	8.63 ± 13.21	-1.98 ± 4.52	$58.61 \pm 15.3^{**}$
TGW	C-I	0.10 ± 0.10	$-0.41 \pm 0.09^{**}$	$-0.69 \pm 0.19^{**}$	$2.96 \pm 0.03^{**}$	-0.01 ± 0.05	$0.44 \pm 0.11^{**}$	$0.34 \pm 0.09^{**}$	$0.26 \pm 0.04^{**}$	-0.08 ± 0.27
	C-II	-0.20 ± 0.11	$0.29 \pm 0.09^{**}$	-0.10 ± 0.18	$3.10 \pm 0.02^{**}$	0.07 ± 0.06	$0.23 \pm 0.04^{**}$	0.18 ± 0.20	$-0.32 \pm 0.03^{**}$	-0.26 ± 0.30
GYP	C-I	-1.69 ± 0.90	$-4.28 \pm 0.93^{**}$	$-5.06 \pm 1.90^{**}$	$4.80 \pm 0.18^{**}$	-0.13 ± 0.42	2.63 ± 1.76	-0.91 ± 1.64	$1.43 \pm 0.28^{**}$	$3.31 \pm 1.29^{*}$
	C-II	$-3.53 \pm 0.91^{**}$	$-3.30 \pm 0.76^{**}$	$-9.20 \pm 1.52^{**}$	$4.54 \pm 0.16^{**}$	$1.47 \pm 0.28^{**}$	$2.80 \pm 0.51^{**}$	2.37 ± 1.38	-0.11 ± 0.52	$7.62 \pm 1.21^{**}$
SM	C-I	-0.15 ± 0.23	0.46 ± 0.28	-0.18 ± 0.49	$1.99 \pm 0.08^{**}$	-0.01 ± 0.07	$-0.30 \pm 0.14^{*}$	–	–	–
	C-II	0.31 ± 0.31	-0.02 ± 0.39	-0.67 ± 0.56	$2.06 \pm 0.11^{**}$	-0.17 ± 0.10	$-0.44 \pm 0.18^{**}$	–	–	–
SN	C-I	$-0.17 \pm 0.07^{*}$	$0.29 \pm 0.07^{**}$	-0.06 ± 0.11	$0.64 \pm 0.01^{**}$	$-0.16 \pm 0.04^{**}$	0.13 ± 0.13	0.18 ± 0.12	$-0.23 \pm 0.05^{**}$	-0.31 ± 0.20
	C-II	$0.28 \pm 0.09^{**}$	$-0.26 \pm 0.10^{**}$	$-0.45 \pm 0.20^{*}$	$0.79 \pm 0.02^{**}$	-0.06 ± 0.05	0.26 ± 0.20	$0.19 \pm 0.04^{**}$	$0.34 \pm 0.03^{**}$	-0.48 ± 0.28

BP = branches/plant; LC = length of capsule; CP = capsules/plant; TGW = 1,000 Grain weight; GYP = grain yield/plant; SM = sesamin; SN = sesamolin; C-I = MKS-I-84001 × White UB2; C-II = White UB2 × Kanchanaburi; *m* = mid-parent; [*d*] = additive effect; [*h*] = dominance effect; [*i*] = additive × additive gene interaction; [*j*] = additive × dominance gene interaction; [*l*] = dominance × dominance gene interaction
* significant different ($p < 0.05$) from zero; ** highly significant different ($p < 0.01$) from zero

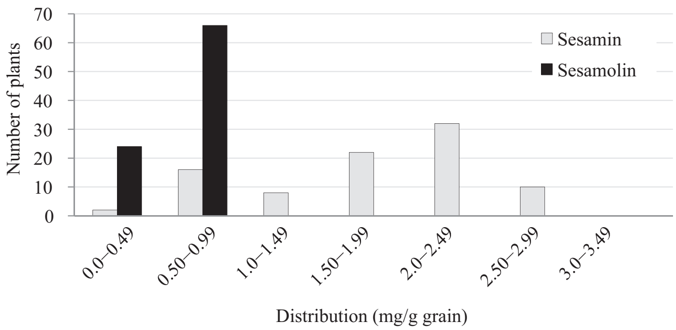

Fig. 1 Distribution of sesamin and sesamolin contents in F_2 population of the MKS-I-84001 × White UB2 cross

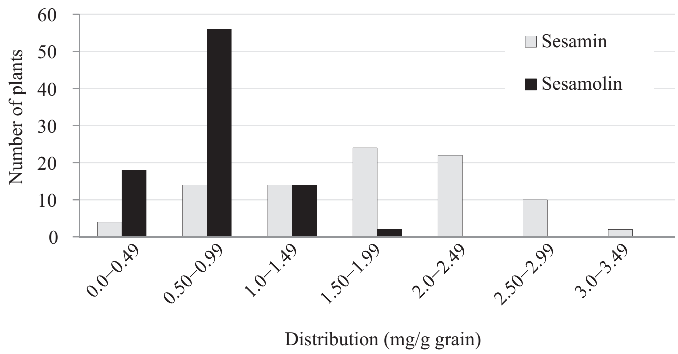

Fig. 2 Distribution of sesamin and sesamolin contents in F_2 population of the White UB2 × Kanchanaburi cross

Broad sense heritability

The estimate of broad sense heritability for agronomic traits and the sesamin and sesamolin contents are presented in Table 3. Branches/plant, the sesamin content in both crosses and capsules/plant for the White UB2 × Kanchanaburi cross exhibited low heritability, indicating that the expression of those traits was sensitive to the environment, with fluctuation of phenotype expression in each generation. In contrast, length of capsule and capsules/plant of the MKS-I-84001 × White UB2 cross, 1,000 grain weight, grain yield/plant and sesamolin content had moderate to relatively high heritability. Traits showing relatively high or high heritability indicated that the variance was more an effect of gene than environment.

Correlation and path coefficient analysis

Correlations among agronomic traits and the sesamin and sesamolin contents are presented in Table 4. Significant positive correlation was found between the sesamin with sesamolin content, indicating that breeding to increase the sesamin content will increase the quantity of sesamolin simultaneously. In contrast, the sesamin and sesamolin contents had significant negative correlations with capsules/plant, 1,000-grain weight and grain yield/plant and no significant correlation with branches/plant and length of capsule. The associations between the sesamin and sesamolin contents with agronomic traits were partitioned into direct and indirect effects based on path coefficient analysis (Tables 5 and 6). Path analysis indicated that the 1,000 grain weight and capsules/plant had a high negative direct effect on both the sesamin and sesamolin contents in sesame. The grain yield/plant had a high negative correlation with the sesamin and sesamolin contents, but its direct effect was low because most effects were indirect via the 1,000 grain weight and capsules/plant.

Table 3 Broad sense heritability of agronomic traits and sesamin and sesamin contents in two crosses of sesame

Trait	Broad sense heritability	
	MKS-I-84001 × White UB2	White UB2 × Kanchanaburi
Branches/plant	0.24	0.31
Length of capsule	0.56	0.68
Capsules/plant	0.56	0.19
1,000 grain weight	0.51	0.75
Grain yield/plant	0.63	0.47
Sesamin	0.40	0.22
Sesamolin	0.57	0.59

Table 4 Correlation coefficients among agronomic traits and sesamin and sesamolin contents of sesame

Trait	Branches/plant	Length of capsule	Capsules/plant	1,000 grain weight	Grain yield/plant	Sesamin	Sesamolin
Branches/plant	1.00	-0.44**	0.17	-0.48**	-0.03	0.05	0.26
Length of capsule		1.00	0.30	0.64**	0.63**	-0.32	-0.21
Capsules/plant			1.00	0.48**	0.70**	-0.55**	-0.41*
1,000 grain weight				1.00	0.61**	-0.54**	-0.59**
Grain yield/plant					1.00	-0.51**	-0.35*
Sesamin						1.00	0.71**
Sesamolin							1.00

* significant different ($p < 0.05$); ** highly significant different ($p < 0.01$)

Table 5 Path analysis showing direct and indirect effects of agronomic traits on sesamin content in sesame

Trait	Direct effect	Indirect effect via					Correlation with sesamin
		Branches/plant	Length of capsule	Capsules /plant	1,000 grain weight	Grain yield /plant	
Branches/plant	-0.08	–	-0.03	-0.05	0.20	0.00	0.05
Length of capsule	0.07	0.03	–	-0.09	-0.27	-0.06	-0.32
Capsules/plant	-0.30	-0.01	0.02	–	-0.20	-0.06	-0.55**
1,000 grain weight	-0.42	0.04	0.04	-0.14	–	-0.05	-0.54**
Grain yield/plant	-0.09	0.00	0.04	-0.21	-0.25	–	-0.51**

** highly significant different ($p < 0.01$)

Table 6 Path analysis showing direct and indirect effects of agronomic traits on sesamolin content in sesame

Trait	Direct effect	Indirect effect via					Correlation with sesamolin
		Branches/plant	Length of capsule	Capsules/plant	1,000 grain weight	Grain yield/plant	
Branches/plant	0.16	–	-0.15	-0.04	0.29	0.00	0.26
Length of capsule	0.34	-0.07	–	-0.07	-0.39	-0.02	-0.21
Capsules/plant	-0.23	0.03	0.10	–	-0.29	-0.02	-0.41*
1,000 grain weight	-0.60	-0.08	0.22	-0.11	–	-0.02	-0.59**
Grain yield/plant	-0.03	0.00	0.21	-0.16	-0.37	–	-0.35*

* significant different ($p < 0.05$); ** highly significant different ($p < 0.01$)

Discussion

Continuous distributions of sesamin and sesamolin were found in F_2 populations, so they were assumed to be polygenically controlled (Yasumoto and Katsuta, 2006). The mean sesamin and sesamolin contents of the F_1 generation of both crosses were less than the mid parent value. Similar results were reported for the sesamin and sesamolin contents in sesame (Ogata and Kato, 2016; Khuimphukhieo and Khaengkhan, 2018) for the cupric ion reducing antioxidant capacity, ferric reducing ability of plasma, β-carotene and chlorophyll-a in cabbage (Parkash et al., 2017) and chlorophyll in cauliflower (Dey et al., 2014).

Component *'m'* was significant for all traits studied, indicating that they are inherited quantitatively (Kere et al., 2013). Capsules/plant, 1,000 grain weight and grain yield/plant were largely controlled by dominance and epistatic gene effects. Similar results were observed by Kumar and Genesan (2004) and Sharmila et al. (2007). The sesamin content was mainly controlled by the dominance gene effect. The negative dominance gene effect found to be controlling the sesamin content implied that it reduced the effect on the performance of the trait. The current results were in agreement with Ogata and Kato (2016) who found that dominance gene effect reduced the sesamin content in sesame, indicating that most hybrids have a lower sesamin content than the parents. Therefore, breeding to increase the quantity of sesamin in sesame seed via the F_1 hybrid method may be ineffective. A similar variation in gene actions observed from the same characters in both crosses showed the presence of similar gene loci and frequencies opposing and reinforcing the traits involved in the crosses (Alam et al., 2014). The additive × dominance interaction effects appeared to provide a major contribution to the inheritance for sesamolin. In addition, the White UB2 × Kanchanaburi cross showed additive × additive interaction effects for the sesamolin content in the F_2 generation, indicating that some alleles were dispersed in the parents used in the current study (Yeboah et al., 2008) because the F_2 population of this cross showed more genetic variation of sesamolin content than the parents. The presence of additive × additive interaction effects implied potential to obtain transgressive segregation in later generations for this cross (Alam et al., 2014). Because of transgressive segregation, outstanding lines that had higher sesamolin contents than their ancestors may be found in this cross. This result suggested that it is possible to develop sesame varieties with high sesamolin contents by selecting transgressive segregation in this cross. In contrast, Ogata and Kato (2016) found that the additive variance exceeded the dominance variance for both sesamin and sesamolin. The varying magnitude of significant genetic components depends on the parents and traits chosen (Alam et al., 2014). The results from the current study showed that selection for important yield components and the sesamin and sesamolin contents in sesame should be deferred to later generations after genes that control desirable traits have been fixed, so breeding methods based on the bulk method and the single seed descent method should be used for improving those traits.

There was moderate to relatively high heritability for agronomic traits in length of capsule, 1,000 grain weight and grain yield/plant. The expression of these traits did not seem to be sensitive to the environment and phenotypic expression was quite stable in each generation. The selection of those traits in the early generation through the pedigree method may be effective. However, those traits are mostly controlled by dominance or epistatic gene effects, so selection in the early generation should be considered very carefully. Sesamin and sesamolin exhibited low and moderate heritability, respectively. Different results were reported by Ogata and Kato (2016) with these traits exhibiting high heritability. The contrasting results may have been due to differences in population sizes, environmental factors and the generations used for evaluation. Broad sense heritability provides information on genetic variation, but it does not provide any indication of the progress expected from selection (Kesmala et al., 2004). The sesamin content exhibited low heritability and the presence of non-additive gene effects could hinder the progress of selection, so the selection of superior genotypes in the F_2 generation would be ineffective (Kesmala et al., 2004).

Significant positive correlation was found between the sesamin and sesamolin contents. Similar results were reported by Yasumoto and Katsuta (2006), Wang et al. (2013), Pathak et al. (2014) and Ogata and Kato (2016), showing that an improvement in the sesamin content will result in a simultaneous improvement in the sesamolin content. In contrast, the sesamin and sesamolin contents had significant negative correlations with capsules/plant, 1,000 grain weight and grain yield/plant, implying that the sesamin and sesamolin contents would increase with decreased seed weight. The current results were in agreement with Khuimphukhieo et al. (2018). In addition, Yasumoto and Katsuta (2006) found that H65 variety had the highest sesamin and sesamolin contents (9.5 and 4.4 mg/g, respectively) with a very small seed size (1,000 grain weight = 0.9 g). Rangkadilok et al. (2010) reported that seed size and the position of capsules affected the contents of sesamin and sesamolin in sesame seed. The presence of associations between traits results from linkage or pleiotropy. Because the associations between the lignan contents and agronomic traits were negative, improvement to increase the quantity of lignan contents may decrease capsules/plant, 1,000 grain weight and grain yield/plant. Therefore, breeding to increase the lignan contents together with good agronomic traits should use different parental lines for the agronomic traits and the lignan contents since the alleles of those traits crossed between those parents will have been segregated in the F_2 progeny (Abbo et al., 2000).

In conclusion, the estimate of gene action through generation mean analysis showed the importance of additive, dominance and epistatic gene effects for the traits studied. The sesamin content was controlled by a dominance gene effect while the grain yield/plant and the sesamolin content were mainly controlled by epistatic gene effects. The sesamin content exhibited low heritability while the sesamolin content exhibited moderate heritability. The current findings showed clearly the complexity in improving the yield and lignan contents of sesame through simple selection procedures or pedigree breeding since the presence of non-additive gene effects and their heritability are not high. The studies on correlation and path analysis indicated that relationships between 1,000 grain weight, capsules/plant and grain yield/plant with the sesamin and sesamolin contents may be obstacles in sesame breeding to increase both important yield components and the lignan contents in sesame.

Conflict of Interest

The authors declare that there are no conflicts of interest

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