

Research Article

Genetic analysis of yield contributing traits and mapping of QTLs in a recombinant inbred line (RIL) population of sesame (*Sesamum indicum* L.)

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Abstract

A population of 188 RIL's derived from a cross involving progenitor species *Sesamum malabaricum* Burm. was used for genetic analysis and mapping of QTLs for yield contributing traits. A total of 60 SSR markers were developed through genomic hybridization assay, of which 12 were found to be polymorphic. Of the total 101 SSR markers screened, 35 markers were found segregating in expected 1:1 ratio and were selected for mapping. The linkage map constructed contained 26 markers in three linkage groups covering a distance of 298.6cM, 694.4cM and 86.4cM respectively. Analysis of population structure identified the presence of 3 clusters (K=3) of parents and recombinants. QTLs for branches/plant, days to 50% flowering, capsules/ node, seed weight per capsule, seed yield per plant, 100 seed weight, internode lengths, stem girth, capsules/ node, days to maturity and node with capsules were mapped.

Key words

Linkage map - Quantitative Trait Loci- *Sesamum indicum*-Yield

Introduction

Sesame (*Sesamum indicum* L.); is an important oil seed crop of the tropics cultivated by poor and marginal farmers. Low productivity and persisting problems of incomplete domestication make this crop quite unattractive from the grower's point of view. Nevertheless, sesame oil is regarded as one of the healthiest vegetable oil with high market demand and the edible seeds are used in confectionaries and as a condiment.

Molecular breeding efforts in sesame pertain to construction of linkage map (Wei *et al.* 2009) and identification of molecular markers linked with important agronomic traits like indehiscence (Uzun *et al.* 2003) and determinate growth (Uzun and Cagirgan, 2009) were also identified by linkage analysis. Transgressive segregants for yield and its component traits were noticed in sesame (Ramya *et al.* 2012). The study also reported positive correlation between yield and number of capsules per plant, 100 seed weight and seed weight per capsule whereas negative correlation existed between yield and internode length L1.

Recently, using next generation sequencing technologies new EST-SSR markers were developed in sesame (Wei *et al.* 2011; Zhang *et al.* 2012). With the reports of a draft genome assembly of *S. indicum* cultivar Zhongzhi No. 13 (Zhang *et al.* 2013) and the haplotype map of sesame genome (Wei *et al.* 2015), sesame genomics is ushered into a new era. The particular study is aimed at fine dissection of yield contributing traits of sesame and mapping of underlying QTLs under Indian conditions.

Materials and methods

Plant materials

A Recombinant Inbred Line (RIL) population of 188 individuals was developed from an original cross MKN6 (E3) X IC 204773 (N1); following Single Seed Descent (SSD) method. The parent MKN6 is an F₈ generation selection from a cross between the exotic accession EC346987 and DLH2; a *S. malabaricum* line. The parental lines differed with respect to height, branching pattern, leaf shape, yield, disease resistance and hairiness. IC 204773 is a photosensitive, late maturing line collected from Nagaland with bushy growth habit and resistance to phyllody and leaf roller.

Evaluation of morphological traits

The morphological characterization of RILs was conducted for two consecutive *khari* seasons of 2008 and 2009 in the fields of NBPGR, New Delhi. Augmented Block design with five blocks was used for field experimentation with spacing of 45x30 cm between lines. The parental lines as well as four standard varieties ('Phulet-1', 'Tapi-A', 'Padma' and HT-1) were used as checks for estimation of error variance. Phenotyping was based on traits; days to flowering, days to 50% flowering, days to capsule formation, leaf shape, hairiness, number of branches per plant, internode lengths from base to top (L1, L2, L3, L4 and L5), number of flowers per node, plant height, stem girth, days to maturity, capsule length, capsule width, number of capsules per node, total number of capsules per plant, seed weight per capsule, seed yield per plant and 100 seed weight.

Genotyping and Mapping of QTLs

SSR markers were used for linkage map construction and QTL mapping. Of the total 101 SSR markers, 27 were constructed based on earlier published sequences by Dixit *et al.* 2005; (GBSSR series), 44 were constructed in the lab by whole genome hybridization assay and the rest were constructed from EST sequences available in the genbank (BKB series). After parental polymorphism survey the identified polymorphic SSR markers were further used for genotyping. The STMS reaction conditions were standardized as 50 ng DNA, 1x PCR buffer with MgCl₂, 0.5 mM MgCl₂, 1U Taq DNA polymerase (Bangalore Genei), 0.25 μM of each of primers and 200 μM of dNTPs. The PCR conditions were; initial denaturation 94°C for 5 minutes, followed by 35 cycles of PCR reactions involving denaturation at 94 minutes for 1 minute, followed by primer annealing at respective temperatures and extension at the rate of 72°C for 2 minutes. After 35 cycles final extension for 10 minutes was given at 72°C. The PCR reactions were carried out in Bioer XP thermal cycler. The products were first resolved in 2.6% agarose gel and later subjected to capillary gel electrophoresis using QIAxcel analyzer.

Data Analysis

The software packages SYSTAT version 12 (Crane Software International Ltd, USA) and GENSTAT version 15 (VSN International Ltd, UK) were used for morphological data analysis. Markers segregating in the expected 1:1 ratio were identified and used for linkage map construction using software MAPMAKER/EXP ver.3.0 (Lander *et al.* 1987). The population genetic structure was analyzed with the help of software STRUCTURE ver.2.3.3 (Pritchard *et al.* 2010). The linkage maps were drawn with the help of software MAPCHART 2.0 (Voorrips, 2002). The combined phenotypic and genotypic data were used for mapping of QTLs using Simple Interval Method with the help of software WinQTL CART ver. 2.5 (Wang *et al.* 2011). A LOD score of 2.5 was used as the threshold to determine the presence of significant QTL. This value was estimated based on a permutation analysis (Churchill and Doerge, 1994) with 1,000 random data shuffles, to provide a genome-wide 0.05 significance level.

Results and Discussion

Phenotyping of Recombinant Inbred Line (RIL) population

The RILs as well as the parents were morphologically characterized for 18 traits under Delhi conditions. For the traits; branches per plant, number of capsules per plant, days to maturity, capsules per plant, seed weight per plant, days to

flowering, seed weight per plant and node with capsules had skewness and kurtosis value greater than 1. The skewness and kurtosis of other traits studied were below 1 indicating the normal distribution of phenotypic data. There was marked difference between the parents for different morphological traits. Between the parents, IC 204773 (N1) produced capsules with more length and diameter while the weight of capsules and number of capsules produced were greater for the parent MKN6 (E3). Transgressive segregation occurred in both the direction for most of the traits implies that both the parents might contribute QTL with positive effects for such traits in the population. The distribution of yield and related traits are given in Fig.1.

Parental Polymorphism Survey

The parents of the RIL population were analyzed with SSR markers to identify polymorphic markers for the purpose of construction of linkage map. Total 101 markers were used for parental polymorphism survey. Out of the 101 primers screened, 43 were found to be polymorphic (Table-1) and were used for genotyping of the RIL population.

Construction of Linkage Map

A linkage map was constructed using SSR markers found polymorphic between the parental lines. In a Recombinant Inbred Line population a co-dominant marker is expected to segregate in the ratio 1:1. The RIL's were classified into parental types based on molecular weight by software BIOCALCULATOR (QIAGEN, USA). The genotypic data was analyzed for segregation distortion and finally 35 markers confirming to the expected ratios were used for linkage map construction. The markers which were excluded from final analysis either due to segregation distortion or due to poor amplification profile were GB-19, GB-5, GB-40, BKB-21, P6B7, P7F4, P21H12 and P12H12.

The linkage map constructed with MAPMAKER ver. 3.0 based on LOD score 5.0 separated the 35 markers into 3 linkage groups with 10, 13 and 3 markers respectively. The 9 markers which were not assigned to any of the linkage group were BKB-08, GB-72, P3D10, P2C2, GB-129, P6H6A, P6H6B, P7B1 and TIL-9. The linkage group 1 covered a total distance of 298.6cM while the linkage group 2 spanned over 694.4cM. The third linkage group was the shortest in terms of distance and length and had only 3 markers covering a total length of 86.4cM. The average marker density for linkage group-1 is 29.86cM; while for linkage group 2 and 3 the marker densities were 53.41cM and 28.8cM respectively. The largest marker

interval observed was between markers P1B4 and P22D11A in linkage group 2 and had a length of 345.4cM.

Genotyping of RILs and Mapping of QTLs

The Recombinant Inbred Line (RIL) population was genotyped with SSR markers which showed clear cut polymorphism between the two parental lines. Assessment of population structure with software STRUCTURE indicated the presence of 3 clusters. The log likelihood increased strongly up to 3 clusters (K=3) which appeared to be the optimum value dividing the data set into both parental types as well as the recombinants (Fig. 2). The RIL population represented the allelic diversity of both the parents. The genotypic and the phenotypic data were combined and used for mapping of Quantitative Trait Loci controlling yield related traits. The software WinQTL CART was used for localization of putative QTL's for agronomically useful traits.

A total of 40 QTLs were identified in the three designated linkage groups controlling 15 traits studied. The LOD score of the QTLs ranged between 2.52 to 45.0. Linkage group-2 contained the maximum number of QTLs (22) followed by linkage group-1 (13 QTLs) and linkage group-3 (5 QTLs). The significant QTLs detected above the threshold level of 2.5 with their positions in the linkage map given in Fig. 3. Table-2 lists the identified QTLs, their positions, LOD scores, gene action and effects.

Fifty percent Flowering (FlwH): For the trait *FlwH*; three QTLs namely *FlwH-1*, *FlwH-2* and *FlwH-3* were present on linkage groups 2 and 3. The QTL *FlwH-1* present on linkage group contributed maximum additive variance of 8.15 while for the other two QTLs the dominance component was more.

Capsules per Plant (Cappl): Three QTLs; *Cappl-1*, *Cappl-2* and *Cappl-3* were identified in linkage groups 1 and 2 controlling the trait 'Capsules per Plant'. These three QTLs were characterized by the presence of high dominance component of variation (more than 129%) while the additive effect accounted for 2.73, 0.83 and -1.34% of variation.

Branches per Plant (BrPl): Two QTLs *BrPl-1* and *BrPl-2* with high LOD scores of 19.38 and 13.35 were discovered in linkage groups 1 and 2 respectively. The QTL *BrPl-2* was found to have higher additive effect of 6.16 while for *BrPl-1*; the dominance component was found to be more (9.36).

Capsule per Node (CapN): The trait *CapN* was found to be under the control of four QTLs namely; *CapN-1*, *CapN-2*, *CapN-3* and *CapN-4*. Two QTLs were present in linkage group-2 while linkage

groups 1 and 3 contained one QTL each. The LOD score for the QTLs ranged between 9.69 and 23.46 while the additive effects estimated ranged between -0.99 to 0.13. The dominance variance ranged between 2.19-2.27%.

Maturity Days (MatD): Three QTLs; *MatD-1*, *MatD-2* and *MatD-3* were identified in linkage groups 1 and 3. These QTLs were characterized by a high LOD score of 34.22-45.0. The QTLs *MatD-1* and *MatD-2* were having additive effect of 0.28 and 0.34 respectively while the additive effect of *MatD-3* was estimated to be -0.02. All three QTLs contributed negative dominance variance to the amount of -9.48 to -0.57.

Node with Capsule (Ndwc): In linkage group-2; two QTLs (*Ndwc-1* and *Ndwc-2*) were identified controlling the trait 'Node with Capsule'. The additive effect of these QTLs ranged from 0.13 to 0.62 while the dominance effect estimated ranged from 0.23 to 13.2.

Stem Girth (StmG): Three QTLs were identified for the trait 'Stem Girth' namely *StmG-1*, *StmG-2* and *StmG-3* present in linkage groups 1 and 2. The LOD score of these QTLs were lowest (2.52-2.88) among all the identified QTLs. The QTLs accounted for additive effect of -0.07 to 0.12 while the dominance effect estimated was 3.12 to 3.68.

Internode length L1 (IntL1): Two QTLs (*IntL1-1* and *IntL1-2*) were detected in linkage groups 1 and 2 respectively. *IntL1-2* had greater additive effect (21.26) than *IntL1-1* (0.71). The estimated dominance effects were 26.14 and 23.34 for *IntL1-1* and *IntL1-2* correspondingly.

Internode length L2 (IntL2): The linkage groups 2 and 3 contained single QTL each for the trait Internode length L2 (*IntL2*). The additive effects of the designated QTLs; *IntL2-1* and *IntL2-2* were 17.68 and -0.47 respectively.

Internode length L3 (IntL3): For the trait 'Internode length L3'; 2 QTLs (*IntL3-1*, *IntL3-2*) with additive effects 6.64 and -0.76, were found to be present in linkage groups 2 and 3. The corresponding dominance effects were -18.97 and 30.5.

Internode length L4 (IntL4): Two QTLs (*IntL4-1*, *IntL4-2*), were discovered in linkage group-2 with additive effects 2.44 and 2.13 respectively.

Internode length L5 (IntL5): Single QTL (*IntL5-1*) in linkage group-1 and two QTLs (*IntL5-2* and *IntL5-3*) in linkage group-2 were discovered controlling the trait 'Internode length L5'. The QTL; *IntL5-2* was found to have higher additive effect (20.03) compared (2.23 and 1.57) to other two QTLs.

Seed weight per capsule (SdwtF): Two QTLs were detected in linkage group-2 (*SdwtF-1* and *SdwtF-2*); with corresponding additive of -0.34 and 0.04. The estimated dominance effects were 0.37 and -

0.01 respectively.

100 Seed weight (100Sd): Linkage groups 1 and 2 contained single QTL each (*100Sd-1* and *100Sd-2*) with additive effects -0.01 and 0.03 for the trait '100 Seed weight'.

Seed weight per plant (Yd5Pl): Three QTLs were discovered in linkage group-1 (*Yd5Pl-1*, *Yd5Pl-2* and *Yd5Pl-3*) and a single QTL in linkage group-2 (*Yd5Pl-4*) controlling the trait 'Seed weight per plant'. The corresponding additive effects estimated were 1.03, 0.92, 1.14 and 1.18.

Problem of low polymorphism

The low level of genetic polymorphism exhibited by cultivars which is the major problem limiting the use of SSR's in sesame breeding still persists [Zhang. et al. 2012]. In the present study also the percentage of polymorphic markers was very low. The earlier linkage map constructed by Wei et al. 2009; used mainly RSAMPL and AFLP markers. The map had only 10 SSR markers. The total length of linkage map was 1232.53 cM and contained 30 linkage groups. Since the markers used in the present study and those reported earlier are different, comparison between linkage maps is not possible.

Saturation of linkage map

Linkage mapping achieves reasonable level of saturation when the number of linkage groups obtained equals the haploid chromosome number of species. For sesame to reach this level there must be 13 linkage groups. In the present study the number of linkage groups obtained was only three which severely affected the precision of mapping. Moreover to locate QTLs accurately it is necessary to have markers at every 10 cM interval. In the map obtained the average marker density ranged from 28.8-53.41 cM which fell much below the requirement. Further, there were many peaks for most of the QTL's mapped which may be erroneous in nature due to the low number of markers used.

In conclusion, utilization of molecular markers had helped enormously in understanding the genetics of complex traits. For Marker Assisted Selection (MAS) and transfer of QTLs the fundamental requirement is a well saturated linkage map. More number of polymorphic markers are necessary to saturate the current map and for greater reliability of map positions. With the advent of next generation sequencing technologies information about large number of EST-SSR markers are now available in the data bases (Wei et al. 2011; Zhang et al. 2012). The release of draft genome sequence of sesame (Zhang et al. 2013) and the haplotype map targeting genes for oil discovery (Wei et al. 2015) opened a new dimension for sesame breeding. When more markers are available a fine

resolution map will be obtained; automatically closing the big gaps and thereby reducing the marker intervals. Especially, more attention must be given to the interval of 345.4cM between PIB4-P22D11 containing 11 QTLs. When more markers are used the spurious peaks can be avoided and the actual position of each QTL can be established.

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Table1. Characteristics of new SSR primers

Sl No	PRIMER	SEQUENCE 5'-3'	Temp	Pdt. Size (bp)	
			(°C)	N1	E3
1	BKB34	F: ACAAGATCGAAGAGAAGTTGGG	49.0	341.0	340.0
		R: CACCTGAATTAATCGCTGTCC			
2	BKB42	F: CTTACTAAGCTGACCAAGGAGC-	55.0	332.0	340.0
		R: ATAATGGGAAACGATAACGG			
3	BKB43	F: CTGGTTAATGGATATTGATCCC-	45.0	372.1	238.9
		R: TTGGCATTTCCTACTCACCC			
4	BKB08	F:CAAGTGAGGAAACACTTACAGGG	45.0	221.0	219.0
		R:TGGAGAGAACAAAGACAGACACG			
5	BKB14	F: TCAAGAAGCTCATGGACTACCC	53.0	416.7	413.2
		R: GCAAATTCGTGACACTGTGG			
6	BKB18	F: CACAAAAATCCCAAACACCC	45.0	396.0	395.0
		R: GATCTGTAGTCCTTGACGAGGG			
7	PAXC12	F: CCGTAAATCTAGGCAGTACCG	48.5	347.0	343.0
		R: AATGGTCATTTTTTCGCAGC			
8	P1B4	F: TCGATTCTCTTAAGCGTGC	47.0	184.0	181.0
		R: TGTCTCTCTCGCTCTCTCC			
9	P2C2	F: TGAAGAAAAGCTTCCTTCACC	47.0	233.0	289.0
		R: TTAAGCGTGCTACTGATGCG			
10	P22D11A	F: ATTATTTGTTGGGTGGCTGC	45.0	345.0	313.0
		R: TTTGTCCAGATCTAAGCAAGAGC			
11	BKB54	F: CTGAGGTTGAATCAGTTCAGC	50.0	301.3	292.1
		R: CGTAATTAACCAACTCAGCTCC			
12	BKB39	F: GAAAATAAGCTAGGAATGTCGG	50.0	226.0	227.0
		R: GCGTCAATCGTGACACCTCC			
13	P3D10	F: AATTCGATTCTCTTAAGCG	50.0	198.0	216.0
		R: CCCACACACCACAAACACACC			
14	P7G8A	F: GGGGAAAGGGCCCAATGAGG	47.0	201.0	214.0

		R: CACGGTTTTTGAGGGTGAGG			
15	P22D5	F: CATGATCCCTTCATGAAACACG	45.0	304.7	306.2
		R: CCCTTGATCGCAGAATTCGC			
16	P22D6A	F: TTCCTTGTTTTCCACTCG	45.0	182.0	158.0
		R: CCCTTGATCGCAGAATTCGC			
17	P2B10	F: ACCCACACACCACACATACA	48.0	324.0	326.0
		R: CCTAATAGGCGTCTTAAGCG			
18	P7B1	F:GACAGACAGACAGACAGACAGACAGC	47.0	175.7	156.8
		R: TCACTAGTGATTTCGTCTTAAGCG			
19	P2C9	F: AATTCGATTTCGTCTTAAGCG	48.0	107.3	143.5
		R: TATTAGGGGGTGGAGTGTGG			
20	P6H6A	F: CCGCGGGAATTCGATTCACC	45.0	184.0	176.0
		R: GTTTTGCTGAACGATGCTCC			

The sequences and annealing temperatures of newly synthesized EST SSRs and SSRs synthesized through hybridization assay. The amplification product sizes of parents (N1 and E3) are also given.

Table 2. The QTLs identified for various traits including their position, LOD peak and effects. The additive effect is given as aH1 and dominance effect as dH2. R² values are given as %

QTL No	Trait Name	Linkage Group	Peak LOD	QTL peak cM	Interval	aH1	dH2	R ²
1	<i>FlwH-1</i>	2	9.72	258.7	P1B4-P22D11	8.15	-8.78	65.7
2	<i>FlwH-2</i>	2	5.5	475.7	P22D11-P7G8	0.94	9.78	55.7
3	<i>FlwH-3</i>	3	4.66	22.4	PAXC12-P22D5	-0.24	9.49	10.1
4	<i>Cappl-1</i>	1	8.88	79.1	BKB42-BKB14	2.73	132.41	10.2
5	<i>Cappl-2</i>	1	9.99	154.9	BKB14-BKB18	0.83	129.62	9.78
6	<i>Cappl-3</i>	2	8.74	38.3	BKB39-GB176	-1.34	135.08	67.3
7	<i>BrPl-1</i>	1	19.38	156.4	BKB18-GB33	0.33	9.36	3.05
8	<i>BrPl-2</i>	2	13.35	297.3	P1B4-P22D11	6.16	0.30	6.4
9	<i>CapN-1</i>	1	20.22	94.6	BKB42-BKB14	0.13	2.27	3.02
10	<i>CapN-2</i>	2	9.69	158.4	BKB18-GB33	-0.04	2.19	4.01
11	<i>CapN-3</i>	2	23.46	158.6	P1B4-P22D11	-0.099	2.19	4.01
12	<i>CapN-4</i>	3	15.08	37.1	PAXC12-P22D5	0.11	2.23	1.01
13	<i>MatD-1</i>	1	44.5	140.2	BKB14-BKB18	0.28	-10.57	3.01
14	<i>MatD-2</i>	1	45.0	155.2	BKB18-GB33	0.34	-10.37	3.22
15	<i>MatD-3</i>	3	34.22	41.5	PAXC12-P22D5	-0.02	-9.48	4.01
16	<i>Ndwc-1</i>	2	4.85	270.7	P1B4-P22D11	0.62	0.23	1.01
17	<i>Ndwc-2</i>	2	8.52	144.2	GB176-P1B4	0.13	13.2	1.09
18	<i>StmG-1</i>	1	2.52	239	GB108-BKB54	-0.07	3.62	2.02
19	<i>StmG-2</i>	2	2.8	84.8	BKB39-GB176	0.12	3.18	69.1
20	<i>StmG-3</i>	2	2.88	493.5	P22D11-P7G8	0.01	3.47	68.9
21	<i>IntL1-1</i>	1	2.59	92.3	BKB42-BKB14	0.71	26.14	1.03
22	<i>IntL1-2</i>	2	4.08	233.8	P1B4-P22D11	21.26	23.34	69.2
23	<i>IntL2-1</i>	2	3.65	278.2	P1B4-P22D11	17.68	16.49	69.5
24	<i>IntL2-2</i>	3	3.52	8.2	PAXC12-P22D5	-0.47	23.15	1.02
25	<i>IntL3-1</i>	2	5.13	246.1	P1B4-P22D11	6.64	-18.97	37.01
26	<i>IntL3-2</i>	3	4.2	13.8	PAXC12-P22D5	-0.76	30.5	1.01
27	<i>IntL4-1</i>	2	4.51	90.9	GB176-P1B4	2.44	32.03	69.1
28	<i>IntL4-2</i>	2	3.58	643.2	P2B10-P2C9	2.13	-2.46	65.1
29	<i>IntL5-1</i>	1	3.9	86.1	BKB12-BKB14	2.23	-2.46	3.02
30	<i>IntL5-2</i>	2	2.72	370.5	P1B4-P22D11	20.03	10.07	71.03
31	<i>IntL5-3</i>	2	3.24	492.8	P22D11-P7G8	1.57	27.07	67.09
32	<i>SdwtF-1</i>	2	4.02	270.7	P1B4-P22D11	-0.34	0.37	69.4
33	<i>SdwtF-2</i>	2	4.12	464.8	P1B4-P22D11	0.04	-0.01	67.9
34	<i>100Sd-1</i>	1	2.68	162.8	BKB18-GB33	-0.01	-0.23	2.02
35	<i>100Sd-2</i>	2	2.65	412.8	P1B4-P22D11	0.03	-0.01	7.06
36	<i>100Sd-3</i>	2	5.51	483.2	P1B4-P22D11	0.02	-0.02	6.75
37	<i>Yd5Pl-1</i>	1	7.75	76.7	BKB34-BKB42	1.03	55.59	1.02
38	<i>Yd5Pl-2</i>	1	7.35	138.4	BKB42-BKB14	0.92	60.53	1.01
39	<i>Yd5Pl-3</i>	1	5.99	184.0	GB33-GB184	1.14	61.77	1.02
40	<i>Yd5Pl-4</i>	2	7.72	488.0	P22D11-P7G8	1.18	56.72	69.9

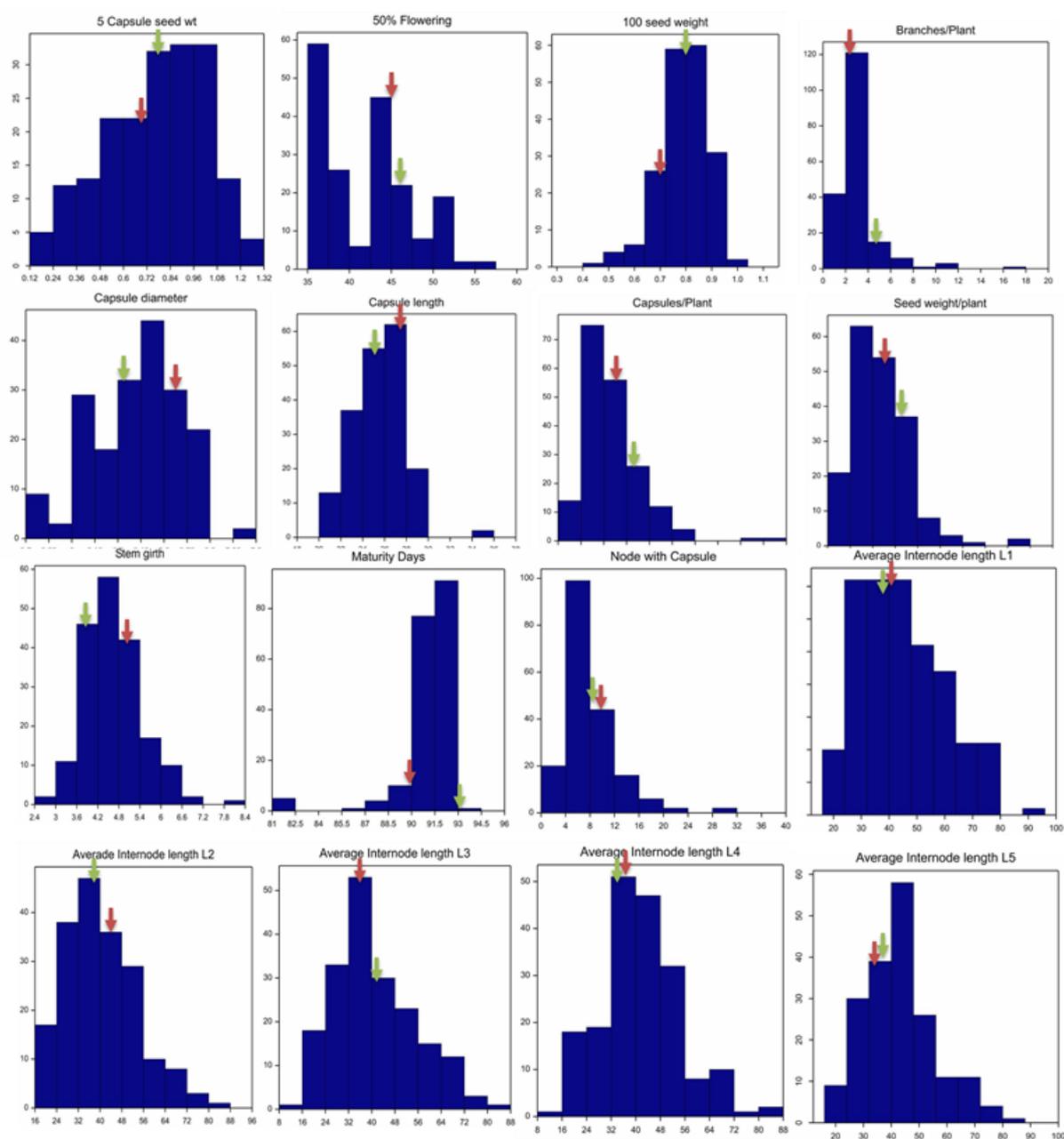


Fig. 1. Distribution of yield and related traits in a Recombinant Inbred Line population of sesame (*Sesamum indicum* L.). The Red arrow indicates parental values for IC 204773 (N1) and green arrow indicates parental values for MKN6 (E3).

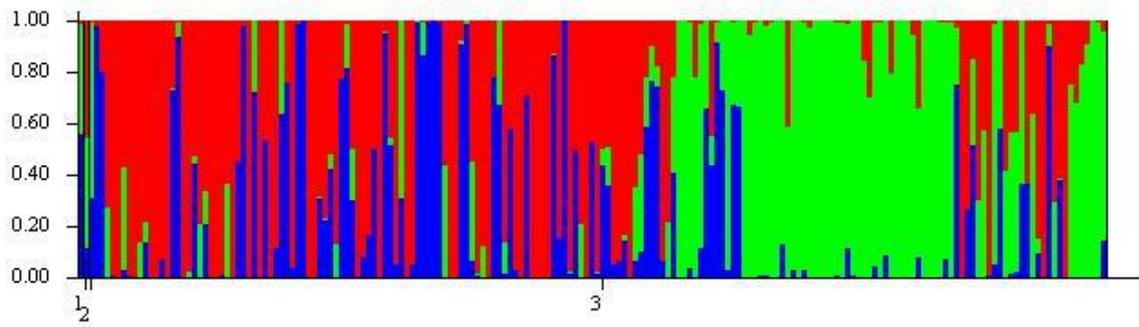


Fig. 2. Structure software results showing the assignment of RIL population into three clusters. The different clusters identified are Parent 1, Parent 2 and the recombinants which are indicated by blue, green and red colors.

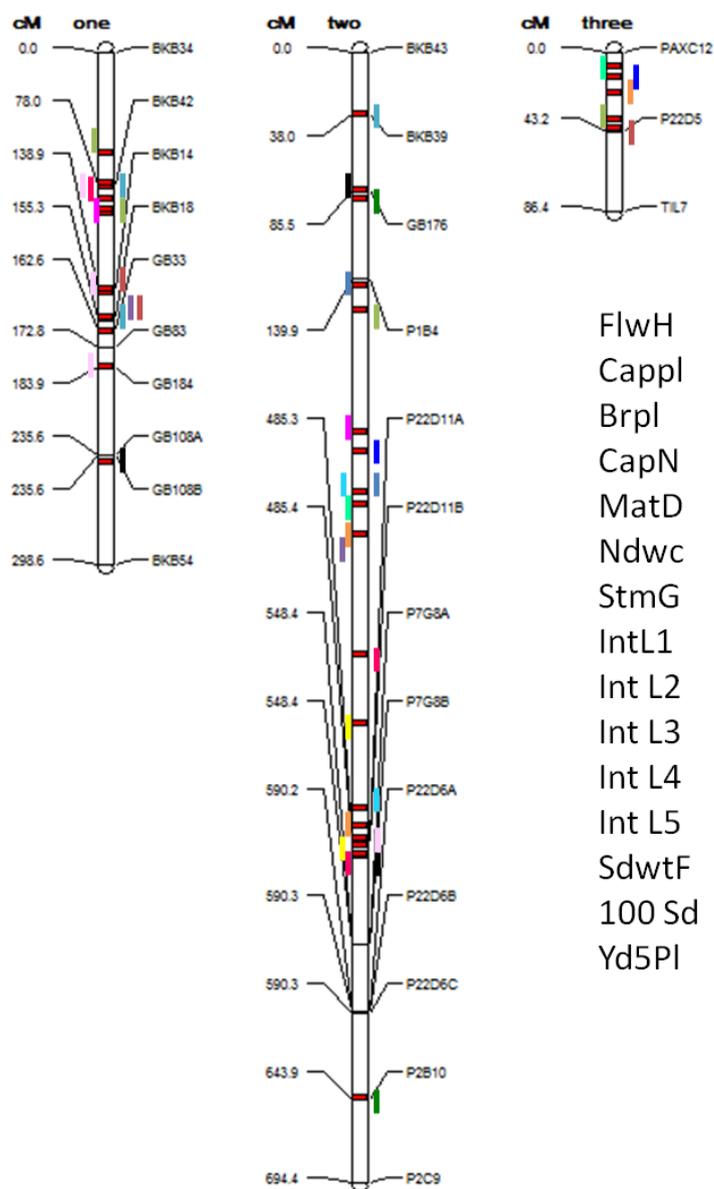


Fig. 3. Linkage map showing the positions of QTLs detected. The marked QTLs include 50% flowering (*FlwH*), capsules/plant (*Cappl*), branches/plant (*Brpl*), capsules/node (*CapN*), maturity days (*MatD*), node with capsule (*Ndwc*), stem girth (*StmG*), internode length L1 (*IntL1*), internode length L2 (*IntL2*), internode length L3 (*IntL3*), internode length L4 (*IntL4*), internode length L5 (*IntL5*), seed weight/capsule (*SdwtF*), 100 seed weight (*100 Sd*) and seed weight/plant (*Yd5Pl*).