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Mapping of QTLs for traits related to leaf pubescence, jassid resistance and yield in cotton (*Gossypium* spp.)

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Abstract

Present investigation was carried out to find the QTLs associated with leaf pubescence, jassid resistance and yield traits in cotton. Available SNP based linkage map was used for QTL analysis. Single marker analysis and simple interval mapping identified 24 and 11 associated QTLs, respectively. Composite interval mapping detected only seven QTLs, of which five were associated with jassid injury resistance and leaf pubesence with 8.83-11.64 % phenotypic variance explained. One QTL each for seed cotton yield and boll weight was detected. These identified QTLs and markers may be used in molecular breeding for improving yield and insect resistance in cotton.

Key words: Abaxial leaf pubescence count, leaf mid-rib pubescence count, quantitative trait loci, single nucleotide polymorphism, cotton

Introduction

Cotton (*Gossypium* spp.) is the principal commercial crop of India since time immemorial. Despite the increasing production of artificial fibers which some time back was thought to threaten the very existence of cotton fiber, the latter has maintained its prime place to this day as the king of fiber crop. Two alloteraploid cotton species, *G. barbadense* L. and *G. hirsutum* L. contribute 90 % of the world production of this natural fibre crop. *G. hirsutum* and *G. barbadense* species belong, respectively to the $(AD)_1$ and $(AD)_2$ genome groups (Hou et al. 2013). Elite cultivars of G and G. barbedense have some history of hybridization, which improves their compatibility in interspecific mapping populations. Trichomes (pubescence) are single-celled structures formed by the unidirectional extension of the outer layer of epidermal cells. They are of central importance to the *Gossypium* (cotton) genus, being its major economic product i.e., lint fiber, an important taxonomic character and a great determinant of sucking pest resistance (Meagher et al. 1997).

Till date, many high density genetic molecular maps have been constructed using both interspecific and intraspecific mapping populations. Molecular dissection of the characters through mapping of QTLs in cotton was concentrated mostly on yield and fiber quality traits such as number of bolls, boll weight, lint yield, (Yu et al. 2013; Gore et al. 2014), fiber length, fiber fineness, fiber tenacity (Yu et al. 2013; Gore et al. 2014). Numerous introgressive breeding programs have been performed over many decades to try to improve fiber quality and yield by interspecific hybridization in cotton (Zhang et al. 2014). In one of the attempts, Wang et al. (2017) genotyped BC_3F_2 families derived from *G. hirsutum* x *G. mustelinum* cross using simple sequence repeat markers for fibre strength and fineness and detected 42 QTLs with percentage variance of 13.86 and 14.06%, respectively. They advocated that new allels could be identified from interspecific hybrids, which may be useful in cotton breeding. However, a problem of linkage drag and reduced tolerance is associated in identifying homozygous wild alleles which makes the task of generating adequate mapping populations difficult (Chandnani et al. 2017; Waghmare et al. 2016). More than 1000 cotton fiber quality QTL have been published, but their use in marker-assisted breeding for cotton improvement has been limited (Said et al. 2015).

However, only few studies were reported the

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QTLs associated with disease (Gutierrez et al. 2011) and insect resistance through limited classical genetic studies and genetic mapping. Five loci (T1-T5) with several additional genes/quantitative trait loci (QTLs) that modify the densities/distributions of leaf trichomes have been identified (Mingquan et al. 2015). Use of SNP (single nucleotide polymorphism) markers in cotton molecular breeding started very recently (Byers et al. 2012; Hulse-Kemp et al. 2015) and gained more popularity due to their abundance in genome and stability (Gupta et al. 2001). However, only a few researchers had reported its use for detecting QTLs in cotton, due to limited available number (Byers et al. 2012; Gore et al. 2014; Zhu et al. 2014) or lower density (Hulse-Kemp et al. 2015; Wang et al. 2014). In recent years, many SNP discovery studies were performed (Young et al. 2015; Sudakara et al. 2017) and new sets of markers have been generated to facilitate the development of the high-resolution genetic map of cotton. SNPs are the most abundant variations in the genome. The main advantage of SNP markers relates to ease of data management along with their flexibility, speed and cost effectiveness. Hulse-Kemp et al. (2015) and Ramesh et al. (2015) have developed inter- and intra-specific maps in cotton by using CottonSNP63K. The array and maps provide a foundation for the genetic dissection of agronomically and economically important traits and crop improvement through genomics-assisted selection. It will also foster positional cloning and genome assembly efforts. The fast-growing contribution of portable markers in cotton furnishes an inexpensive way for gene isolation and linkage mapping for breeding cotton to obtain desirable objectives.

In the present study recombinant inbred lines derived from the inter-specific cross between *G. hirsutum* var. DS-28 and *G. barbadense* var. SBYF-425 which are diverse with respect to morphology, jassid resistance, yield and fibre traits, were used in the mapping of QTLs for leaf pubescence, jassid resistance, and yield traits.

Materials and methods

Plant material and phenotypic analysis

Two hundred recombinant inbred lines in F_{12} generation derived from an interspecific cross between *G. hirsutum* var. DS-28 and *G. barbadense* var. SBYF-425 were grown under field conditions during *kharif* 2015-16 at Agricultural Research Station, Dharwad Farm, University of Agricultural Sciences Dharwad. Observations for different pubescence traits on the plants were recorded based on qualitative grading (pubescence rating) and quantitative measurement (trichome density and trichome length). The pubescence evaluation through qualitative grading system was carried out during September using a hand lens (4X magnification). In the RIL populations, from each plant, two leaves were screened for pubescence and the average value of these two leaves was taken for statistical analysis. The 0-9 point scale for pubescence as given by Bourland et al. (2003) was used for screening.

Quantitative measurement of trichomes such as number and length of trichomes were recorded. Number of trichomes on leaf lamina, mid-rib and vein were recorded with the help of stereomicroscope. Average of two leaves (from the top fourth node) count per plant was used for statistical analysis (Bourland et al. 2003; Hornbeck and Bourland 2007). Length of hair was measured from leaf lamina. Two samples of hairs from each leaf were taken. A sample of hair was peeled off with the help of the razor and mounted on a slide. The slide was observed under a compound microscope to determine the length of hair by using an ocular micrometer.

Evaluation for jassid infestation

The jassids nymph population and jassid injury were recorded to screen the RILs for jassid resistance. Observations were recorded at 120 days after sowing. Jassids nymph population was taken on three plants in each RIL. In each plant three leaves one each from the top, middle and bottom parts of the plant were taken for recording observations. The observations were recorded during October when jassid incidence was at peak or at its ETL *i.e*., 2 nymphs per leaf. The density of nymphs was counted by visually observing the abaxial surface of the leaves. The average value of three leaves per plant was taken for the statistical analysis. Observations for jassid damage were

Grade	Description of jassid damage
Grade-1	Entire foliage free from crinkling or curling with no yellowing
Grade-2	Crinkling and curling of few leaves in the lower portion of plant and marginal yellowing of leaves
Grade-3	Crinkling and curling of leaves almost all over the plant and plant growth hampered
Grade-4	Extreme curling, crinkling, yellowing, bronzing and drying of leaves

recorded based on the symptoms and 1-4 grades were used to score the symptoms caused by jassids as follows.

Statistical analysis of yield and yield related traits

The plants in a plot of one row were harvested and seed cotton yield was expressed in kilogram (kg) per hectare (ha). The number of bolls on the plant, which contributed to seed cotton yield was counted on five plants and an average was recorded. Seed cotton obtained from bolls on five plants in each RIL was used to determine the average boll weight in grams (g). Analysis of variance (ANOVA) was performed for leaf pubescence, jassid resistance and yield components to test the significance between RILs. To assess the genetic variability among the RILs, phenotypic coefficient of variance (PCV), genotypic coefficient of variance (GCV) and heritability in the broad sense (h^2 bs) and frequency distribution were estimated. Statistical analyses were carried out using SPSS 16^{th} version software package.

High density genetic linkage maps construction

The high density linkage map was constructed (Ramesh 2015) using the genotype scores of 178 RILs for identified polymorphic SNP markers by multipoint analysis software with a minimum LOD of 3.0 and maximum recombination fraction of 0.372. The Kosambi mapping function was used to convert the recombination frequencies into centiMorgan (cM) map distance (Kosambi 1943). The constructed genetic maps were validated by MadMapper software (Kozik 2006) and Check Matrix. The marker group analysis was calculated pair-wise recombination values between markers using the MadMapper RECBIT Python program V248. The markers grouping and order were carried out using RECORD win software (Van et al. 2005). Check Matrix (py_matrix_2D_V248_RECBIT.py) Python script (version 248) was used for visualization and validation of constructed linkage map using two-dimensional heat-plots and graphical genotyping of all linkage group.

QTL analysis and mapping by SNP markers

The QTL mapping and analysis was performed by single marker analysis, simple interval mapping and composite interval mapping by IciMapping 3.2/4.0 based on stepwise regression by considering all the marker information simultaneously. The 'Deletion' command was used to accommodate the missing phenotypes and the step size chosen 1.0cM was claimed to be significant at a LOD value of 3. The QTL map was drawn by MapChart software.

Results

Genetic variability for leaf pubescence, jassid injury and seed cotton yield

The analysis of variance showed significant differences among the genotypes for all the characters studied. The presence of significant differences among the RILs for leaf pubescence traits (Abaxial leaf pubescence count, leaf mid-rib pubescence count, leaf vein pubescence count and trichome length), jassid injury and yield traits indicate the presence of genetically diverse lines in these RILs. The *per se* performance of each genotype for leaf pubescence and yield characters were presented in Table 1. A wide range of variability was recorded for several characters *viz.,* ALFPc (1.25-61.50), LFMPc (4.00-63.50), LFVPc

Table 1. Estimation of genetic parameters for leaf pubescence, jassid injury and yield traits among recombinant inbred lines

Parameters	$ALFP_C$	$LFMP_C$	$LFVP_C$	Trichome length (µm)	Leaf pubescence score	Jassids/ leaf	Jassid injury	Seed cotton yield (kg/ha)	No. of bolls/ plant	Boll weight (g)
Mean	24.36	31.80	19.87	35.94	2.17	6.63	3.005	1637.77	6.96	4.28
Maximum	61.50	63.50	51.75	66.55	5.00	26.67	4.00	3618.60	14.60	7.89
Minimum	1.25	4.00	2.75	10.68	1.00	0.33	1.00	155.80	2.00	1.18
GCV (%)	73.31	67.60	69.52	23.51	49.081	72.46	32.25	46.33	40.47	26.39
PCV (%)	97.82	68.65	73.28	25.58	59.33	83.76	46.09	56.83	40.26	29.13
h^2(bs)	0.56	0.97	0.90	0.84	0.68	0.74	0.49	0.91	0.01	0.82
GA	35.50	43.68	27.005	16.008	1.925	8.572	1.365	1482.132	0.562	2.084
GAM (%)	145.73	140.90	135.93	44.51	88.47	129.26	44.59	90.49	8.07	48.59

ALFPc = Abaxial leaf pubescence count; LFMPc = Leaf mid-rib pubescence count; :FVPc = Leaf vein pubescence count

(2.75-51.75), trichome length (10.68-66.55µm), leaf pubescence score (1.00-5.00), jassids/leaf (0.33-26.67), jassid injury (1.00-4.00), seed cotton yield (155.00-3,618.60 kg/ha), no. of bolls per plant (2.00-14.60) and boll weight (1.18-7.89g). Based on *per se* performance, the RILs-39, 57, 91, 99, 118, 134, 151, and 152 were identified as potential jassid resistant with highest mean values for leaf pubescence. One hundred and eighty RILs recorded significantly higher yield as compared to the superior parent DS-28. From these, the RILs which were showing resistance to jassid injury can be used for further development of cotton varieties with high yield and jassid resistance *viz*., RILs-39, 57, 100, 118, 134, 149, 151 and 152.

Among the 200 recombinant inbred lines, a wide range of genetic diversity existed for leaf pubescence, jassid injury and yield traits. In the present investigation, RILs with high GCV and PCV for jassids/leaf, jassid injury, $ALFP_C$, $LFMP_C$, $LFVP_C$, hair length and leaf pubescence were recorded. Based on pubescence rating or trichome density selection for desirable genotypes can be made. In the RILs, the heritability was high for all the traits except for no. of bolls per plant. Similarly, high heritability was observed for all the leaf pubescence traits except ALFPc which was moderate (Table 1). The frequency distribution based on the mean data for jassid injury, boll weight and number of bolls per plant showed near normal distribution pattern. The frequency distribution for ALPCs, LVPCs, trichome length, jassids/leaf and seed cotton yield was skewed positively (left), whereas LMPCs was skewed negatively (Fig. 1).

QTL analysis and mapping for leaf pubescence and yield traits

Using SNP genotypic and phenotypic data (178 RILs genotypic data and leaf pubescence) some QTLs were detected. The QTLs and flanking markers detected by composite interval mapping graphically represented in Fig 2. In single marker analysis, 25 QTLs were mapped on eight chromosomes. Among the 25 QTLs, ten were governing the leaf pubescence traits explaining 7.70 to 9.19 per cent phenotypic variation with peak LOD score range of 3.09 to 3.72 and fifteen QTLs were showing association with yield and yield contributing traits, explaining 7.61 to 13.60 per cent phenotypic variation with peak LOD score ranging from 3.07 to 5.65. For the leaf mid-rib pubescence, ten QTLs were identified on chromosomes 12 and 16. The range of LOD score for these QTLs was 3.09 to 3.72 with a phenotypic variability of 7.70 to 9.19 per cent. Twelve QTLs were identified for seed cotton yield on 6 chromosomes (3, 9,15,19, 20 and 24). The range of LOD score was 3.07 to 5.65 with a phenotypic variability of 7.65 to 13.60 per cent. Three QTLs were detected for the trait boll weight on chromosome 24 with a LOD ranging from 3.06 to 3.39 and the phenotypic variability 7.61 to 8.39 per cent.

In simple interval mapping, a total of eleven QTLs were detected on 10 chromosomes with a phenotypic variance and LOD score ranging from 7.61 to 18.88 per cent and 3.08 to 5.79, respectively. Among the eleven QTLs, one QTL was responsible for leaf pubescence, two were controlling jassid injury and

Table 2. Trait wise QTLs along with flanking markers, position on chromosome, LOD, phenotypic variance and additive effect by simple interval mapping method

Trait	QTL name	Chromo-some	Left marker	Right marker	Position (cM)	LOD score	PVE (%)	Additive
LFMPc	*q-LFMPc-16-1*	16	i43776Gh	i49389Gh	144.00	3.55	9.05	3.76
Jassid injury	*q-JI-12-1*	12	i29317Gh	i16245Gh	19.00	3.53	8.23	3.83
	q-JI-12-2	12	i35524Gh	i08330Gh	139.00	3.58	10.24	3.06
Seed cotton yield	*q-SCY-3-1*	3	i03341Gh	i03339Gh	127.00	3.15	8.28	196.05
	q-SCY-9-1	9	i38265Gh	i51322Gb	14.00	3.62	10.22	234.46
	q-SCY-11-1	11	i06826Gh	i06723Gh	9.00	3.08	9.87	242.55
	q-SCY-15-1	15	i23609Gh	i11371Gh	221.00	5.79	18.88	295.12
	q-SCY-19-1	19	i59560Gb	i62239Gt	100.00	3.04	7.61	-206.49
	q-SCY-20-1	20	i34581Gh	i20100Gh	37.00	3.16	8.18	217.07
	q-SCY-24-1	24	i03997Gh	i52405Gb	297.00	4.18	10.79	232.90
	q-SCY-25-1	25	I10730Gh	i17162gh	404.00	3.52	14.29	-259.92

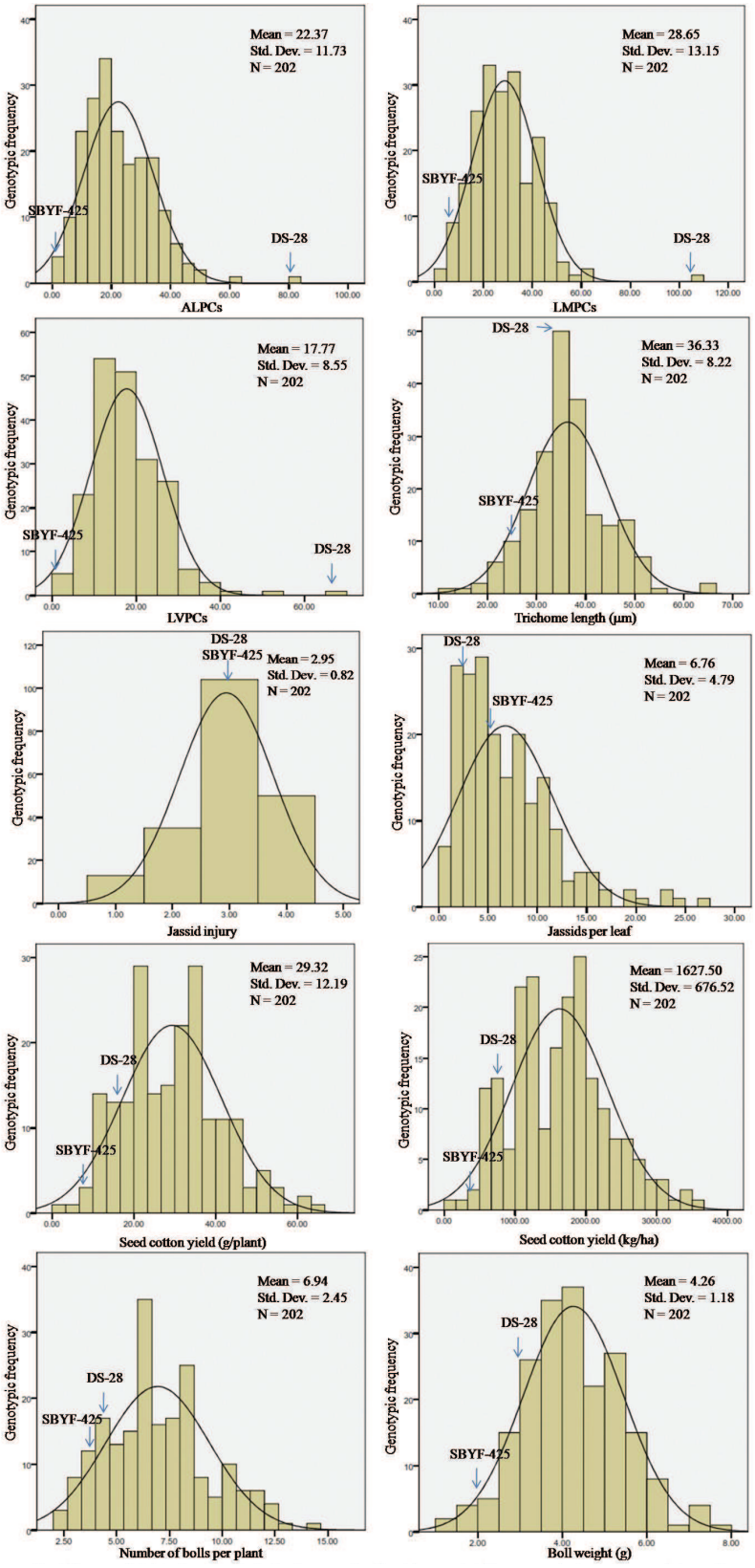

Fig. 1. The normal distribution curve for leaf pubesence, jassid resistance and yield components. Arrows represents the position of parental genotypes (DS-28 and SBYF-425)

remaining eight were for seed yield traits (Table 2). Single QTL detected for leaf mid-rib pubescence which was mapped on chromosome 16 (*qLFMPc-16-1,* i43776Gh-i49389Gh). The QTL *qLFMPc-16-1* was detected at peak LODs 3.55 explaining the phenotypic variances of 9.05 per cent. The QTL *qLFMPc-16-1* recorded the positive additive value of 3.76. The two QTLs, *q-JI-12-1* (i293117Gh-i16245Gh) and *q-JI-12-2* (i35524Gh-i08330Gh) were detected for jassid injury on chromosome 12. QTLs *q-JI-12-1* and *q-JI-12-2* were detected at peak LODs of 3.53 and 3.58; explaining the phenotypic variance of 8.23 and 10.24 respectively. A total of eight QTLs were detected for the seed cotton yield. Among the eight QTLs, one each of them was mapped on chromosome 3 (*q-SCY-3-1*, i03341Gh-i03339Gh), chromosome 9 (*q-SCY-9-1,* i38265Gh-i51322Gb), chromosome 11 (*q-SCY-11-1,* i06826Gh-i06723Gh), chromosome 19 (*q-SCY-19-1,* i59560Gb-i62239Gt), chromosome 20 (*q-SCY-20-1,* i34581Gh-i20100Gh), chromosome 24 (*q-SCY-24-1*, i03997Gh-i52405Gb), chromosome 25 (*q-SCY-25-1,* i10730Gh-i17162Gh) and chromosome 15 (*q-SCY-15-1,* i23609Gh-i11371Gh). The QTLs *q-SCY-3-1, q-SCY-9-1, q-SCY-11-1, q-SCY-19-1, q-SCY-20-1, q-SCY-24-1*, *q-SCY-25-1* and *q-SCY-15-1* were detected at peak LODs of 3.15, 3.62, 3.08, 3.04, 3.16, 4.18, 3.52 and 5.79; explaining the phenotypic variances of 8.23, 10.22, 9.87, 7.61, 8.18, 10.79, 14.29 and 18.88, respectively.

In composite interval mapping method seven QTLs were detected (Table 3). All the seven QTLs were found to be affect the different traits, explained 4.42 to 18.88 per cent phenotypic variation

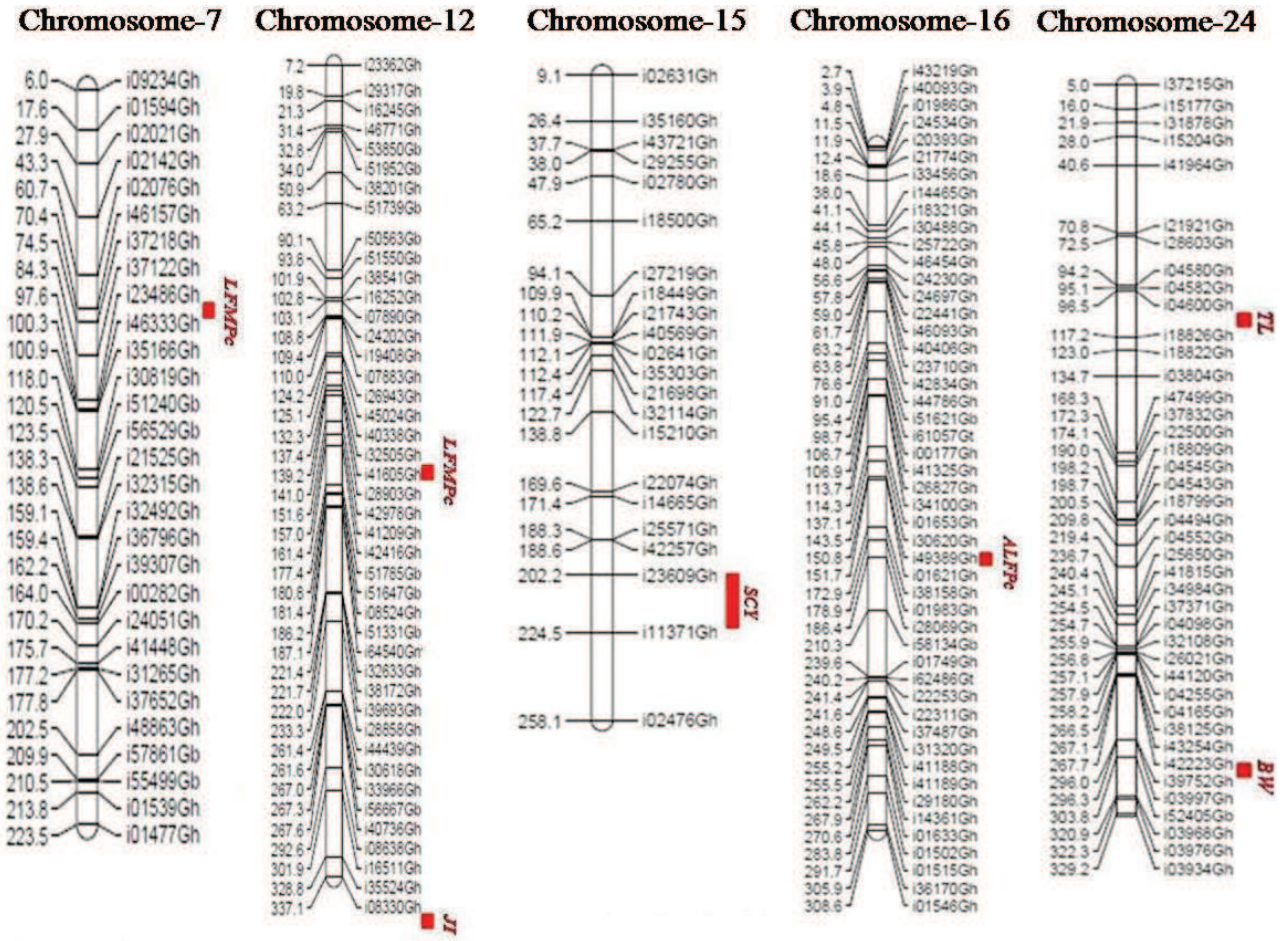

Fig. 2. Graphical representation of chromosomal positions of QTLs and flanking markers detected by composite interval mapping

and were located on chromosomes 16, 7,12,24,15 and 24. For the abaxial leaf trichomes only one QTL was detected with LOD 3.41, which was mapped on chromosome 16 (i43776Gh-i49389Gh, *q-ALFPc-16-1*). It explained 8.83 per cent phenotypic variance and an additive effect of 3.48. A total of two QTLs were detected for the leaf mid-rib trichomes, of which one mapped on chromosome 7 (*q-LFMPc-7-1,* i39581Gh-i46333Gh) and another on chromosome 12 (*q-LFMPc-12-1,* i45939Gh-i41605Gh). The QTLs *q-LFMPc-7-1*

Table 3. Trait wise QTLs, along with flanking markers, position on chromosome, LOD, Phenotypic variance and additive effect by composite interval mapping method

Trait	QTL name	Chromo-some	Left marker	Right marker	Position (cM)	LOD score	PVE (%)	Additive
ALFPc	*q-ALFPc-16-1*	16	i43776Gh	i49389Gh	149.00	3.41	8.83	3.48
LFMPc	*q-LFMPc-7-1*	7	i39581Gh	i46333Gh	100.00	3.21	7.42	3.53
	q-LFMPc-12-1	12	i45939Gh	i41605Gh	139.00	4.96	11.64	-4.12
Jassid injury	*q-JI-12-2*	12	i35524Gh	i08330Gh	339.00	3.58	10.24	3.06
Trichome length	*q-TL-24-1*	24	i04600Gh	i18826Gh	117.00	4.11	9.9	2.73
Seed cotton yield	*q-SCY-15-1*	15	i23609Gh	i11371Gh	221.00	5.79	18.88	295.12
Boll weight	*q-BW-24-1*	24	i42223Gh	i39752Gh	296.00	3.38	8.42	0.35

and *q-LFMPc-12-1* detected at peak LOD scores of 3.21 and 4.96 explained the phenotypic variance of 7.42 and 11.64, respectively. The QTL *q-LFMPc-7-1* recorded additive effect (3.53). One QTL was detected for trichome length on chromosome 24 (*q-TL-24-1,* i04600Gh-i18826Gh) with LOD score of 4.11. It explains that this trait with 9.9 per cent phenotypic variance had an additive effect of 2.73. One QTL was detected for jassid injury on chromosome 12 (*q-JI-12-2*) which was flanked by the markers i35524Gh and i08330Gh with 4.03 LOD score. It explained 10.63 per cent phenotypic variance with an additive effect of 3.74. One QTL was detected for seed cotton yield on chromosome 15 (*q-SCY-15-1*) which was flanked by the markers i23609Gh and i11371Gh with LOD 5.79. Phenotypic variance of 18.88% with an additive effect of 295.12 was recorded for this QTL. One QTL was detected for the boll weight on chromosome 24 (*q-BW-24-1,* i042223Gh-i39752Gh) with LOD 3.38, which explained 8.42 per cent phenotypic variance and with an additive effect of 0.35. Six QTLs recorded with additive effects contributing the favourable alleles for the traits expression.

Discussion

Genetic variability for leaf pubescence, jassid injury and seed cotton yield

Genetic variability was observed for leaf pubescence, jassid injury and yield characters in the RIL population. The range can provide a preliminary idea about the variability but it is the coefficient of variation which is reliable as it is independent of any unit of measurement. The *per se* performance gives ample opportunity to select RILs with a desirable amount of trichomes and high yield, which is an important morphological character for sucking pest tolerance. This present findings supports the results of Bhatti (2015). The extent of variability as measured by PCV and GCV also gives information regarding the relative amount of variation existing in the genetic material. This kind of wide range of genetic variability gives good chance to select RILs with a desirable amount of trichomes. Jassid injury tolerance has been observed due to the presence of more $ALFP_C$, $LFMP_C$, and $LFVP_C$ in cotton. The results of present study also support the findings of Murugesan and Kavitha (2010).

QTL analysis and mapping for leaf pubescence and yield traits

Though the trichomes are visible to our eyes it is important to map the QTLs for leaf pubescence to improve the utility of the QTL in marker assisted selection (MAS), and to move towards the positional cloning of candidate genes, where the mapping of the QTL to a smaller region of the chromosome is necessary (Wang et al. 2011). Keeping in view, the extensive use of cotton and its products, there is a need for breeding varieties by incorporating the gene for hairiness into promising cotton genotypes, which will not only minimize possible insect pest attack and insecticide usage but also helps to improve yield and fibre quality attributes.

QTL mapping can be considered in various levels of increasing complexity. The first level is a test of association between trait values and the genotypes of marker loci i.e., singlemarker analysis (SMA). The second level of QTL mapping, called simple interval mapping (SIM), requires the prior construction of a marker genetic map. SIM evaluates the association between the trait values and the expected contribution of a hypothetical QTL at multiple analysis points between each pair of adjacent marker loci. The third level is called composite interval mapping (CIM) or multiple QTL mapping (MQM). Like simple interval mapping, CIM evaluates the possibility of a target QTL at multiple analysis points across each inter-marker interval. However, at each point, it also includes the effect of one or more background markers. The inclusion of a background marker in the analysis helps in one of two ways depending on whether the background marker and the target interval are linked. If they are not linked, an inclusion of the background marker makes the analysis more sensitive to the presence of a QTL in the target interval. If they are linked, inclusion of the background marker may help to separate the target QTL from other linked QTLs on the far side of the background marker. Among the three methods of QTL analysis, highest numbers of QTLs (25) were detected in single marker analysis followed by simple interval mapping (11) and composite interval mapping (7). Although SMA and SIM can detect more number of QTLs, CIM is more powerful, precise and can minimize the bias that would normally be associated with a QTL that is linked to the position being tested. Among the leaf pubescence traits, number of QTLs were identified for leaf mid-rib trichomes *i.e*., 14 QTLs followed abaxial leaf trichomes and only one QTL was identified for trichome length, each trait both by the single marker analysis and interval mapping method. It indicates that genetic variability for mid-rib pubescence is more.

Using single marker analysis method, 25 QTLs were detected, out of which ten affect the LFMPc, twelve affect the seed cotton yield and three affect the boll weight. By simple interval mapping method, eleven QTLs were identified, out of which one affects the LFMPc, two affect jassid injury and seven affect the seed cotton yield, whereas by composite interval mapping seven QTLs were identified, among which one affects the ALFPc, two affect the LFMPc, one affects the trichome length, one affects the jassid injury and other two traits seed cotton yield and boll weight were affected by two independent single QTLs. QTL ifdentification for fibre quality and yield in a population of 107 RILs applying a large number of SNPs was carried out by Keerio et al. (2018). They identified a total of 74 QTLs out of which five QTL clusters were identified that could be used for breeding program for improving fibre quality and yield in upland cotton. The QTLs identified in the present investigation for different traits are useful and may be utilized in breeding cotton cultivars with high yield and fibre quality.

Authors' contribution

Conceptualization of research (ISK); Designing of the experiments (ISK, RP); Contribution of experimental materials (ISK); Execution of field/lab experiments and data collection (MS, MPJ, SA); Analysis of data and interpretation (MS, MPJ, RP, SA); Preparation of manuscript (MS, MPJ, SA, RP, ISK).

Declaration

The authors declare no conflict of interest.

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