High-resolution genetic map construction and QTL analysis of important fiber traits in kenaf using RAD-seq

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Abstract

Quantitative trait locus (QTL) mapping is a useful method for revealing the mechanism of complex genetic traits and identifying new genomic information to accelerate crop improvement. In the present study, 154 $F_{2:3}$ strains and their parents were used for restriction site-associated DNA sequencing, single-nucleotide polymorphism (SNP) identification, and genetic map construction. After filtering based on stringent filtering standards, 297.5 Gb of clean data were obtained. Further, 5,191 polymorphic SNP markers were identified from each sample, of which 1,997 polymorphic SNP markers were successfully mapped onto 18 different linkage groups. Six QTLs (QPH, QFBW, QDBW, QFW, QFT, and QFC) were identified based on the genetic map using the multiple QTL mapping (MQM) method, which were then assigned to three linkage groups, LG16, LG8, and LG3. QPH, QFBW, QDBW, and QFW were related to fiber yield, while QFT and QFC were related to fiber quality. This is the first study of its kind to map QTL of fiber yield and fiber quality, which will facilitate further understanding of the molecular genetic basis of these traits. However, there are limitations regarding the utilization of this map because several large gaps remain in some linkage groups. Therefore, additional markers need to be developed to further narrow these regions.

Introduction

Kenaf (*Hibiscus cannabinus* L.) is an important natural fiber crop. The main purpose of kenaf planting is to harvest bast fibers. Kenaf fibers can be used as textile materials, carpet backing, packing materials, paper pulp, and biocomposite materials (Li et al. 2019; Muniandi et al. 2018; Ahmad et al. 2020), and are permeable and possess antibacterial and biodegradable properties (Li et al. 2016). With global deterioration of the natural environment and the enhancement of people's awareness of environmental protection, the demand for natural fiber is increasing worldwide. Kenaf fiber is an important natural fiber; therefore, improving both the quality and yield of the fiber is an essential task in kenaf breeding.

It is common knowledge that the agronomic traits of fiber yield and quality are controlled by polygenes. It is difficult to further increase the fiber yield and quality using traditional breeding strategies, such as hybrid breeding, which are the main methods currently used to improve these traits. Marker-assisted selection breeding is an efficient method to improve both fiber yield and quality.

In kenaf, the first genetic linkage map was constructed in 2011 using sequence-related amplified polymorphism (SRAP), inter simple sequence repeats (ISSR), and random amplified polymorphic DNA (RAPD) markers, which comprised 307 loci (Chen et al. 2011). Due to the limitation of the number of traditional markers when constructing the genetic linkage map, the map cannot achieve sufficient resolution for quantitative trait locus (QTL) mapping or map-based cloning. However, single-nucleotide polymorphism (SNP) markers, which are widely distributed in plant genomes, have been previously used to construct genetic maps and map QTLs in many crops, such as jute, upland cotton, alfalfa, Hawthorn, and soybean (Yang et al. 2019; Li et al. 2017; Zhang et al. 2019; Zhao et al. 2020; Liu et al. 2017).

The combination of next-generation sequencing technology (NGS) and restriction enzyme digestion has facilitated the development of SNP markers and genotyping processes (Hohenlohe et al. 2011). Restriction site-associated DNA sequencing (RAD-seq) is an efficient method to develop SNP markers for high-throughput genotyping, and does not require a reference genome. To date, RAD sequencing has been used to construct high-density linkage maps and QTL maps for important agronomic traits in many species, such as barley and *Barbarea vulgaris* (Chutimanitsakun et al. 2011; Liu et al. 2019). However, high-density genetic linkage maps have been constructed for kenaf using RAD-seq technology.

In this study, we developed a high-density genetic linkage map with SNP markers, using an $F_{2:3}$ population derived from a cross between Taihong763 (♀) and F71 (♂). This is the first attempt to use SNP markers to construct high-density genetic linkage maps. We first identified six QTLs for both fiber yield and quality agronomic traits based on this genetic map. These results will be fundamental for marker-assisted gene selection in kenaf breeding programs.

Materials And Methods

Plant material

A tall female parent Taihong763 with a plant height of 466 cm and a short male parent F71 with a plant height (360 cm) were supplied by the Institute of Bast Fiber Crops, Chinese Academy of Agricultural Sciences. Hybridization occurred between Taihong763 (♀) and F71 (♂), which were planted in Changsha, in Hunan Province during the summer of 2017. The hybrid seeds were harvested, and these were planted in eight rows (each row was 10 m long, 0.6 m apart) and self-pollinated to produce the F2 generation in Sanya, Hainan Province, in 2019. In 2020, we selected 154 $F_{2:3}$ plant strains and planted them in Changde, Hunan Province. The two parents and the 154 $F_{2:3}$ plant strains were used to construct high-density genetic linkage map and to map QTLs. Young leaf tissues from the two parents and 154 $F_{2:3}$ plant strains were collected for genomic DNA extraction.

Fiber yield and fiber quality phenotypic measurements and analysis

The $F_{2:3}$ population was planted in Changde, Hunan, in the summer of 2020. Ten individual plants of each $F_{2:3}$ plant strain were randomly selected for measuring their agronomic traits. The following six agronomic traits related to fiber yield and quality were investigated in this study: plant height (PH), fresh bast weight (FBW), dry bast weight (DBW), fiber weight (FW), fiber strength, (FS), and fiber count (FC). pH was measured in mature plants as the distance (cm) from the root to the top of the plant. FBW was determined based on the weight (g) of the whole plant's fresh bast. DBW was determined by the weight (g) of the whole plant's dry bast. FW was measured as the weight (g) of the whole plant's bast fiber. FS (N/tex) was measured using an Instron 3350 instrument. FC (N) was measured using an OFDA 2000 instrument. SPSS software (version 21.0) was used for statistical analysis of phenotypic data. The field trial experiments were performed in Changde, Hunan, in the summer of 2020, following completely

random block design with three replications. The average value was calculated as the final phenotypic value.

DNA extraction, RAD library construction and sequencing

Young leaves from $F_{2:3}$ individuals and their parents were collected and used to extract genomic DNA following the manufacturer's protocol of the Plant Genomic DNA extraction Kit (Tiangen Biotech, Beijing, China). DNA concentration and purity were assessed using a NanoPhotometer® NP 80 spectrophotometer (IMPLEN, CA, USA).

The RAD-seq library was developed based on a previously described protocol (Baird et al. 2008; Guo et al. 2015). Genomic DNA of the $F_{2:3}$ strains and their parents were digested by EcoRI (New England Biolabs, Ipswich, MA, USA) and were then ligated to a P1 adapter containing a nucleotide barcode for individual labeling. The digested DNA and the P1 adapter from different samples were pooled together and randomly sheared. The 400–700 bp fragments were selected and ligated with the P2 adapter. Several rounds of PCR amplification were performed to enrich the adapter-ligated DNA fragments, and DNA fragments within the 400–700 bp range were selected and purified for library construction. The qualified library was sequenced on HiSeq4000 platform using the PE150 strategy.

SNP discovery and genotyping

The raw data were segregated to each individual of the $F_{2:3}$ population or the parents according to their nucleotide barcodes. The raw reads were filtered to the trimmed P1 and P2 adapter sequences, and the low quality sequences were removed, according to the standards described by Nie et al. (2017). SNP identification and genotyping were performed using the Stacks software (Catchen et al. 2011). The SNPs of the two parents and individuals of the $F_{2:3}$ population were identified by aligning the clean reads to the reference RAD tags. Polymorphic SNPs were selected according to the following stringent filtering standards: (a) homozygous sites with polymorphism between parents were screened, (b) the loci with missing parental information were filtered out, and (c) the loci with >10% unidentified nucleotides were removed from the offspring population. Genotypes of each $F_{2:3}$ plant strain were obtained by comparing these genotypes with the parental genotypes. Polymorphic SNP markers, which conformed to the above standards and with <10% missing data among the 154 $F_{2:3}$ strains, were used to construct the genetic map.

Genetic linkage map construction

Polymorphic SNP markers with more than a 10% deletion rate in the $F_{2:3}$ plant strains were removed and further filtered using the parameters of segregation distortion ($p < 0.01$). The value of logarithm of odds (LOD) ranged from 2.0 to 20.0 using the maximum likelihood method. Joinmap 4.1 software was used to separate filtered markers into 18 linkage groups. The distance between the polymorphic SNP markers was then calculated using Kosambi mapping function. MapChart 2.2 software was used to draw the visualized linkage map (Voorrips 2002).

QTL mapping and analysis

The fiber yield and quality data were used to map QTLs based on the high-density genetic map using MapQTL6.0 (Van Ooijen and Kyazma 2009). A multiple QTL mapping (MQM) model was used to scan the QTLs. A permutation test (1000 replications) at 5% level of significance was conducted to achieve the LOD threshold, which was in turn used to determine the existence of QTLs. QTLs were detected with an LOD threshold of ≥4.0. Moreover, the location of the QTL was determined according to its peak LOD location and the surrounding region over the score threshold. The analysis results indicated the additive effects of QTLs and explanation rate of phenotypic variation by QTLs.

Results

Phenotypic analyses of fiber yield and quality traits

Fiber yield and quality phenotypic data showed continuous positive distribution or positively skewed distribution (Fig. 1). As shown in Fig. 1, the six agronomic traits are quantitative traits controlled by multiple genes. Transgressive segregation in the $F_{2:3}$ population was observed for the six traits, which suggested that there were allelic genes, which had positive effects on the six agronomic traits. The correlation analysis (Table 1) showed that there was a positive correlation between FW and PH, FBW, and DBW ($p < 0.01$). This is because the kenaf fiber originates from the bast of the plant, and the FW is closely related to the bast weight. Taller the plant, more is the weight of the fiber. There was also a positive correlation between the FW and FS ($p < 0.01$). However, there was a negative correlation between FW and FC ($p < 0.01$). There was no correlation between the FS and FC.

Table 1
Phenotypic correlation coefficients between the six agronomic traits

	PH	FBW	DBW	FW	FS	FC
PH	1.000					
FBW	0.599**	1.000				
DBW	0.544**	0.951**	1.000			
FW	0.541**	0.919	0.984**	1.000		
FS	0.116	0.282**	0.365*	0.394**	1.000	
FC	-0.069	-0.160*	-0.191	-0.186	-0.001	1.000
'PH', 'FBW', 'DBW', 'FW', 'FS', and 'FC' represent 'plant height', 'fresh bast weight', 'dry bast weight', 'fiber weight', 'fiber strength', and 'fiber count', respectively.						
'**' and '*' represent significance at p <0.01 and $p < 0.05$.						

Rad Sequencing And Genotyping

There were 156 RAD-seq libraries that were constructed from 154 $F_{2:3}$ strains and their parents, which were then sequenced on the Illumina HiSeq4000 platform. A total of 305.93 Gb of raw data were obtained and assigned to each sample according to their nucleotide barcode. After filtering and trimming the adapter sequence and removing the low-quality sequences, 297.5 Gb of clean data were obtained. There were 196,389 RAD tags that were found and used as reference tags. The SNP loci of each sample were identified. According to stringent filtering standards, 5,191 polymorphic SNP markers were identified and used to construct the genetic map. The number of SNP markers in each sample is shown in Table S1.

Genetic Linkage Map Construction

After filtering, 1,997 polymorphic SNP markers were successfully mapped onto 18 different linkage groups (Table 2, Fig. 2). This map covered a genome length of 1282.045 cM, with an average marker distance of 0.642 cM. The genetic length of each linkage group ranged from 2.939 cM (LG18) to 139.106 cM (LG12). Among these linkage groups, the densest linkage group was LG1 with an average density of 0.05 cM, containing 214 SNP loci, whereas the sparsest linkage group was LG17 with an average density of 2.526 cM, containing only 33 SNP loci. The maximum gap length was 42.452 cM, which occurred in LG12, and the minimum gap length was 0.504 cM, which occurred in LG18. According to these results, the linkage distance distribution and resolution in this genetic map were much better than the genetic map constructed using SRAP, ISSR, and RAPD markers.

Table 2
Distribution of mapped SNP markers on the 18 linkage groups of kenaf

Linkage group	No. of SNPs	Total genetic distance(cM)	Average inter-loci distance (cM)	Max gap(cM)
LG1	214	10.759	0.05	3.335
LG 2	160	40.111	0.251	11.152
LG 3	129	99.27	0.77	33.635
LG 4	91	109.957	1.208	19.156
LG 5	71	88.229	1.243	27.268
LG 6	229	46.305	0.202	12.102
LG 7	112	48.622	0.434	13.036
LG 8	201	100.312	0.499	16.129
LG 9	33	39.121	1.185	33.196
LG 10	27	53.816	1.993	30.55
LG 11	128	61.088	0.477	19.474
LG 12	78	139.106	1.783	42.452
LG 13	247	54.963	0.223	4.821
LG 14	135	136.153	1.009	27.631
LG 15	27	30.906	1.145	7.03
LG 16	62	137.034	2.21	23.939
LG 17	33	83.354	2.526	27.422
LG 18	20	2.939	0.147	0.504
Total	1997	1282.045		

Fiber Yield And Quality Qtl Analysis

The fiber yield and quality-related traits, which showed a continuous distribution (Fig. 1), were controlled by polygenes. Overall, six QTLs (QPH, QFBW, QDBW, QFW, QFT, and QFC) were detected with the genetic map using the MQM method (Fig. 2, Table 3). Among the six QTLs, QPH, QFBW, QDBW, and QFW were associated with fiber yield, and QFT and QFC were associated with fiber quality. On LG16, two QTLs (Q1 and Q2) were detected, QPH1 and 2, QFBW2, and QFW3 were located at the same locus (Q1), and QFC was located at the Q2 locus. QPH, with two closely related markers (un_59437998 and un_24745703), explained 13.8% and 13.5% of the PH phenotypic changes, respectively. QFBW, with two closely related

markers (un_37170711, un_59437998), explained 10.7% and 11.9% of the FBW phenotypic changes, respectively. QFW, with closely related marker un_59437998, explained 10.5% of the phenotypic variance of the FW. QFC, with closely related marker un_25677623, could explain 12.3% of the phenotypic variance of the FC. On LG8, one QTL was identified, and QDBW and QFW 1 and 2 were located at the same locus (Q3). QDBW, with the closely related marker un_56233383, could explain 11.8% of the phenotypic variance of the DBW. QFW, with two closely related markers un_56233383 and un_36391475, could explain 14.7% and 14.0% of the phenotypic variance of the FW, respectively.

Table 3
QTL mapping results for fiber yield and quality in kenaf

Traits	QTL	Linkage group	Related marker name	Related marker genetic distance(cM)	LOD	Additive effect (%)
PH	QPH1	16	un_59437998	30.196	4.97	13.8
	QPH2			29.912	4.84	13.5
			un_2474 5703			
FBW	QFBW1	3,16	un_37170711	17.494	4.32	10.7
	QFBW2		un_59437998	30.196	4.24	11.9
DBW	QDBW	8	un_ 56233383	41.339	4.18	11.8
FW	QFDW1	8,16	un_ 56233383	41.339	5.32	14.7
	QFW2		un_ 36391475	41.220	5.04	14.0
	QFW3		un_59437998	30.196	4.39	10.5
FT	QFT	3	un_ 14650517	17.154	5.47	15.1
FC	QFC	16	un_25677623	60.502	4.38	12.3
PH: plant height, FBW□fresh bast weight, DBW□dry bast weight, FW□fiber weight,						
FT: fiber strength, FC□fiber count						

In LG3, two QTLs (Q4 and Q5) were identified, and QFBW (Q5), with the closely related marker un_37170711, could explain 10.7% of the phenotypic variance of the FBW. QFC (Q4), with the closely related marker un_14650517, could explain 15.1% of the phenotypic variance of the FS.

Discussion

A high-density genetic linkage map is useful to map important agronomic QTL, which can discover valuable alleles and reveal genetic mechanisms. Traditional molecular markers, such as RAPD and AFLP, have been used to construct genetic linkage maps of important crops (Yu et al. 2012; Ferreira et al. 2000;

Dong et al. 2019; Riaz et al. 2004). However, the genetic linkage maps constructed using traditional molecular markers have a lower resolution and lower genome coverage than the genetic map constructed using SNP markers. With the development of sequencing technology, RAD-seq technology has been used for identifying SNPs and constructing genetic maps without a reference genome. To date, there have been no reports on a high-density genetic linkage map of kenaf, which was constructed using SNP markers obtained by RAD-seq. In this study, we developed a large number of SNP markers with the RAD-seq method and constructed a SNP genetic map for kenaf. There are 5,191 polymorphic SNP markers, which were obtained from 154 $F_{2:3}$ offspring and two kenaf parents. Of the polymorphic SNP markers, 1,997 SNP markers were successfully segregated to 18 linkage groups, corresponding to 18 chromosomes of kenaf. Compared with previously published genetic map with 307 loci constructed using ISSR, SRAP, and RAPD markers (Chen et al. 2011), the marker number and quality of the present genetic map achieved a new milestone. Moreover, the current version of the genetic map can be used for QTL mapping and locating important genes of kenaf. However, many large gaps remain in some linkage groups that may limit its application in some aspects. Therefore, we need to develop additional markers to further narrow the gaps in these regions.

The main purpose of kenaf planting is to harvest bast fibers. Therefore, continuously improving fiber yield and quality are important breeding targets for kenaf. QTLs of agronomic traits related to yield have been detected in many crops, such as rice and maize (Shi et al. 2020; Yang et al. 2020). However, there are no previous reports on fiber yield QTLs in kenaf. In the present study, we found six QTLs of fiber yield and quality based on the genetic map. These six QTLs were assigned to three linkage groups, namely LG3, LG8, and LG16. QPH1, QDBW2, and QFW3 were located in the same region in LG16 and were closely associated with the same SNP marker un_59437998. The results showed that the three agronomic characters were closely related. Moreover, QDBW and QFW1 were located in the same region in LG8 and were closely associated with the same SNP marker un_56233383. These results showed that fiber yield and quality-related genes may have pleiotropic effects. The SNP markers un_59437998 and un_56233383 were closely linked to fiber yield agronomic trait, suggesting that the two SNP markers can be candidate molecular markers for determining the fiber yield during breeding.

To the best knowledge of the authors, this is the first study of its kind to perform QTL mapping for both fiber yield and fiber quality. Six QTLs were identified that were assigned to three linkage groups, namely LG3, LG8, and LG16, among which QPH, QFBW, QDBW, and QFW were related to fiber yield, and QFS and QFC were related to fiber quality. The QTLs obtained in the present study will facilitate further understanding of the molecular genetic basis of these traits.

Statements And Declarations

Ethics approval and consent to participate: NA

Consent for publication: NA

Availability of data and materials: NA

Competing Interests: The authors declare no competing interests.

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Author contributions:

CG conceived the project; CL, TJ, PG, JH, WN measured and collected the data of field agronomic characters; LH, HQ wrote the initial draft, LB revised the manuscript. All authors had read and approved the final manuscript

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Figures

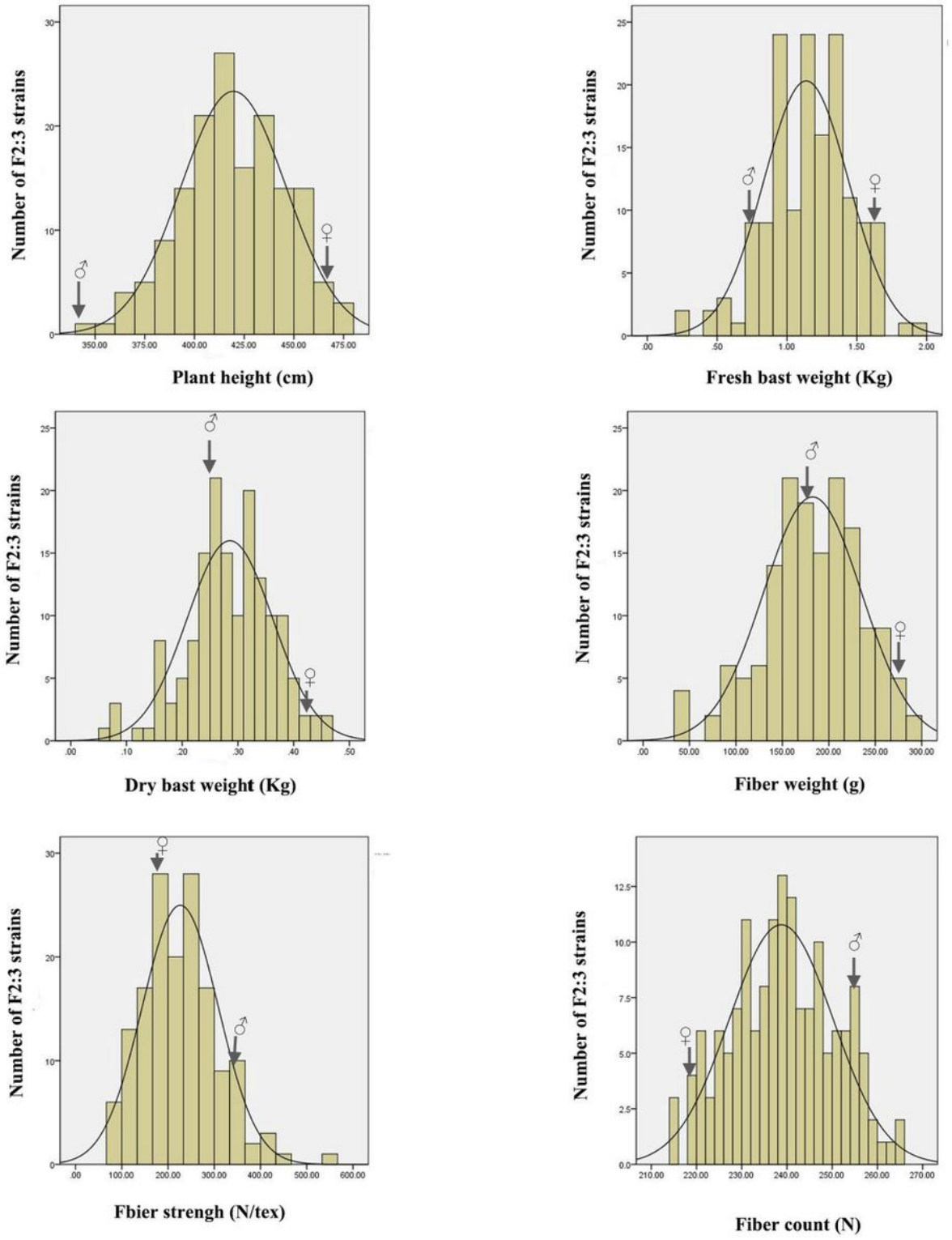

Figure 1

Phenotypic distribution of six traits among the 154 F2:3 strains

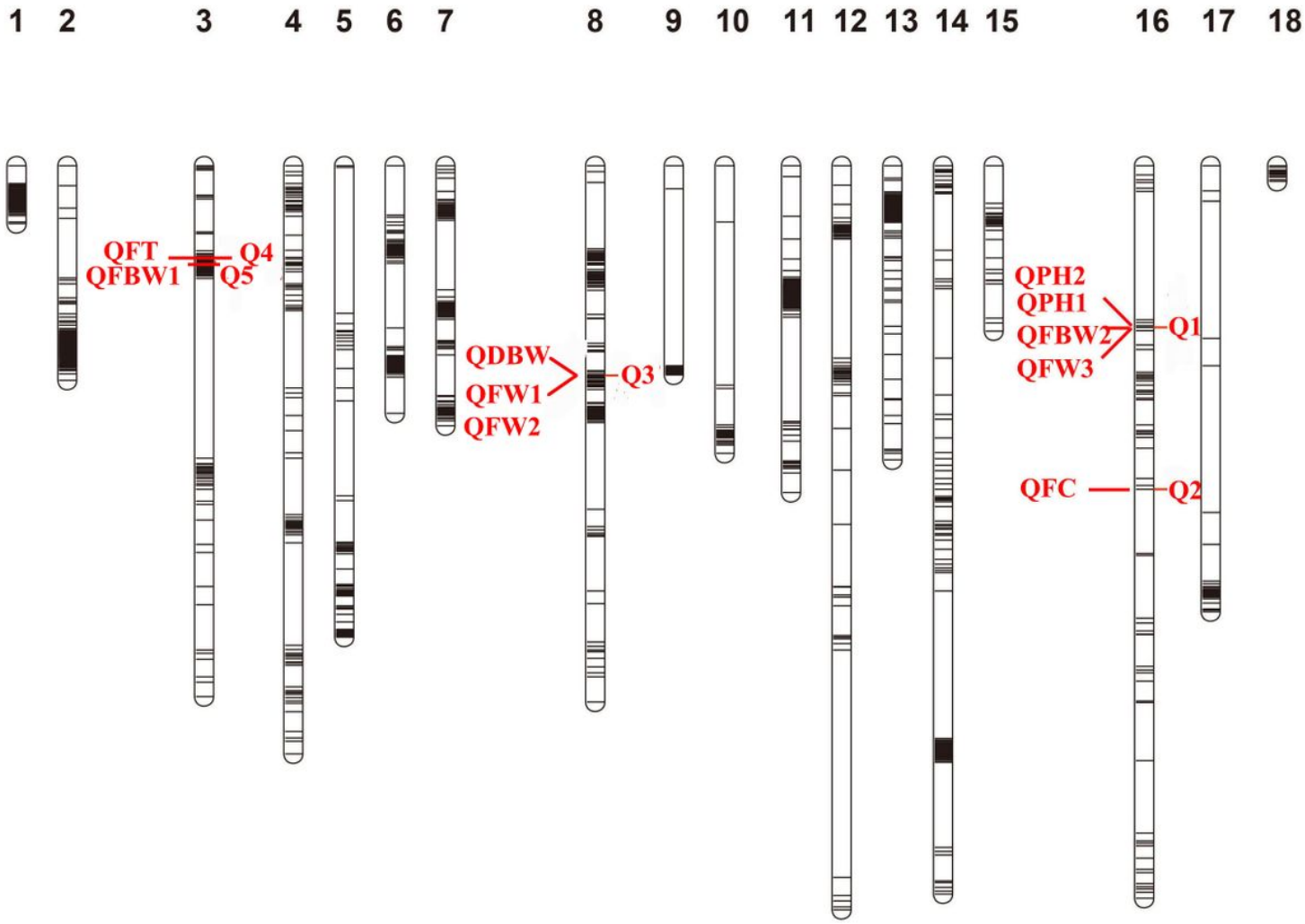

Figure 2

Identification of fiber yield and fiber quality-related QTL using a high-density genetic map in kenaf. Each black line represents a SNP locus. Q1, Q2, Q3, Q4, and Q5 represent the name of the QTL locus

Supplementary Files

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- S1Table.xls