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A COMPLETE GENETIC LINKAGE MAP AND QTL ANALYSES FOR BAST FIBRE QUALITY TRAITS, YIELD AND YIELD COMPONENTS IN JUTE (*CORCHORUS OLITORIUS* L.)

We report the first complete microsatellite genetic map of jute (Corchorus olitorius L.; 2n = 2x = 14) using an F_6 recombinant inbred population. Of the 403 microsatellite markers screened, 82 were mapped on the seven linkage groups (LGs) that covered a total genetic distance of 799.9 cM, with an average marker interval of 10.7 cM. LG5 had the longest and LG7 the shortest genetic lengths, whereas LG1 had the maximum and LG7 the minimum number of markers. Segregation distortion of microsatellite loci was high (61 %), with the majority of them (76 %) skewed towards the female parent. Genomewide non-parametric single-marker analysis in combination with multiple quantitative trait loci (QTL)-models (MQM) mapping detected 26 definitive QTLs for bast fibre quality, yield and yield-related traits. These were unevenly distributed on six LGs, as colocalized clusters, at genomic sectors marked by 15 microsatellite loci. LG1 was the QTL-richest map sector, with the densest co-localized clusters of QTLs governing fibre yield, yield-related traits and tensile strength. Expectedly, favorable QTLs were derived from the desirable parents, except for nearly all of those of fibre fineness, which might be due to the creation of new gene combinations. Our results will be a good starting point for further genome analyses in jute.

Introduction. Jute is one of the most important ligno-cellulosic bast fibre crops and produces one of nature's strongest vegetable fibres only next to cotton in production.

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Besides its traditional roles in woven industry and geotextiles, it is increasingly being used in automotive and paper industries [1]. It belongs to the genus *Corchorus* in the family Sparrmanniaceae [2] and is represented by the two diploid ($2n = 2x = 14$) cultivated species, viz., *C. capsularis* L. (white jute) and *C. olitorius* L. (dark jute). However, the latter represents the predominant jute crop in the world occupying more than 80 % of the total jute growing area because it is not only high yielder but also ideally suited to transplanted paddy-based crop rotation [3].

Jute is a self-pollinated crop. For strong sexual incompatibility combined with a dearth of compatible breeding resources [4], conventional pedigree breeding is the preferred means for jute improvement. However, it is a typical short-day plant for flowering, but requires long-day for bast fibre production; fibre matures at 120 d, while seed at 150–180 d after sowing [5]. Hence, there is an inherent problem in plant selection because fibre and seed cannot be obtained from the same jute plant. Selection on the basis of highly correlated bast fibre yield components, such as plant height, stem base diameter, number of nodes, etc. is the standard practice in jute breeding [3, 6, 7]. Although these traits are quantitative in nature and show non-additive genetic variance [8], they exhibit moderately

high heritability and genetic advance [7]. In contrast, bast fibre quality traits like fibre fineness and tensile strength are complex under polygenic control with low to medium heritability, and thus the gain in selection for these characters is relatively much slow [7]. In view of these factors, jute is perhaps the premier example of a crop plant in which marker-assisted selection (MAS) appears to be almost indispensable even in a small resource-poor breeding program in a developing country.

Despite its small haploid genome size (~ 300–450 Mb) amongst the economically important crop species [9, 10], genomics research has not progressed much in jute as compared to other important crop species including cotton and allied bast fibre crops like flax and kenaf. Only in the last decade, various DNA markers, such as inter-simple sequence repeat (ISSR), random amplified polymorphic DNA (RAPD), simple sequence repeat (SSR) and sequence tagged microsatellite site (STMS) were developed for jute [11–16]. A large number of genomic microsatellites was enriched in *C. olitorius* [17, 18], which were used for genetic diversity analyses and for tagging traits of agronomic importance [17, 19, 20].

However, complete genetic maps of the two cultivated jute species could not be constructed, although elementary maps resolving few linkage groups based on few ISSR or RAPD or microsatellite markers continued to be published over the past several years [21–23]. These efforts proved to be more of academic interest than of any practical breeding use. More recently, Das et al. [24] used an incomplete linkage map of *C. olitorius*, with six linkage groups, to analyze quantitative trait loci (QTLs) for bast fibre quality and yield traits. However, a framework genetic map with complete coverage of the genome as expected on the basis of haploid chromosome number of jute ($n = 7$) is yet to be developed. And this continues to be the primary challenge limiting the progress of QTL analyses and the implementation of MAS in jute, particularly when it does not even have any supporting classical linkage map and cytogenetic stocks that can be used to align the linkage groups to chromosomes.

We report here the first complete genetic linkage map of jute by mapping a set of 83 highly polymorphic microsatellite loci on an F_6 recombinant inbred line (RIL_6) population from a cross of an *olitorius* cultivar with one phenotypically distinct *olitorius* selection. This microsatellite genetic map could not only be resolved into seven linkage groups with a total genetic distance of 799.9 cM, but also was reliably used for the detection of QTLs for bast fibre quality traits, yield and yield components.

Material and methods. *Mapping population*. The mapping population was developed from a cross of JRO 524 (♀), a leading *C. olitorius* cultivar that has saturated about 80 % of the jute area in the world [3], with PPO4 (♂), a selection from *C. olitorius* exotic accession OIJ 154 [25]. This selection is characterized by a phenotypic marker of redtinted pale green stem that becomes crimson red at maturity as compared to the green stem of JRO 524. In addition, PPO4 produces fine fibre (1.5 tex) of high tensile strength (19.7 g tex^{-1}) with low lignin content (13.8 %) as compared to JRO 524 [25]. The haploid genome size of PPO4 (315.8 Mb) is smaller than that of JRO 524 (327.8 Mb) [10]. The RIL_6 population comprising 120 genotypes was developed by single seed descent.

Phenotyping. The mapping population was raised in the CRIJAF (Kolkata, India) experimental field (22.45° N, 88.26° E; 3.14 m above msl) during the summer (March-September; mean day/night temperature: 32.7/24.2 °C; RH: 68.8–93.7 %) following the recommended cultural practices. The trial was laid out in a randomized complete block design (RCBD) with three replications. Each genotype was represented by three rows of 10 plants each at a spacing of 10 cm in rows 30 cm apart per replication. At 120 d after sowing, 10 healthy plants were harvested per replication, and observations were recorded on plant height (PH; cm), number of nodes (NN), stem diameter base (SDB; cm), stem diameter mid (SDM; cm), stem diameter top (SDT; cm) and green biomass yield (GBY; g $plant^{-1}$). For bast fibre extraction, the harvested plants were steep-retted in a water tank. After drying, fibre and wood yields (FY and WY; g $plant^{-1}$) were determined. Bundle strength and airflow fineness testers (NIRJAFT, Kolkata) were used to measure tensile strength (TS; g tex^{-1}) and fibre fineness (FF; tex in a decreasing 0–5 scale), respectively.

Microsatellite genotyping. High-quality mucilage-free genomic DNA was isolated from leaf tissues as described by [26]. A total of 403 microsatellite

markers representing the four genomic libraries of *C. olitorius* cv. JRO 524 [18] was screened to detect polymorphisms between the two parental lines. Altogether, 83 polymorphic markers were identified, and these were used for genotyping the mapping population. The 83 microsatellite sequences were amplified according to [26] using a PCR protocol consisting of 30 cycles at 94 °C for 1 min, T_a °C [17, 18] for 1 min and 72 °C for 1 min followed by a final extension at 72 °C for 5 min. Amplified products were separated in 10 % denaturing polyacrylamide (19:1) gels in 1.0 × TBE buffer at 80 V cm^{-1} constant voltage, silver-stained [27] and recorded under an AlphaImager (Cell Biosciences, Santa Clara) gel documentation unit. Alleles were scored for size in bp and coded as codominant markers.

Genetic map construction. Linkage analysis and genetic map construction were carried out using various options in JoinMap 4 [28]. The genotype frequencies for each microsatellite locus were calculated, and its segregation ratio was tested against the expected ratio using the chi-square goodness of fit test. For linkage analysis, grouping was initially done using independence logarithm of the odds (LOD) thresholds (3–10; step 1.0) based on the G^2 statistic [28] and finally using a recombination frequency threshold of 0.250–0.200 (step –0.050). The linkage group assignment of loci was verified using the strongest cross link (SCL) function. The genetic recombination map was constructed using the multipoint maximum likelihood (ML) algorithm [29] that exclusively uses the mapping function of Haldane.

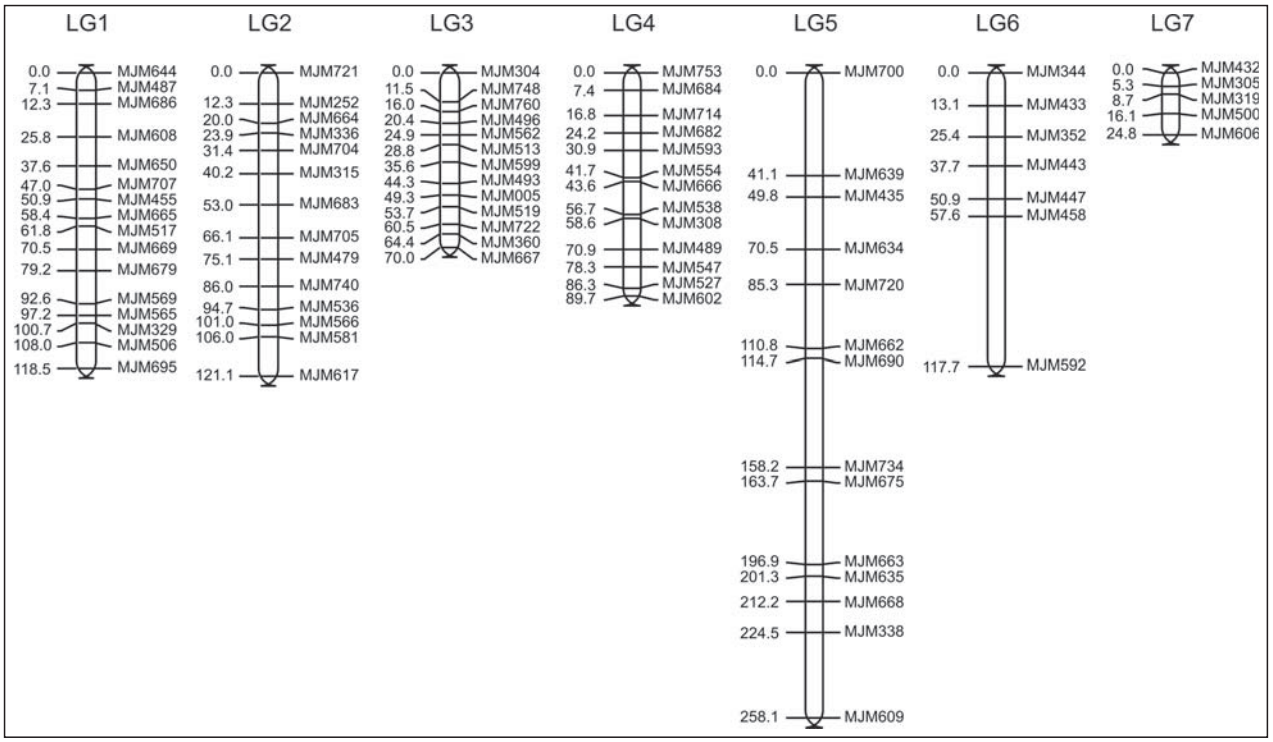
Phenotypic data analyses. For each trait, adjusted entry means for all RILs were calculated using the statistical model: $y_{ij} = \mu + \mathrm{RIL}_i + e_{ij}$, where y_{ij} was the phenotypic observation of the *i*th RIL in the *j*th block, μ was the general mean, RIL_i was the effect of the *i*th RIL (fixed) and e_{ij} was the residual. For estimation of variance components, all effects were considered as random. Heritability on an entry mean basis was calculated according to [30]

$$h^2 = \sigma_g^2/(\sigma_g^2 + \overline{w}/2),$$

where σ_g^2 was the genotypic variance and $\overline{w}$ was the mean phenotypic variance of the difference between two adjusted entry means. Trait associations were estimated by Spearman's nonparametric method of rank correlation using original non-transformed data. Normality (Shapiro-Wilk test) and equal variance (Bartlett's test) assumptions were tested for phenotypic data for each character, and accordingly they were transformed into logarithmic scales: FS, FY, GBY, NN, PH and SY into $\log_{10}$, while FF, SDB, SDM and SDT into $\log_{10}(x+1)$. Data analyses were performed using GenStat Version 7.2.0.220 (VSN International Ltd., Oxford, UK) and PLABSTAT Version 3A [31].

QTL analyses. QTL analyses were performed using various functions in MapQTL 6 [32] based on log-transformed mean values over the three biological replicates. Both chromosomewide and genomewide LOD significance thresholds at P = 0.05 were estimated by the permutation test [33], with at least 1,000 permutations. For estimating single marker influence, the Kruskal-Wallis rank-sum test was performed for each locus separately using original non-transformed mean values of each trait. QTLs were detected using the mixture model option for multiple-QTL models (MQM) that conduct a genomewide one-dimensional search for segregating QTLs while simultaneously fitting the selected cofactors [34]; a single segregating QTL was fitted in the background of cofactors. Cofactors were chosen by backward selection using the automatic cofactor selection (ACS) option. QTLs were considered significant if their LOD scores reached only a genomewide level of significance, and they were designated according to [35]. QTL intervals and graphs were drawn using MapChart 2.2 [36].

Results. *Genetic linkage mapping.* Genetic mapping of the *C. olitorius* RIL_6 population using 83 (1 locus MJM681 unmapped) polymorphic microsatellite loci identified seven linkage groups (LG1-LG7) that covered a total genetic distance of 799.9 cM (Figure). The map was characterized by an average marker interval (AMI) of 10.7 cM, with 96.9 % of genome within 20 cM to the nearest marker. The longest genetic distance was resolved for LG5 (258.1 cM) with an AMI of 18.4 cM, while the shortest for LG7 (24.8 cM) with an AMI of 5.0 cM. The distribution of markers between the linkage groups was unequal, with LG1 having the maximum (16) and LG7 the minimum (5) number of markers. LG2 to LG5 comprised 13–14 markers each. However, no relationship could be established between the number of markers and the genetic distance covered. With only 7 markers, LG6 covered a gene-



A microsatellite-based genetic recombination map of *Corchorus olitorius* JRO 524 × PPO4 F_6 recombinant inbred lines. Genetic distances of markers are shown in centiMorgan (cM)

tic distance of 117.7 cM (16.8 cM AMI) that nearly corresponds to the genetic distance of LG1 (118.5 cM) or LG2 (121.1 cM). LG5 and LG6 were obviously characterized by big gaps, e. g., as high as 60.1 cM on LG6 (Figure), which could be saturated by increasing the number of microsatellite loci.

Marker segregation distortion. The 83 microsatellite loci used to construct the genetic map represented 76.8, 17.1, 1.2 and 4.9 % of di-, tri-, tetra- and penta-nucleotide motifs, respectively. Of the 82 loci eventually mapped, 50 loci (61 %) significantly ($P \leq 0.05$) deviated from the expected 1:1 Mendelian segregation ratio. Distorted loci were distributed throughout the entire length of the genome. The regions of segregation distortion extended to the complete genetic distance of LG7 and the majority of the genetic distance of LG2 (71.4 %) and LG5 (78.6 %). The least segregation distortion was for LG3 (46.1 %) and LG4 (38.5 %). Among the distorted loci, 38 loci (76.0 %) skewed towards the female parent, while 12 loci (24 %) towards the male parent. The genomic regions or linkage groups were distinguished by a distinct pattern in the direction of segregation distortion. All distorted loci on LG1, LG5, LG6 and LG7 skewed in favor of the female alleles and those on LG3 in favor of the male alleles. The majority of the distorted loci on LG2 (80 %) skewed in favor of the female alleles, whereas the segregation distortion was more or less equi-directional on LG4. No specific distribution pattern of the distorted loci was observed on the map, except on LG3 and LG6 where the distorted loci formed clusters at the distal ends of the genetic distance.

Phenotypic variation. The phenotypic values for bast fibre traits and yield components of the RIL_6 population are shown in the Table 1. Analyses of variance showed significant variation ($P \leq 0.001$) among RILs for all traits, with minimum variation observed for PH and SDB as evident from ranges and coefficients of variation (data not shown). All traits had absolute skewness values around or less than 1. However, the absolute values of kurtosis for SDB, SDM, FF, FY and TS were greater than one.

Heritability estimates were moderately high for all traits, with FF showing the least. Spearman's rank correlations, presented in Table 2, showed that bast fibre yield had significant ($P \leq 0.001$) positive associations with all yield components, particularly PH, SDB, GBY and WY. Between the two fibre quality traits, TS had significant ($P \leq 0.05$) positive correlations only with SDB and FY. However, no significant ($P \leq 0.05$) correlations were present between FF and the other traits.

QTL mapping. A total of 26 'definitive QTLs' (genomewide LOD ~ ≥ 2.5 estimated for all characters by the permutation test) was detected; however, 'suggestive QTLs' with chromosomewide significant LOD scores (~ ≥ 1.7) were ignored. Their summary statistics are shown in Table 3. For FY, two QTLs were identified, and their peaks were associated with the MJM650 and MJM602 regions of LG1 and LG4, respectively. Together, they explained 21.2 % of the phenotypic variation, and

Table 1

Phenotypic values for bast fibre quality traits, yield and yield components of *Corchorus olitorius* JRO 524 × PPO4 RIL_6 mapping population

Trait	Mean ± SD	Min	Max	Skewness	Kurtosis	h^2	Minimum magnitude of additive QTL effect to explain phenotypic variance	
							> 5 %	> 10 %
Fibre fineness	2.34 ± 0.23	1.70	3.20	0.57	1.31	0.57	0.07 (0.01)	0.10 (0.01)
Fibre yield	15.92 ± 4.33	5.40	31.90	0.31	1.25	0.67	1.37 (0.04)	1.94 (0.06)
Green biomass yield	209.76 ± 54.90	78.60	350.10	0.06	0.20	0.67	17.36 (0.04)	24.55 (0.06)
Number of nodes	69.05 ± 6.43	51.90	84.80	−0.32	−0.27	0.65	2.03 (0.01)	2.88 (0.02)
Plant height	337.50 ± 23.68	253.70	398.60	−0.21	0.94	0.65	7.49 (0.01)	10.59 (0.01)
Stem diameter base	1.55 ± 0.18	1.10	2.30	0.93	1.51	0.65	0.06 (0.01)	0.08 (0.01)
Stem diameter mid	1.24 ± 0.13	0.70	1.60	−0.26	1.11	0.59	0.04 (0.01)	0.06 (0.01)
Stem diameter top	0.30 ± 0.05	0.20	0.50	0.87	0.31	0.64	0.02 (0.01)	0.02 (0.01)
Tensile strength	19.91 ± 2.84	14.40	29.20	0.85	1.14	0.66	0.897 (0.02)	1.27 (0.03)
Wood yield	32.99 ± 10.27	10.80	63.00	0.52	0.57	0.67	3.25 (0.04)	4.59 (0.06)

Note. ANOVAs show significant ($P \leq 0.001$) differences between the RILs for all traits. Values within parenthesis represent magnitudes based on log-transformed phenotypic data used for QTL analysis.

Table 2

Associations among bast fibre quality traits, yield and yield components in *Corchorus olitorius* JRO 524 × PPO4 RIL_6 mapping population

Trait	Plant height	Stem diameter base	Stem diameter mid	Stem diameter top	Number of nodes	Wood yield	Fibre yield	Tensile strength	Fibre fineness
Green biomass yield	0.753**	0.787**	0.807**	0.396**	0.619**	0.873**	0.803**	0.172^{ns}	-0.157^{ns}
Plant height		0.569**	0.682**	0.334**	0.776**	0.747**	0.723**	0.147^{ns}	-0.140^{ns}
Stem diameter base			0.823**	0.263**	0.410**	0.677**	0.670**	0.206*	-0.146^{ns}
Stem diameter mid				0.322**	0.577**	0.744**	0.658**	0.070^{ns}	-0.117^{ns}
Stem diameter top					0.307**	0.384**	0.339**	0.014^{ns}	-0.047^{ns}
Number of nodes						0.666**	0.578**	0.134^{ns}	-0.067^{ns}
Wood yield							0.871**	0.169^{ns}	-0.114^{ns}
Fibre yield								0.228**	-0.115^{ns}
Tensile strength									-0.050^{ns}

Note. Non-parametric Spearman's rank correlations were used to estimate trait associations. *, ** and ^{ns} = significant at $P \leq 0.05$, 0.01 and non-significant at $P \leq 0.05$, respectively. n−1 = 120−2 = 118 d. f.

increased FY was conferred by the allele from the higher fibre-yield female parent. Only a single QTL for TS was detected at the MJM644 region of LG1. It explained 11.0 % of the observed variation, and increased TS was conferred by the male (high TS) allele. A total of four QTLs was identified for FF. The peaks of the two associated with the MJM566 and MJM635 regions of LG2 and LG5 explained 9.2 and 8.1% of the phenotypic variation, respectively. Increased FF (lower tex value) was conferred by the female (coarse fibre) allele at these two loci. The two most significant FF QTLs were located at the distal end of LG3. They were linked in the coupling phase and together explained 32.4 % of the observed variation. At *qFF-l3-2*, increased FF was conferred by the male (fine fibre) allele.

Among the bast fibre yield components, maximum QTLs were detected for PH and SDT followed by SDB and WY. Increased PH was conferred by the female (taller) allele at three loci (LGs 1, 2 and 5) and the male (shorter) allele at one locus (LG7). The *qPH-l7* accounted for 11.8 %, while to-

Table 3

Summary statistics for quantitative trait loci (QTLs) of bast fibre quality traits, yield and yield components detected in *Corchorus olitorius* JRO 524 × PPO4 RIL_6 mapping population

Trait	QTL	Nearest marker	Linkage group	Position (cM)	LOD score	R^2 (%)	Additive effect
			Bast fibre quality traits and yield				
Fibre fineness	*qFF-l2*	MJM566	2	100.704	3.15	9.2	−0.0095
	qFF-l3-1	MJM722	3	58.707	5.07	19.2	−0.0191
	qFF-l3-2	MJM667	3	69.961	4.48	13.2	0.0157
	qFF-l5	MJM635	5	199.889	2.68	8.1	−0.0086
Fibre yield	*qFY-l1*	MJM650	1	37.572	3.74	12.2	0.0583
	qFY-l4	MJM602	4	89.675	2.83	9.0	0.0400
Tensile strength	*qTS-l1*	MJM644	1	0.000	3.00	11.0	−0.0266
			Bast fibre yield components				
Green biomass yield	*qGBY-l2*	MJM581	2	113.031	3.93	21.5	−0.0787
	qGBY-l4	MJM602	4	89.675	3.13	9.9	0.0411
Number of nodes	*qNN-l1*	MJM679	1	81.188	3.90	16.6	0.0174
Plant height	*qPH-l1*	MJM679	1	79.188	3.13	8.3	0.0098
	qPH-l2	MJM536	2	93.968	2.88	8.6	0.0136
	qPH-l5	MJM635	5	201.345	2.53	6.7	0.0088
	qPH-l7	MJM305	7	4.000	3.40	11.8	−0.0198
Stem diameter base	*qSDB-l1*	MJM650	1	39.572	3.19	8.9	0.0172
	qSDB-l2	MJM581	2	111.031	4.36	12.0	−0.0209
	qSDB-l7	MJM305	7	5.290	2.66	7.3	−0.0154
Stem diameter mid	*qSDM-l3*	MJM722	3	60.478	3.71	10.8	0.0130
	qSDM-l7	MJM500	7	16.058	3.78	12.7	−0.0099
Stem diameter top	*qSDT-l1*	MJM679	1	79.188	2.90	9.3	0.0056
	qSDT-l3-1	MJM513	3	27.885	2.61	7.9	0.0071
	qSDT-l3-2	MJM722	3	60.478	3.98	11.3	0.0087
	qSDT-l5	MJM668	5	217.152	3.14	12.0	−0.0061
Wood yield	*qWY-l1*	MJM650	1	37.572	2.77	7.8	0.0442
	qWY-l4	MJM602	4	89.675	2.91	8.2	0.0426
	qWY-l5	MJM663	5	192.744	4.20	25.0	0.0959

Note. The percentage of the phenotypic variance explained by a QTL (R^2) was estimated at the highest probability peak. Positive additive value indicates that JRO 524 alleles at that marker increase the trait value, while negative additive value indicates that PPO4 alleles increase the trait value.

gether the other three accounted for 23.6 % of the phenotypic variation. Of the three SDB QTLs, the most significant one was flanked by MJM581 and MJM617 at the distal end of LG2 and explained 12.0 % of the observed variation. Increased SDB was conferred by the female allele at one locus (LG1) and the male allele at two loci (LGs 2 and 7). Only one QTL for NN was detected at the MJM679 region of LG1 that explained 16.6 % of the phenotypic variation; increased NN was conferred by the female allele.

Two QTLs were detected for SDM on LGs 3 and 7, which together accounted for 23.5 % of the phenotypic variation. Increased SDM was conferred by the female and male alleles at respective loci of LG3 and LG7, respectively. Four SDT QTLs were detected, and together they explained 40.5 % of the observed variation. Increased SDT was conferred by the female allele at three loci (LGs 1 and 3) and by the male allele at one locus (LG5). The three WY QTLs were located at the MJM650, MJM602 and MJM663 regions of LGs 1, 4 and 5, respectively, and together they explained 41 % of the phenotypic variation. Increased WY was conferred by the female allele at all the three loci. The two GBY QTLs were associated with the MJM581 and MJM602 regions of LGs 2 and 4, respectively, which explained 31.4 % of the phenotypic variation; the former had negative and the latter positive additive effects.

Discussion. Ours is the first microsatellite genetic map of jute with a complete coverage of the genome in agreement with the haploid number of chromosomes. This framework map is likely to be a good starting point for further genome analyses in jute. All previous mapping efforts in jute could coalesce only 2–3 linkage groups, with a total genetic distance of as low as 87.3 cM [21] and as high as 463.7 [22] to 628.4 cM [23]. Recently, Das et al. [24] have mapped 36 microsatellite loci on six linkage groups that covered a total genetic distance of 784.5 cM, with an AMI of 21.8 cM. Although no microsatellite loci were common between the two maps and altogether different mapping algorithms were used to construct them, the total length of our genomewide genetic map (799.9 cM) is commensurate with that of Das et al. [24]. This shows the accuracy and reliability of the present map. Since a stringent grouping algorithm in combination with cross-linkage validation of the loci was employed in the present map, we have been unsuccessful in saturating it with the 36 loci of Das et al. [24] in JoinMap 4. Nevertheless, additional markers are required to enrich it, particularly to bridge the gaps on LG5 and LG6.

Despite the recent availability of a large number of microsatellites [17, 18], jute is characterized by relatively fewer alleles at each microsatellite locus, with unexpectedly low polymorphism information content [17]. This in combination with an inherently narrow genetic base [14] limits the usefulness of microsatellites in constructing a high-density genetic map in jute. In the present study, only 20.6 % of microsatellite loci were polymorphic between the two parents, even though they were phenotypically distinct. Surprisingly, the same level of parental polymorphism was reported by Das et al. [24] using an entirely different set of microsatellite markers. Expressed sequence tag (EST)-SSR and genomewide or candidate-gene single nucleotide polymorphism (SNP) markers can be used to saturate the present map resulting in a denser genetic map with potential functional association [37].

In our study, an unusually high degree of marker segregation distortion was observed, which was slightly lower than that reported by Das et al. [24]. Segregation distortions are widespread in interspecific [38] as well as intraspecific crosses [39] commonly used to construct mapping populations [40]. What was, however, interesting in our study was the observation that segregation distortion was much more skewed towards the female (76 %) than the male (24 %) parent. Our results are consistent with that of a recent report in kenaf, where 68.8 % of the distorted loci skewed towards the female parent [41]. Since megasporocytes are more tolerant of genetic imbalance than microsporocytes, some sorts of gametic selection occur in favor of the female gametes. Thus the apparent marker-segregation distortion is, in fact, a reflection of the segregation distortion of the gametes or zygotes passing to the F_2 progenies [42]. Interestingly, in jute, a skewed distribution of the recombinant types towards the female parent in F_2 and F_3 is a common phenomenon [43, 44]. This could well explain the basis of a rather high level of marker segregation distortion in our study and that in Das et al. [24]. Nevertheless, the distorted microsatellite loci did not influence the map order or statistical confidence in any of the linkage groups

when mapped together with the neighboring normally segregating loci, in accordance with results obtained in other crops [41, 45].

Despite the fact that the RIL population was primarily developed for mapping bast fibre quality traits, we observed wide variation among the RILs for bast fibre yield and yield-related traits. Transgressive segregation was observed for some of the important traits like FY, PH and TS, but not for FF despite its being the most distinguishing trait between the two parents of the mapping population. However, for cotton, transgressive segregation was reported not only for fibre yield and yield components [46], but also for fibre quality traits [47] including fibre fineness [48]. This reveals a restricted scope for fibre-fineness improvement in jute through selection for transgressive segregants in the progenies of a specific cross, besides confirming the complexity of this trait in agreement with results from classical genetical studies [7]. This is rather obvious because jute fibre, as opposed to purely cellulosic seed trichomes (fibres) of cotton, represents a composite of ligno-cellulosic phloem-fibre cell bundles, the fineness of which is controlled by several factors and their coordination [49] including the post-harvest retting process [1, 6].

Our genomewide QTL search could detect fewer number of QTLs than that reported by Das et al. [24]. This is not unexpected because we did consider only the definitive QTLs, whereas Das et al. [24] not only employed a less restrictive threshold (LOD > 2.0), but also considered suggestive QTLs (LOD < 2.0). The 26 QTLs were distributed on six linkage groups at genomic regions specified by 15 nearest-neighbor markers. The LG1 represented the QTL-richest map-sector because 7 QTLs for the most important FY and yield components (PH, NN, SDB, SDT and WY) including TS were co-localized on it at genomic regions specified by only three markers MJM644, MHM650 and MJM679. This vindicates not only a classical genetic basis of selection in jute for bast fibre yield based on these correlated traits [3, 7, 17], but also a significant association between FY and TS, as observed in this study. Furthermore, a QTL of FY was co-localized on LG4 with those of GBY and WY at the MJM602 region. Most interestingly, in continuation of what we have discussed in the preceding paragraph, a QTL of FF was co-localized with those of PH, SDB and WY at the distal end of LG2 bracketed by three markers, and another on LG5 with that of PH at the specified genomic region. Such co-localized QTL clusters have been reported in a number of crop species [50–53]. However, QTL fine-mapping could settle as to whether these co-localized QTL-clusters entail numerous tightly-linked QTLs or a pleiotropic QTL, for different traits.

Alleles from the male (PPO4) and female (JRO 524) parents increased trait values at 10 and 16 loci, respectively. All favorable QTLs for FY and yield-attributing traits of LG1 and LG4 clusters were derived from the expected female parent, suggesting a scope for parallel improvement of these traits based on these co-localized QTLs because the desirable alleles are contributed by a single parent [52, 54]. Incidentally, this female parent has been extensively used over the years to breed improved dark jute varieties since its release in 1977 [3]. Between the two bast fibre quality traits, the sole QTL for TS was derived from the expected male parent, however, an appreciable exception was observed for FF. Of the four favorable FF QTLs, three were derived from the coarse-fibre female parent, not from the desired fine-fibre male parent. Increased fibre fineness (low micronaire value) in cotton was also reported to be partly conferred by the undesirable female parent than by the desirable male parent [55, 56], presumably due to the creation of new gene combinations [55]. The male parent of our mapping population was a selection from OIJ 136, an exotic type from Tanzania, while the female parent was the derivative of a cross from Sudan Green (an exotic type from Sudan) with JRO 632, a selection from an indigenous type [3]. Therefore, the possibility of the creation of new gene combinations in the RIL population cannot be ruled out.

In conclusion, our study initiates the first genomewide QTL mapping in jute using a microsatellite genetic map based on an RIL population from a cross between two phenotypically distinct and geographically divergent parental genotypes. We could reliably dissect the genetic basis of bast fibre quality traits, yield and yield components. However, there is a need to validate these QTLs, particularly those of bast fibre quality traits, in additional populations across environments. It is expected that variability in the number and locations of QTLs for these traits will be observed in different environments. Notwithstanding, our results would

not only facilitate the use of trait-linked microsatellite markers in MAS for concurrent improvement of a number of traits, but also accelerate the genetic dissection of bast fibre development mechanisms in jute. Recent results from our laboratory show that fibre fineness in jute is conditioned by the architecture of the mostly triangular fibre cell bundle wedges (FCBs), which is governed by a balanced growth between radially elongating FCBs and tangentially expanding ray cells due to development-specific activation of the cambium [57]. QTL mapping for some of these important anatomical traits and cambial function will be highly rewarding in future, for understanding the complex genetics of fibre fineness and accelerating the development of jute cultivars with improved fibre fineness.

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ПОЛНАЯ КАРТА СЦЕПЛЕНИЯ ГЕНЕТИЧЕСКИХ ПРИЗНАКОВ И QTL АНАЛИЗ ПРИЗНАКОВ КАЧЕСТВА ВОЛОКНА, УРОЖАЙНОСТИ И ЭУКОМПОНЕНТОВ У ДЖУТА (*CORCHORUS OLITORIUS* L.)

Впервые приводится полная генетическая карта микросателлитов джута (*Corchorus olitorius* L.; $2n = 2x = 14$), полученная с помощью рекомбинантной инбредной популяции F_6. Из изученных 403 микросателлитных маркеров 82 были картированы в семи группах сцепления, которые в целом занимают генетическую дистанцию в 799.9 сМ со средним интервалом между маркерами 10.7 сМ. По генетической дистанции самой длинной была группа сцепления 5, самой короткой группа 7, в то время как максимальное число маркеров имела группа 1, а минимальное – группа 7. Для 61 % микросателлитных локусов наблюдали нарушение расщепления, в 76 % случаев преимущество при передаче имел аллель материнского организма. Геномный непараметрический одномаркерный анализ в комбинации с моделью множественных QTL картировал 26 локусов, отвечающих за качество лубяного волокна, урожайность и признаки, связанные с урожайностью. Они неравномерно распределены в шести группах сцепления как ко-локализованные кластеры в генетических секторах, маркированных 15 микросателлитными локусами. Группа сцепления 1 была сектором, наиболее обогащенным QTL, с плотно расположенными кластерами QTL, отвечающими за выход волокна, и за признаки, связанные с урожайностью и прочностью. Как и ожидалось, в результате возникновения новых комбинаций генов от соответствующих родителей получены сочетания благоприятных локусов, за исключением почти всех локусов, определяющих тонкость волокна. Результаты являются хорошей основой для дальнейшего анализа генома джута.

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ПОВНА КАРТА ЗЧЕПЛЕННЯ ГЕНЕТИЧНИХ ОЗНАК І QTL АНАЛІЗ ОЗНАК ЯКОСТІ ВОЛОКНА, ВРОЖАЙНОСТІ ТА ЕУКОМПОНЕНТІВ У ДЖУТА(*CORCHORUS OLITORIUS* L.)

Вперше наводиться повна генетична карта мікросателітів джуту (*Corchorus olitorius* L.; $2n = 2x = 14$), отримана за допомогою рекомбінантної інбредної популяції F_6. З 403 вивчених мікросателітних маркерів 82 були картовані в семи групах зчеплення, які в цілому займають генетичну дистанцію в 799.9 сМ із середнім інтервалом між маркерами 10.7 сМ. За генетичної дистанції найдовшою була група зчеплення 5, найкоротшою група 7, в той час як максимальне число маркерів мала група 1, а мінімальне – група 7. Для 61 % мікросателітних локусів спостерігали порушення розщеплення, в 76 % випадків перевага при передачі мав алель материнського організму. Геномний непараметричний одномаркерний аналіз в комбінації з моделлю множинних QTL картував 26 локусів, що відповідають за якість луб'яного волокна, врожайність і ознаки, пов'язані з урожайністю. Вони нерівномірно розподілені в шести групах зчеплення як ко-локалізовані кластери в генетичних секторах, маркованих 15 мікросателітними локусами. Група зчеплення 1 була сектором, найбільш збагаченим QTL, з щільно розташованими кластерами QTL, що відповідають за вихід волокна, та за ознаки, пов'язані з врожайністю і міцністю. Як і очікувалося, в результаті виникнення нових комбінацій генів від відповідних батьків були отримані поєднання сприятливих локусів, за винятком майже всіх локусів, що визначають тонкість волокна. Результати є хорошою основою для подальшого аналізу геному джуту.

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