Analysis of genetic diversity and population structure of a worldwide collection of *Corchorus olitorius* L. germplasm using microsatellite markers

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ABSTRACT

Jute (*Corchorus* spp.) is the second most important global natural fiber crop after cotton. Analyses of the genetic diversity and population structure of the germplasm are useful for improving *Corchorus* breeding. Recently, limited studies on genetic diversity and population structure in jute have been carried out. In the present study, the genetic diversity and population structure of 453 accessions in *Corchorus olitorius* L., including cultivars, landraces, genetic materials and wild germplasm, were analyzed using 39 SSR markers. The results showed that *C. olitorius* populations have moderate genetic diversity with an average gene diversity (h_e) value of 0.322 and polymorphic information content (PIC) value of 0.270 in all accessions. Regarding the geographic distribution, the average h_e and PIC values were highest in Kenya (0.332, 0.273), followed by Nepal (0.307, 0.259), and China (0.303, 0.253). Among the different germplasm types, the wild germplasm showed higher genetic diversity with an average h_e value of 0.362 and PIC value of 0.299. The population structure analysis revealed two populations, Pop1 and Pop2; Pop1 was further divided into three subpopulations, and Pop2 was further divided into two subpopulations. These populations were verified by F_ST statistics, principal coordinate analysis (PCoA) and neighbour-joining trees. This study contributes to the knowledge about levels and distribution of genetic diversity of *C. olitorius* worldwide and provides clues about the origin of *C. olitorius*.

Introduction

Jute (*Corchorus* spp.) is the second most important global natural fiber crop after cotton. It is a diploid annual crop (2n = 14) and was originally classified in Tiliaceae and now in the family Malvaceae according to the Angiosperm Phylogeny Group (APG) system [1,2]. Jute consists of approximately 50–60 species that grow in the tropics, subtropics and warm temperate regions of the world (mainly in Asia and Africa) [3]. However, only two cultivated species, *C. capsularis* L. and *C. olitorius* L., are mostly used commercially with an annual global production of 2.65 million tonnes [4]. The increasing demand for jute worldwide is due to its broad-spectrum application and environmentally-friendly characteristics [5–7]. However, cultivars of the two species possess narrow genetic diversity since there are limited breeding parent combinations and only a few varieties are cultivated. For example, only five varieties (JRO878, JRO7835, JRO524, Chinsurah Green and D154) were widely cultivated in the last century in India, which increased to 22 varieties in 2005 (12 of *C. capsularis* and 10 of *C. olitorius*) [8]. However, only four major cultivars (D154 and Yueyuan5hao for *C. capsularis*, and Cuigreen and Guangfengchangguo for *C. olitorius*) have been cultivated in the last century in China. Therefore, to promote jute breeding, it is important to expand the genetic basis of the breeding populations.

More than 2,000 jute accessions are stored in the National Bast Fiber Germplasm Middle-term Storage, Changsha, China. Analysis of genetic diversity and population structure of the germplasm plays an important role in improving breeding, expanding the genetic basis of breeding, and association mapping, similarly to that of other crops [9–11]. Recently, limited studies on genetic diversity in jute have been carried out with morphological traits and some molecular markers. Ghosh et al. [12] investigated the genetic diversity and population structure of 63 jute genotypes from *C. capsularis* and *C. olitorius* using simple sequence repeat (SSR) and amplified fragment length polymorphism...
(AFLP). Basu et al. [13] assessed the genetic diversity of 160 jute (C. capsularis and C. olitorius) genotypes using 14 organelle DNA markers. Banerjee et al. [14] assessed the genetic diversity and population structure in 292 genotypes (C. capsularis L. and C. olitorius L) using 172 SSRs markers. Rana et al. [15] studied the genetic diversity of 31 cultivars of jute belonging to two cultivated species by 43 sequence related amplified polymorphism (SRAP) marker. Zhang et al. [16] analyzed the population structure and relationships of 159 jute accessions using 63 SSRs.

Although some of these studies estimated the genetic diversity and population structure in jute (Corchorus spp.), most of the studies were performed on a limited number of accessions and germplasm types, and the accessions used in the studies included two species of Corchorus spp. [14,17] simultaneously. Therefore, a comprehensive analysis of Corchorus spp. focusing on only one species involving a global collection of cultivars, landraces, genetics materials and wild germplasm is still needed to assess the genetic diversity and population structure for effective breeding programs in jute. Consequently, in the present study, the genetic diversity and population structure of 453 accessions in C. olitorius including cultivars, landraces, genetic materials and wild germplasm were analyzed using 39 SSR markers. The objectives of this study were to examine the genetic diversity and population structure of C. olitorius in relation to its origin.

Materials and methods

Plant materials

We analyzed a total of 453 accessions of C. olitorius L. including cultivars, widely cultivated varieties developed through various breeding methods; landraces which were selected and developed by local farmers and planted continuously only in certain places; genetic materials referring to number or structure variation of chromosomes or genes with particular value which could be transmitted to offspring and including intermediate breeding lines, such as sterile, aneuploid, substitution lines, etc.; and wild germplasm. All accessions were stored in the National Bast Fiber Germplasm Middle-term Storage of China. A total of 232 accessions, 128 of which were known in terms of germplasm types, were collected from Nepal, India, Thailand, Vietnam, Bangladesh, Pakistan, Kenya, Tanzania, Russia, the United States and China. The geographic source of the other 221 accessions was unknown. Detailed information about the 453 accessions of C. olitorius used in the present study are provided in Online Resource 1 (codes 1–453).

DNA isolation

Genomic DNA was extracted from leaves of the 453 C. olitorius accessions using the DNAeasy plant mini prep kit (Tiangen, Tiangen biotech Co.LTD. Beijing, China). The extracted DNA was diluted to approximately 20 ng/mL for the working concentration needed for SSR genotyping.

Genotyping of jute accessions using SSR markers

A total of 600 primer pairs, which were randomly selected from the primer pairs developed using transcriptome sequencing data of C. olitorius, were used for amplification 11 randomly selected C. olitorius accessions (one in each country). A total of 39 primer pairs which showed polymorphism in any two of the 11 randomly selected C. olitorius accessions were used for genotyping the whole panel of 453 samples. The primer sequences are shown in Online Resource 2. Polymerase chain reaction (PCR) amplifications of each genomic DNA of the 453 samples were carried out in 10 µL reaction volumes with 1 µL 10X PCR buffer, 0.3 mmol/L deoxynucleoside triphosphates (dNTP), 0.15 µL (2 U/µL) Taq DNA polymerase (Tiangen), 0.5 µL µmol/L of each primer, 1.5 µL DNA and 5.99 µL ddH2O. The following PCR program was used: 5 min at 94 °C; followed by 33 cycles of 30 s at 95 °C, 40 s at 55 °C, 60 s at 72 °C, and a final extension of 10 min at 72 °C. The PCR products were electrophoretically separated in 8% polyacrylamide gels, and silver staining was carried out according to Zhang et al. [18]. The clear bands from PCR products were used for genotyping.

Statistical analysis

Genetic diversity was evaluated using the program PowerMarker V3.25 [19]. It measured the number of alleles (n_i), the major allele frequency and expected heterozygosity (gene diversity, h_e) [19]. When a gene locus had r alleles and the i_th allele frequency was p_i, then he was defined as:

\[ h_e = 1 - \sum_{i=1}^{r} p_i^2 \]

The polymorphic information content (PIC) for each locus [20] was defined as follows, supposing that p_i, p_j, and m, respectively, represent the frequencies of the i_th, the j_th alleles and the number of alleles in a locus:

\[ PIC = 1 - \sum_{i=1}^{m} p_i^2 - \sum_{i=1}^{m-1} \sum_{j=i+1}^{m} 2p_i^i p_j^j \]
The major allele frequency ranged from 0.328 to 0.993 with an average value of 0.754. The gene diversity ($h_e = 0.729$) and PIC (0.273) varied greatly in this study with a low mean value, both lower than 0.325 (Table 1). For the subsets based on countries, Kenya possessed the maximum mean value of gene diversity (0.332) and PIC (0.273), followed by Nepal (0.300), but higher than the values reported by Zhang et al [16] ($h_e = 0.307$, PIC = 0.259) and China ($h_e = 0.303$, PIC = 0.253), and the minimum mean value was in Vietnam ($h_e = 0.178$, PIC = 0.138). The mean value of the major allele frequency in each country was more than 0.7, and only in China and Kenya, the mean allele number was >2. In terms of germplasm types, the highest mean of gene diversity and PIC were present in wild germplasm, which was significantly different from the other three types. Similar to the above subset, all germplasm types showed a high major allele frequency (mean value 0.709–0.789). The allele number ranged from 1 to 4 for every germplasm type, with averages of >2.

In comparison, the number of samples, germplasm types and geographical sources have been relatively low in previous studies [16,24,25]. To the best of our knowledge, before the present study, the largest number of samples used for assessment of the genetic diversity in *C. olitorius* was 140 [14]. In the present, more comprehensive and representative study, the results showed that *C. olitorius* has moderate genetic diversity. This is in agreement with Zhang et al. [16] ($h_e = 0.350$, PIC = 0.300), but higher than the values reported by Benor et al. [17] ($h_e = 0.0763$, Rana et al. [15] (PIC ranging from 0.196 to 0.425, $h_e = 0.072$) and Banerjee et al. [14] ($h_e = 0.262$, PIC = 0.203), and lower than that

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**Table 1. Statistical analysis of major allele frequency, allele number ($n_e$), gene diversity ($h_e$) and PIC in worldwide accessions of *C. olitorius* L.**

| No. | Category name | Number of accessions | Major allele frequency | Number of alleles ($n_e$) | Gene diversity ($h_e$) | PIC |
|-----|---------------|----------------------|------------------------|--------------------------|------------------------|-----|
| 1   | All accessions| 453                  | 0.328–0.993 (0.754)    | 2–5 (2.923)              | 0.014–0.729 (0.322)   | 0.014–0.679 (0.270) |
| 2   | Nepal         | 12                   | 0.333–1.000 (0.761)   | 1–3 (1.949)              | 0.059–0.307 (0.257)   | 0.047–0.259 (0.198) |
| 3   | India         | 11                   | 0.273–1.000 (0.809)   | 1–4 (1.892)              | 0.076–0.252 (0.210)   | 0.070–0.210 (0.150) |
| 4   | Thailand      | 4                    | 0.500–1.000 (0.834)   | 1–3 (1.556)              | 0.625–0.204 (0.160)   | 0.555–0.160 (0.120) |
| 5   | Vietnam       | 4                    | 0.500–1.000 (0.848)   | 1–3 (1.405)              | 0.611–0.178 (0.138)   | 0.536–0.138 (0.108) |
| 6   | Bangladesh    | 13                   | 0.375–1.000 (0.784)   | 1–4 (1.974)              | 0.688–0.285 (0.238)   | 0.630–0.238 (0.198) |
| 7   | Pakistan      | 8                    | 0.375–1.000 (0.789)   | 1–4 (1.811)              | 0.688–0.273 (0.233)   | 0.630–0.223 (0.188) |
| 8   | China         | 30                   | 0.375–1.000 (0.734)   | 1–5 (2.237)              | 0.714–0.332 (0.273)   | 0.663–0.273 (0.203) |
| 9   | Tanzania      | 3                    | 0.375–1.000 (0.796)   | 1–3 (1.639)              | 0.656–0.251 (0.200)   | 0.582–0.200 (0.160) |
| 10  | Russia        | 11                   | 0.273–1.000 (0.798)   | 1–4 (1.921)              | 0.748–0.264 (0.220)   | 0.701–0.220 (0.180) |
| 11  | USA           | 9                    | 0.438–1.000 (0.792)   | 1–4 (1.895)              | 0.672–0.275 (0.265)   | 0.612–0.226 (0.215) |
| 12  | China         | 127                  | 0.335–0.994 (0.763)   | 2–5 (2.641)              | 0.012–0.724 (0.303)   | 0.012–0.674 (0.253) |
| 13  | Cultivars     | 51                   | 0.333–1.000 (0.786)   | 1–4 (2.158)              | 0.722–0.278 (0.238)   | 0.671–0.238 (0.198) |
| 14  | Landraces     | 43                   | 0.305–1.000 (0.772)   | 1–4 (2.237)              | 0.738–0.296 (0.246)   | 0.690–0.246 (0.206) |
| 15  | Genetic materials | 11            | 0.350–1.000 (0.775)   | 1–4 (2.077)              | 0.705–0.290 (0.260)   | 0.665–0.260 (0.210) |
| 16  | Wild germplasm| 23                   | 0.313–1.000 (0.709)   | 1–4 (2.216)              | 0.744–0.362 (0.299)   | 0.697–0.299 (0.269) |
| 17  | Pop1          | 247                  | 0.344–1.000 (0.778)   | 1–4 (2.434)              | 0.716–0.284 (0.235)   | 0.664–0.235 (0.205) |
| 18  | Pop1–1        | 83                   | 0.373–1.000 (0.811)   | 1–4 (2.128)              | 0.688–0.245 (0.203)   | 0.631–0.203 (0.165) |
| 19  | Pop1–2        | 93                   | 0.337–1.000 (0.815)   | 1–4 (2.333)              | 0.719–0.256 (0.216)   | 0.668–0.216 (0.178) |
| 20  | Pop1–3        | 70                   | 0.322–1.000 (0.815)   | 1–4 (2.103)              | 0.732–0.264 (0.205)   | 0.683–0.205 (0.165) |
| 21  | Pop2          | 206                  | 0.309–0.992 (0.750)   | 2–5 (2.795)              | 0.016–0.741 (0.326)   | 0.016–0.694 (0.273) |
| 22  | Pop2–1        | 147                  | 0.325–1.000 (0.792)   | 1–4 (2.205)              | 0.724–0.274 (0.226)   | 0.673–0.226 (0.195) |
| 23  | Pop2–2        | 59                   | 0.352–1.000 (0.716)   | 1–5 (2.744)              | 0.744–0.370 (0.314)   | 0.700–0.314 (0.265) |

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**Results and discussion**

**Genetic diversity in the germplasm**

The study detected 2–5 alleles, with an average of 2.923 alleles per locus using 39 EST-SSRs in the 453 accessions.
reported by Ghosh et al. [12] (PIC = 0.45). These differences in may result from the materials source and marker types. The present study and that of Zhang et al. [16] included some common Chinese accessions and used SSR markers. Most of the PIC values in the above-mentioned studies range from 0.25 to 0.5, which demonstrates that *C. olitorius* shows a moderate degree of genetic diversity.

The scientific community continues to debate on the origins of *C. olitorius*. Some authors support that this species is native to India, Indo-Burma or Sri Lanka [25,26]. However, Africa is also widely assumed as the center of origin of *C. olitorius* [27]. In our study, the highest genetic diversity was found in Kenya, which implies that the origin center of *C. olitorius* may be Africa. Wild germplasm showed the highest genetic diversity, which was significantly higher (>17.8%) than that in the other three types, with similar genetic diversity in them. This is in agreement with the results of Yuan et al. [28] and but in contrast with those of Benor et al. [17], who found that the genetic diversity of wild accessions was similar to that of cultivated plants. However, different materials and fewer markers (only 6 AFLP markers) were used by in the study of Benor et al. [17].

**Population structure and cluster analysis**

The results from Structure V2.3.4 software analysis indicated that Δ*K* peaked when the *K* value was 2 (Figure 1a). Therefore, the optimal value of *K* should be *K* = 2. That is, the 453 *C. olitorius* accessions could be divided into two populations (Figure 2a), Pop1 and Pop2. Pop1 included 246 accessions from different countries mainly comprising Nepal (4/12), India (6/11), Thailand (1/4), Vietnam (3/4), Bangladesh (0/13), Pakistan (5/8), Kenya (3/30), Tanzania (1/3), Russia (2/11), the United States (5/9), China (61/127) and some of unknown origin (155/221). In comparison, the 207 accessions in Pop2 mainly comprised accessions from Nepal (8/12), India (5/11), Thailand (3/4), Vietnam (1/4), Bangladesh (13/13), Pakistan (3/8), Kenya (27/30), Tanzania (2/3), Russia (9/11), the United States (4/9), China (66/127) and some of unknown origin (66/221) (Table 2). To analyze the population structure in depth, each of the two populations was subdivided into subpopulations using the same methods, inferring three subpopulations in Pop1 (Figures 1b and 2a) named Pop1–1 (83/246), Pop1–2 (93/246) and Pop1–3 (70/246), and two subpopulations in Pop2 (Figures 1c and 2a) named Pop2–1 (147/207) and Pop2–2 (60/207) (Online Resource 1 and Table 2). For the 128 accessions with known germplasm types, most wild germplasm was assigned to Pop2 (17/23). Pop2 (28) included more landraces than Pop1 (15). Pop2–2 only held 1 cultivar and 22 comprised the other three types of accessions. Only 4 accessions of known germplasm types were assigned to Pop1–3 (Table 2). The results from AMOVA and *F* ST indicated that most of the variation (65%) came from inter-individual variation among the different populations (‘among individuals’), followed by the intra-individual variation (28%) within
the same population (‘within individuals’); whereas differences between the two populations were relatively low (7%) (Figure 2b, Table 3), which indicated that a much greater proportion of the variation accounted for inter-individual variation among the populations. Pairwise $F_{ST}$ values showed significant differentiation between the two populations and among the pairs of all subpopulations ranging from 0.069 to 0.231 (Table 4), which indicated that the populations and the subpopulations were significantly different. Pop1–3 and Pop2–2 were more differentiated from each other according to the $F_{ST}$ value (0.231), followed by Pop1–3 and Pop2–1 ($F_{ST} = 0.204$). The genetic diversity, major allele frequency, allele number, gene diversity and PIC were computed through PowerMarker. All four indices suggested that the genetic diversity of Pop2 was higher than that of Pop1 (Table 1). For the five subpopulations, Pop2–2 showed the highest genetic diversity, gene diversity (0.370) and PIC (0.314), which were significantly higher than those of the other four subpopulations and two populations.

PCoA indicated that the first and second principal coordinate (PCo) explained 11.99% and 6.54% variation, respectively. The first principal coordinate (PCo1) separated 453 accessions into two groups. Pop1 was mainly grouped in quadrants 1 and 3 and Pop2 in quadrants 2 and 4. The second principal coordinate (PCo2) showed that Pop1 was divided into three subsets (Pop1–1, Pop1–2 and Pop1–3) and Pop2 into two subsets (Pop2–1 and Pop2–2) (Figure 2c), which was similar to the result from $F_{ST}$ and population structure analyses.

An NJ tree of the all 453 accessions was constructed based on Nei’s genetic distance, which ranged from 0.011 to 0.786 (average = 0.26). All the accessions were

### Table 3. Analysis of molecular variance (AMOVA) of *C. olitorius* populations.

| Source               | df | SS   | MS    | Est. Var. % |
|----------------------|----|------|-------|-------------|
| Among populations    | 1  | 303.464 | 303.464 | 0.643 | 7 |
| Among individuals    | 451 | 6734.943 | 14.933  | 6.148 | 65 |
| Within individuals   | 453 | 1195.000 | 2.638  | 2.638 | 28 |
| Total                | 905 | 8233.406 | 321.035 | 9.428 | 100 |

Note: Among individuals: inter-individual variation among different populations. Within individuals: intra-individual variation within the same population.

### Table 4. Pairwise population differentiation of *C. olitorius* populations measured by $F_{ST}$ using GenAlEx6.502.

| Population | Pop1 | Pop1–1 | Pop1–2 | Pop1–3 | Pop2–1 |
|------------|------|--------|--------|--------|--------|
| Pop2       | 0.073** |        |        |        |        |
| Pop1–1     |      | 0.111** |        |        |        |
| Pop1–2     |      |      | 0.118** | 0.082** |        |
| Pop1–3     |      |      |      | 0.069** | 0.204** |
| Pop2–1     |      |      |      |      | 0.190** |
| Pop2–2     |      |      |      |      |      |

** Significant at $P < 0.01$ after 999 permutations.
assigned to the two main clusters: I and II (Figure 3). The clustering of accessions in the NJ tree was generally in agreement with the population structure identified by the analyses discussed above. The accessions of Pop1 (80.58%) were mostly located in cluster I, whereas those of Pop2 (67.60%) were in cluster II.

There were more accessions in Pop1 than in Pop2, but more wild accessions and landraces in Pop2 (17 and 28) than in Pop1 (15 and 6). Therefore, there was higher genetic diversity in Pop2. In the five subpopulations, the highest proportion (78.26%) of wild accessions and landraces was in Pop2–2, accounting for the highest genetic diversity. All the accessions from Bangladesh and most of the accessions from Kenya and Russia were grouped into Pop2. The other accessions were relatively homogeneously distributed between Pop1 and Pop2, which suggests that genetic diversity of the accessions did not always correlate with their geographical origins. This phenomenon agrees with results reported by Zhang et al. [16] and might be caused by germplasm exchange across country boundaries.

Conclusions

In summary, our study provides a comprehensive genetic diversity and population structure analysis of Corchorus olitorius focusing on only one species involving a global collection of cultivars, landraces, genetic materials and wild germplasm. These results contribute to the knowledge about the levels and distribution of genetic diversity and the population structure in jute worldwide. The study provides clues in support of African origin of C. olitorius. The obtained data will play an important role in the protection and application of the jute germplasm genetic diversity, and may be beneficial for making progress in developing optimal jute breeding strategies.

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Disclosure statement

There are no conflicts of interest to declare.

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