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Construction of RFLP-based maps of foxtail millet, *Setaria italica* (L.) P. Beauv.

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Abstract An RFLP-based map consisting of 160 loci was constructed in an intervarietal cross of foxtail millet [*Setaria italica* (L.) P. Beauv.], Longgu 25 × Pagoda Flower Green. The map comprises nine linkage groups, which were aligned with the nine foxtail millet chromosomes using trisomic lines, and spans 964 cM. The intraspecific map was compared to an interspecific map, constructed in a *S. italica* × *S. viridis* cross. Both the order of the markers and the genetic distances between the loci were highly conserved. Deviations from the expected 1 : 2 : 1 Mendelian segregation ratios were observed in both the intra- and inter-specific populations. The segregation data indicate that chromosome VIII in the Longgu 25 × Pagoda Flower Green cross carries a gene that strongly affects gamete fertility.

Key words Foxtail millet · Genetic map · Primary trisomics · RFLP · *Setaria italica* · *Setaria viridis*

Introduction

Foxtail millet, *Setaria italica* (L.) P. Beauv., is an important grain crop in India, China and Japan, and is grown for hay and silage in North and South America, Australia and North Africa. The crop is relatively drought-tolerant and well adapted to arid and semi-arid growing conditions. In China, the largest producer of foxtail millet, the crop covers an area of 1 867 400 hectares and yields an average of 1814 kg/ha (Yearbook of Chinese Agriculture Editorial Board 1993). Over 250 varieties have been released since 1950 (Li and Diao 1994, and personal communication).

Foxtail millet is a self-pollinating crop ($2n = 2x = 18$) with a haploid nuclear DNA content estimated to be 0.82 pg by Sivaraman and Ranjekar (1984). The small genome size and diploid nature of foxtail millet should have made it a suitable organism for genetic and molecular studies. However, as the crop is considered a minor cereal of only regional importance, genetic studies have lagged behind those of other staple cereals. Since the start of foxtail millet research in the 1930s, a number of morphological traits (Ayyangar and Narayanan 1931, 1932, 1933 a, b; Ayyangar and Sharma 1993; Ayyangar et al. 1993 a, b, 1935; Krishnaswami and Ayyangar 1935; Li et al. 1935; Kishimoto 1938; MacVicar and Parnell 1941; Darmency and Pernès 1987; Darmency et al. 1987; Till-Bottraud and Brabant 1990) and isozymes (de Cherisey et al. 1985; Jusuf and Pernès 1985) have been studied but, to-date, no detailed linkage maps have been available.

An important component of plant breeding programmes has been crop improvement through the introduction of novel genes from wild relatives. *S. viridis* (L.) P. Beauv. or green foxtail, a weed occurring throughout China, carries the same genome (A) as *S. italica* and is the likely progenitor of the domesticated crop. *S. viridis* hybridizes easily with cultivated foxtail millet and produces semi-fertile hybrids (Kihara and Kishimoto 1942; Li et al. 1942, 1945). In order to study the introgression and location of traits such as herbicide resistance, carried by *S. viridis* (Darmency and Pernès 1985, 1989; Jasieniuk et al. 1994), and those associated with domestication, interspecific *S. italica* × *S. viridis* genetic maps are needed. This paper

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reports on the construction and comparison of genetic maps in an intraspecific *S. italica* cross and an interspecific *S. italica* × *S. viridis* cross, and the aligment of linkage groups with the nine foxtail millet chromosomes.

Materials and methods

Plant material

Thirty *S. italica* and one *S. viridis* accession were tested for levels of polymorphism. Following these tests, the *S. italica* accessions Longgu 25 and Pagoda Flower Green were chosen as parents for the intraspecific mapping population, and *S. italica* acc. B100 × *S. viridis* acc. A10 as parents for the interspecific mapping population. Morphological characteristics that distinguish the parents are green vs purple pigmentation of the leaf sheath for Longgu 25 and Pagoda Flower Green, and yellow, single stemmed vs green and tillering seedlings for B100 and A10. The female parent, B100, is also highly male-sterile which should be an aid to the collection of F_1 grain.

Prior to hybridization the plants were grown in controlled environments at 70% humidity, 16 h daylength and a day/night temperature of 28/20°C. Artificial hybridization between the parents was carried out according to Li et al. (1935) with the following modifications. Florets that were not expected to flower within the next few days were removed from the top half of a panicle from accession Longgu 25, the female parent, using fine-tipped scissors. The top half of the panicle was then immersed in hot water (47°C for 10 min) and bagged prior to the introduction of pollen collected from the male parents, Pagoda Flower Green and A10, within a glassine bag. The lower half of the panicle was bagged for selfing. Emasculation was not necessary for the male-sterile accession B100. F_1s were identified by the presence of dominant morphological markers, transmitted from the male parents, and later verified using RFLPs (Fig. 1). A single F_1 plant was selfed to produce each F_2 population, consisting of 138 plants for the intraspecific cross and 127 plants for the interspecific cross. Each F_2 plant was selfed to provide F_3 families.

A set of primary trisomic lines, developed at the Institute of Millet Crops at Hebei, China (Wang et al. 1994), were used to assign the linkage groups to chromosomes. Selfed seed was sown at JIC and putative trisomic progeny, identified by morphology, were selected for verification by chromosome counts. At least two trisomic plants were confirmed for each line, with the exception of Triplo-VI for which only a single trisomic plant was identified.

RFLP probes

DNA from the *S. italica* variety Gaolan Aubergine-headed White was digested with *Pst*I and fragments in the size range 500–2500 bp were ligated into the plasmid vector pUC18. After transformation and blue/white selection, 850 recombinant clones were submitted to PCR amplification using M13 forward and reverse sequencing primers (Pharmacia). Amplification products (5 µl) were separated on 0.8% agarose gels, transferred to Hybond N^+ membranes (Reed and Mann 1985), and hybridized to ^{32}P-labelled total genomic DNA. Inserts displaying positive signals were assumed to contain highly repeated sequences and were discarded. The remaining clones were tested for their ability to detect polymorphism in the sample of foxtail millet accessions.

In addition to the foxtail millet genomic clones (prefix 'PSF'), anonymous pearl millet ('PSM') and wheat ('PSR') probes, and two known function clones identifying the waxy locus, *Xpsr470*(*Wx*) (Rhode et al. 1988), and the carboxypeptidase locus, *Xwia483*(*Cxp1*) (Doan and Fincher 1988), were also employed.

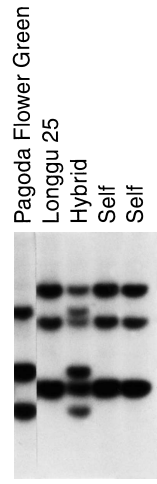


Fig. 1 Identification of a F_1 hybrid of the intraspecific cross Longgu 25 × Pagoda Flower Green using RFLP markers

RFLP procedures and linkage analysis

DNA was extracted from fresh leaf material using the method described by Sharp et al. (1988). Aliquots of 2 µg of DNA were digested with the restriction enzymes *Eco*RI, *Eco*RV, *Dra*I and *Hin*dIII according to the supplier's recommendation and separated on 0.8% agarose gels. For radioactive detection, Southern blotting, probe labelling and filter hybridization were carried out as described by Laurie et al. (1993). For chemiluminescent (ECL-Amersham) detection, Southern blotting, probe labelling, filter hybridization and detection were carried out as described by the manufacturer. Linkage analyses were carried out using the programme Mapmaker vs 3.0 (Lander et al. 1987). Linkage groups were established at LOD ≥ 3. The most likely marker orders were determined using three- and multi-point analyses, and manually checked for critical cross-overs. Recombination fractions were converted to centimorgan (cM) distances using the Kosambi function. Locus names followed the rules for Wheat Gene Nomenclature (McIntosh et al. 1995).

Trisomic analysis

Three probes that detected loci in different linkage groups were hybridized simultaneously to filters containing restricted DNA from euploid foxtail millet and two sets of trisomic lines. Autoradiographs were scanned with a GS-690 Imaging Densitometer (Bio-Rad) and the intensity of the hybridization signals was determined using the software package 'Molecular Analyst' (Bio-Rad). A correction for loading differences was carried out and loci were assigned to chromosomes by an assessment of intensity differences of the hybridizing fragments.

Results

Levels of polymorphism

Of the initial 850 recombinant foxtail millet genomic DNA clones, 510 (60%) yielded PCR-amplification insert products. About 13% of the inserts gave positive signals after hybridization with ^{32}P-labelled total genomic DNA and were discarded. The remaining 406 probes were tested for their ability to reveal polymorphism between the parents of the mapping crosses. One

hundred and eighty probes (44.3%) detected variation between Longgu 25 and Pagoda Flower Green with at least one of the four restriction enzymes used, and 304 probes (75%) detected variation in the interspecific cross, *S. italica* acc. B100 × *S. viridis* acc. A10.

Linkage maps

Of the 180 probes polymorphic in the intraspecific cross, 143 were used for mapping, and these detected a total of 144 co-dominant and 16 dominant loci. These loci were grouped into nine linkage groups, which were assigned to cytogenetically identified chromosomes (Wang et al. 1994) using the primary trisomic lines (I to IX) (Fig. 2). The total map comprises a length of 964 cM, with the length of individual chromosomes ranging between 69 (chr. VIII) and 152 (chr. IX) cM. Interestingly, the shortest chromosome, VIII, has the highest density of markers, several of which are duplicated within that chromosome. Similarly, 91 co-dominant and 20 dominant loci, detected by 90 probes, were mapped in the interspecific population. Of these, 62 loci were in common between the two maps to allow their comparison. This comparison of the intra- and inter-specific maps revealed very similar map lengths. Distances between the most distal common markers in the intra- and inter-specific crosses amounted to 92 and 75 cM for chromosome I, 88 and 78 cM for chromosome II, 71 and 67 cM for chromosome III, 107 and 96 cM for chromosome IV, 98 and 90 cM for chromosome V, 85 and 105 cM for chromosome VI, 55 and 46 cM for chromosome VII, 59 and 57 cM for chromosome VIII, and 122 and 113 cM for chromosome IX, respectively.

Distorted segregation ratios

Deviations from the expected 1 : 2 : 1 and 3 : 1 segregation ratios were observed both for markers in the intra- and inter-specific crosses (Fig. 2) The segregation distortions were mainly due to a large number of homozygotes of the female parental type (AA) compared to the male parental type (BB). In the intraspecific cross, deviations from Mendelian inheritance ratios were observed for markers on chromosomes VI and VII with AA : BB ratios reaching 2 : 1 and 3 : 1 respectively, and were most severe on chromosome VIII, where, from top to bottom, the ratio AA : BB gradually increased from 1 : 1 to 2 : 0, with all homozygous plants being of the AA type at the locus *Xpsf114* (Fig. 3). Five chromosome regions were affected in the interspecific cross with segregration ratios (AA : BB) > 2 : 1 on chromosomes III and V, and up to 9.5 : 1, 7.5 : 1 and 11 : 1 in regions of chromosomes IX, IV and II respectively. No correspondence was found between the intra- and inter-specific cross in the regions affected.

Discussion

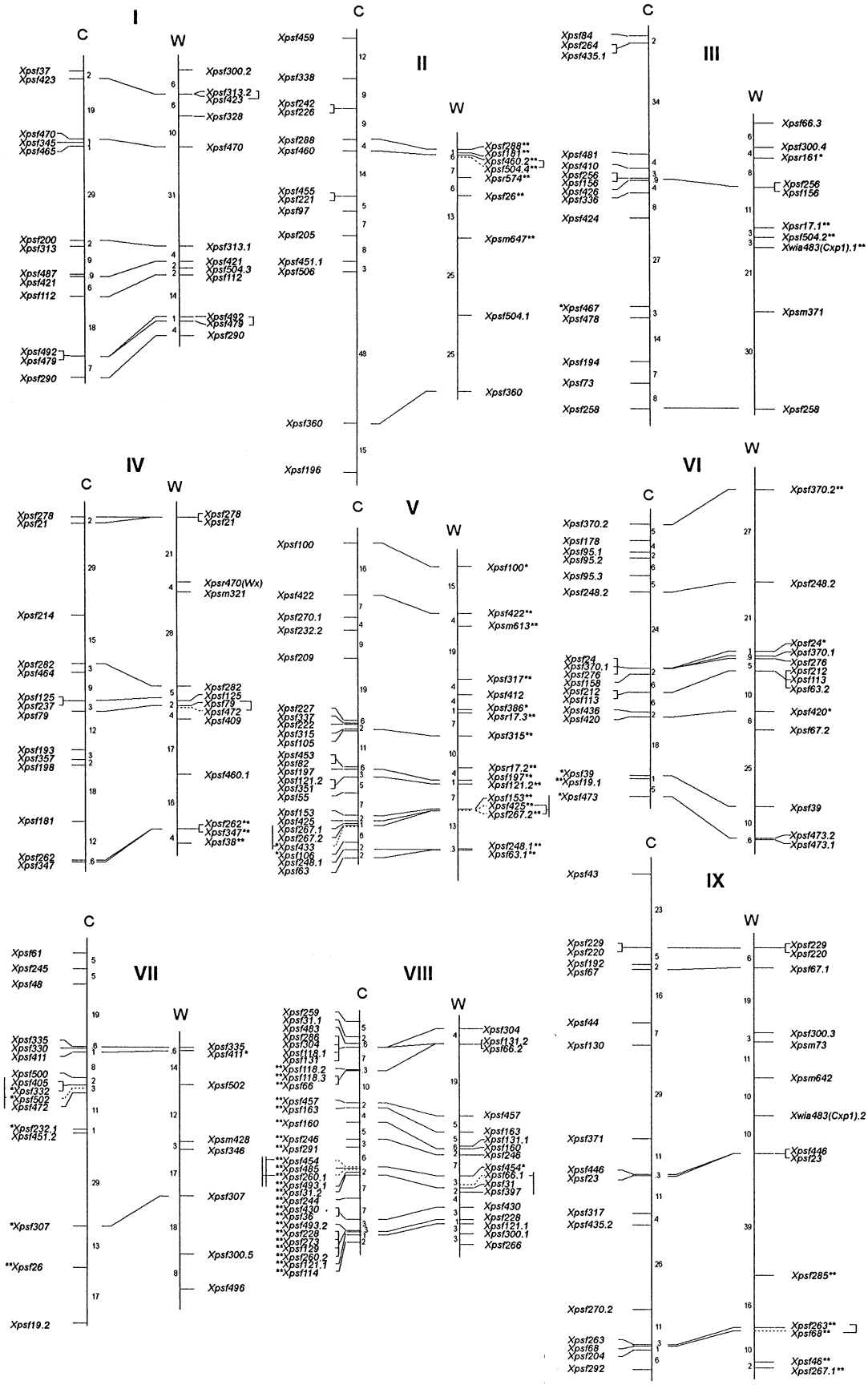
The foxtail millet genome

Our survey of *S. italica* accessions demonstrated a considerable level of RFLP polymorphism, although earlier work had showed limited variation in isozymes (Jusuf and Pernès 1985) or storage proteins (de Wet et al. 1979). The mean value of 44% polymorphism at any locus, observed with four restriction enzymes, can be compared to a mean value of 8.7% in wheat with 13 restriction enzymes (Chao et al. 1989). Thus, although *Setaria* is an inbreeder, RFLP polymorphism levels are relatively high and thus have potential for use in breeding research using crosses between adapted genotypes.

The total genetic length of the foxtail millet map is, on the other hand, very similar to the values obtained with other inbreeding cereals at, on average, 107 cM per chromosome compared to 122 cM in wheat (Gale et al. 1995) and 131 cM for rice (Kurata et al. 1994). By analogy this indicates that, although the map has not yet been capped with mapped telomeres, we can expect to have achieved around 80% coverage.

S. italica compared with *S. viridis*

In these experiments the wide interspecific cross was constructed and mapped as an insurance against the possibility that the intraspecific cross may not have revealed adequate polymorphism. Although the wide cross was much more polymorphic (75% relative to 44%), we were able to construct both maps with comparative ease. The construction of both an intra- and inter-specific map should allow us to observe any rearrangements between the wild and cultivated forms, or possibly the presence of any translocations or inversions that may have been present in our intraspecific cross. A comparison of the maps, as judged by the equivalent genetic lengths between common distal chromosomal markers, shows them to be similar at 777 cM for the intraspecific and 727 cM for the interspecific maps. Moreover, although a few localised differences in recovered linkage intervals were observed, there was no evidence of major chromosomal rearrangements, such as translocations or inversions, between the genomes of three *S. italica* and *S. viridis* genotypes. This result, and the similarity in the degree of chromosomal pairing as judged by the total genetic map lengths, is consistent with the results of the comparative study of Jusuf and Pernès (1985) between *S. italica* and *S. viridis*, which showed that the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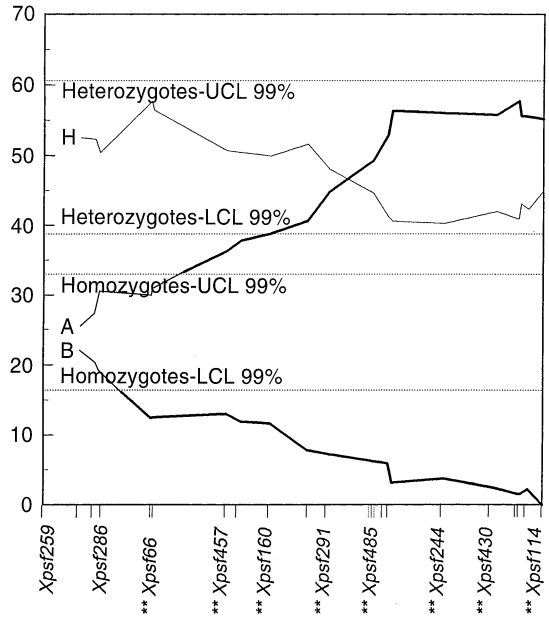

Fig. 3 Percentage of heterozygotes (H), AA (A) and BB (B) homozygotes along chromosome VIII. Dotted lines indicate 99% confidence levels (UCL: upper confidence level; LCL: lower confidence level). Levels that are significantly (**) deviant from the expected values are indicated in bold

differentiation between the two genotypes was regional rather than taxonomical in that *S. italica* and *S. viridis* from the same region were more closely related than *S. italica* accessions from different regions. Our results also support the suggestion of Harlan and de Wet (1971) that *S. italica* and *S. viridis* are taxonomically the same species and should be considered as subspecies.

Alignment of linkage groups and chromosomes

Hybridization of an RFLP probe to a line trisomic for the critical chromosome, i.e. the one carrying the sequence from where the probe was generated, is expected to show a 1.5-times stronger hybridization signal compared to a disomic. Such an assessment of hybridization intensities assumes that each track contains identical quantitities of DNA. To circumvent possible problems associated with any inaccuracies in DNA concentration measurements leading to unequal DNA loading, three probes belonging to different linkage groups were hybridized simultaneously, and the relative intensities of the hybridization signals in each track were compared. In a few cases, assignment of a locus to a chromosome was simplified by heterozygosity of the trisomic lines. Heterozygous loci displayed two fragments of near equal intensity in non-critical trisomic lines, while two alleles with an intensity ratio of 1: 2 were displayed when three copies of the hybridizing chromosome were present.

Fig. 2 Comparative genetic maps constructed in an intraspecific (C) and interspecific (W) cross. The extent of possible locations for loci that could not be mapped unambiguously are indicated with vertical bars. Loci with non-Mendelian segregation ratios are indicated with asterisks ($P < 0.05$*, < 0.01**)

Segregation distortion

Deviations of Mendelian segregation ratios may be due to selection at pre-zygotic or post-zygotic stages. Although our experiments do not allow us to identify the precise cause of the distorted segregation ratios, the deviation of the number of homozygotes, but not heterozygotes, from the expected values is most consistent with gametic selection. Moreover, the severe distortion observed on chromosome VIII suggests the presence of a gametocidal gene. At the top of chromosome VIII, segregation ratios do not significantly differ from 1 : 2 : 1 ($P > 0.01$); however, moving towards the bottom of chromosome VIII, the proportion of AA homozygotes increases from 25% to about 55% while that of BB homozygotes decreases from 25% to 0% (Fig. 3). In wheat, gametocidal genes (*Gc*) have been identified which in a hetero- or hemi-zygous condition kill gametes lacking *Gc* genes (King et al. 1991). These genes affect both male and female gametogenesis. The number of plants heterozygous for the markers along the length of chromosome VIII did not differ greatly from the expected value of 50%. Thus it appears that the gene on chromosome VIII that may control gamete fertility, or even abortion, affects only male or female gametogenesis.

Duplications in the *Setaria* genome

Increasingly, evidence is emerging of ancient duplications in genomes previously assumed to be true diploids, such as in rice where a highly conserved duplicated region covering part of the short arms of chromosomes 11 and 12 has been described by Nagamura et al. (1995). Similar evidence is not apparent between chromosomes in foxtail millet where most of the 27 probes for which at least two loci were mapped appear to be dispersed at random around the genome. A possible exception, which requires further confirmation as an intra-chromosomal duplication, is on chromosome VIII where six loci detected with probes PSF31, PSF66, PSF118, PSF131, PSF260 and PSF493 are duplicated, albeit not in two obviously co-linear blocks.

In conclusion, our maps provide molecular markers for the analysis of the foxtail millet genome with immediate practical applications for breeders of the crop in China. This small and apparently simple genome with high levels of polymorphism, particularly in the

wide cross, will also provide a useful intermediate in the longer term synthesis of grass comparative genetics (Moore et al. 1995) and provides the first example of a genetic map of a grass genome with a haploid chromosome number of nine.

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