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The effect of genome and sex on recombination rates in *Pennisetum* species

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Abstract The effects of homoeology and sex on recombination frequency were studied in crosses between cultivated pearl millet, *Pennisetum glaucum*, and two wild subspecies, *P. violaceum* and *P. mollissimum*. For the two wild×cultivated crosses, reciprocal three-way crosses were made between the F_1 hybrid and an inbred line (Tift $23DB_1$). The three-way cross populations were mapped to produce a female map of each wide cross (where the F_1 was the female) and a male map (where the F_1 was the male). Total genetic map lengths of the two inter-subspecies crosses were broadly similar and around 85% of a comparable intervarietal map. In the *P. glaucum*×*P. mollissimum* crosses, the map was further shortened by a large (40 cM) inversion in linkage group 1. Comparison of the recovered recombinants from male and female meiocytes showed an overall trend for the genetic maps to be longer in the male (~10%) in both inter-subspecific crosses; however, analysis of individual linkage intervals showed no significant differences. Gametophytic selection was prevalent, and sometimes extreme, for example 12:1 in favour of 'wild' alleles in the *P. glaucum*×*P. mollissimum* male recombinant population. One of the loci which determines panicle type in cultivated pearl millet and wild relatives, *H*, was mapped 9 cM from *Xpsm812* on linkage group 7 in the *P. violaceum* cross.

Key words *Pennisetum* · Gene transfer · Sex · Gametophytic competition · Linkage maps · Domestication syndrome

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Introduction

The sexual transfer of desirable genes from wild relatives to cultivated crops by recombination is a widely used technique in plant breeding. Two major potential limitations to successful introgression are a low frequency of homoeologous recombination, leading to linkage drag and the simultaneous incorporation of undesirable genes (Gale and Miller 1987), and the presence of structural rearrangements in the alien genome relative to that of the cultivated crop which can lead, following transfer, to unbalanced genotypes (Devos et al. 1993).

Recombination frequency can also be regulated by major genes (Riley et al. 1959; Temin and Marthas 1984). Overall, and in specific chromosomal regions, it can also differ between egg and pollen mother cells (Robertson 1984; de Vicente and Tanksley 1991), and this will be reflected in differences in map distances estimated from male or female gametes. Knowledge of the effect of the meiocyte in which recombination takes place can be conveniently exploited in both genetic studies and breeding practice. Unfortunately, previous results on this subject vary depending on the species studied. In humans (Donis-Keller et al. 1987) and most animal species (Johnson et al. 1987; Graf 1989), less recombination occurs in male gametogenesis. In plants, the results are less consistent. For example, in maize less recombination occurs in female gametogenesis (Robertson 1984), while in tomato, the opposite is the case (de Vicente and Tanksley 1991). In pearl millet, recombination was found to be little affected by sex in an intraspecific cross, with differences in only a few genomic regions, where it was slightly higher in the male (Busso et al. 1995).

In the study presented here, differences in recombination rates both between the sexes and between *Pennisetum* intraspecific and inter-subspecific crosses in pearl millet were investigated. These latter were crosses between cultivated *P. glaucum* and the wild subspecies, *P. violaceum* and *P. mollissimum*, both of which are potentially important gene donors for pearl millet improvement (Hanna

1987). No apparent genetic barrier exists between the cultivated and wild forms since they cross easily and form highly fertile hybrids (Brunken 1977; Marchais and Pernès 1985; Robert et al. 1991). Hence, Brunken (1977) concluded that these wild subspecies form a single biological species with cultivated pearl millet and proposed to include both of the wild forms as subspecies *monodii* of the cultivated form *P. americanum* (synonym *P. glaucum*).

Materials and methods

Plant materials

Two cultivated *P. glaucum* accessions (IP 6271 and IP 12070) and two accessions of two wild subspecies (*P. violaceum*, often referred to as subspecies *monodii*, IPW 2; and *P. mollissimum*, IPW 250) were used to make two F_1 hybrids.These inter-subspecific hybrids were reciprocally crossed to an inbred line of *P. glaucum*, Tift $23DB_1$ (Burton 1969), to produce two pairs of three-way (3 W) crosses (*viol*3W♀ and *viol*3W♂, and *moll*3W♀ and *moll*3W♂). They were:

*viol*3W♀: (*P. violaceum* IPW 2×*P. glaucum* IP 6271)$_{F1}$ ×*P. glaucum* Tift $23DB_1$

*viol*3W♂: Tift $23DB_1$×(IPW 2×IP 6271)$_{F1}$

*moll*3W♀: (*P. glaucum* IP 12070×*P. mollissimum* IPW 250)$_{F1}$ ×Tift $23DB_1$

*moll*3W♂: Tift $23DB_1$×(IP 12070×IPW 250)$_{F1}$

Tift $23DB_1$ was obtained from Dr. P. Ozias-Akins, University of Georgia, and all the other parental genotypes were provided by the Genetic Resource Division, ICRISAT.

The parents were grown and crossed in growth cabinets maintained at 60% humidity, at 28°C/25°C in a 12-h day/12-h night cycle. A single F_1 plant was used to produce each pair of reciprocal three-way crosses. In both of the *viol*3W crosses the population analysed comprised 107 plants; there were 98 plants in both of the *moll*3W crosses. Compared with F_2 or backcross populations, "off-type" plants resulting from outcrossing or selfing can be easily identified in the three-way cross progeny (Fig. 1). About 3% of the plants were excluded from the analysis because they did not show the restriction fragment(s) characteristic of the appropriate male parents.

DNA probes and RFLP analysis

Sixty genomic single-copy clones selected from a pearl millet *Pst*I genomic library were used to map the crosses. Most of these probes were selected on the basis of an existing RFLP map (Liu et al. 1994) to cover the pearl millet genome. Initially, probes were screened on DNA from six three-way F_1 plants from each of the *viol*3W♀ and *moll*3W♀ populations to identify polymorphic probe-enzyme combinations.

Methods for plant DNA isolation, restriction enzyme digestion, gel electrophoresis, Southern transfer, probe labelling and filter hybridisation and stripping were as described by Sharp et al. (1988), with the following modifications: (1) Hybond N^+ nylon membranes were used; (2) after hybridisation the membranes were washed twice in 2×SSC/1% SDS for 15 min each at 65°C, followed by two washes in 0.2×SSC/1% SDS for 15 min each at 65°C; and (3) membrane stripping was carried out by adding a boiling solution of 0.1×SSC/0.5% SDS and agitating for 15 min.

Isozymes

Five isozyme loci were mapped: esterase, *Est-1* and *Est-2* using methods described by Liu and Gale (1994); aminopeptidase, *Amp* as in Koebner and Martin (1989), malic enzyme, *Mal* as in Liu and Gale (1988); and β-amylase, *β-Amy* as in Ainsworth et al. (1983).

Linkage analysis

Data were analysed using the computer programme MAPMAKER (version 3.0) supplied by E.S. Lander, Whitehead Institute for Biomedical Research, Cambridge, Massachusetts. Linkage groups were obtained using two-point analysis with a LOD score of 4 and a maximum recombination fraction of 0.30. Multipoint analysis was then used for markers in each individual group to determine their relative order with a LOD threshold ≥33. Recombinant fractions were converted to centiMorgans (cM) using the Haldane mapping function.

The experimental design used allows for the separate analysis of recombination in male and female gametogenesis. Recombination rates in male and female linkage intervals were compared by testing the significance of differences in recombination fractions using a heterogeneity chi-square test with Yates' correction.

Map comparisons

The analyses concentrated on two comparisons: sex differences when recombination had been restricted either to the male pollen cells or the female egg cells, and narrow versus wide crosses in which maps made from intervarietal *P. glaucum* crosses were compared with maps made from inter-subspecific crosses. Sex differences were analysed in two pairs of reciprocal three-way inter-subspecific crosses involving *P. violaceum*×*P. glaucum* and *P. glaucum*×*P. mollissimum*. The "narrow" cross maps used in the second type of comparison were the *P. glaucum* intervarietal, LGD-1-B-10×ICMP 85410

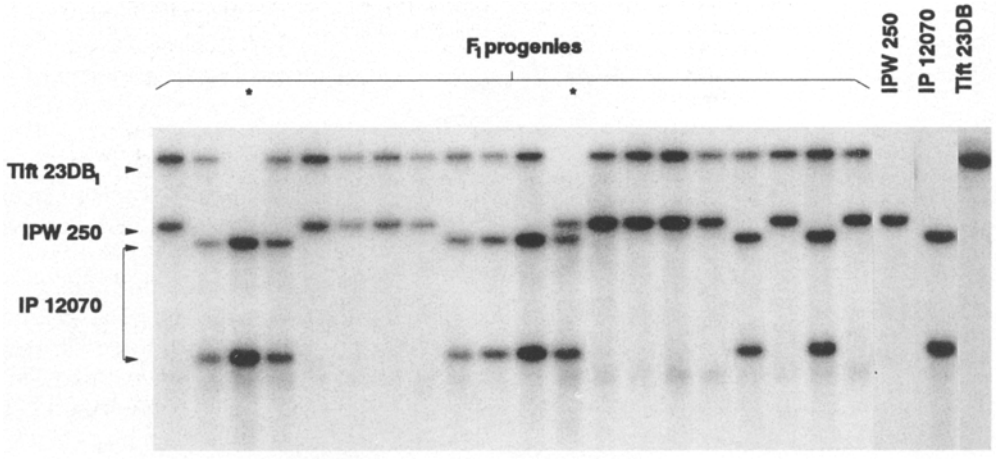

Fig. 1 Autoradiogram showing segregation patterns of three-way F_1 progeny from *moll*3W♀. Plant DNAs were digested with *Hin*dIII, and the filter was probed with PSM318. "True-to-type" plants in three-way F_1 populations should possess the restriction fragment from the third parent (Tift $23DB_1$), together with either the allele from the cultivated (IP 12070) or the wild (IPW 250) parent, but never both. The individuals indicated with * have been generated through selfing

and Tift 23DB$_1$×WSIL F2 populations already published by Liu et al. (1994). The latter cross was used only for comparisons involving linkage group 1 (LG1), since the former cross displayed a putative translocation involving LG1 and LG2.

Results

Skewed allele segregations

P. violaceum×*P. glaucum populations*

Of the 50 loci mapped in *viol*3W♀, 12 located on linkage groups 2 and 5 showed distorted allelic segregations (Table 1). All were skewed in the direction of IPW 2, the wild female parent. The average ratio between alleles of IP 6271 (the male) and IPW 2 (the female) was 1:1.7 on linkage group 2 and 1:3 on group 5.

Table 1 Loci showing distorted segregation for alleles in the three-way F_1 populations and their locations on the linkage groups

Locus	Linkage group	Ratio of alleles (cult:wild)	
		*Viol*3W♀	*Viol*3W♂
Xpsm565	1	45:53	69:37**
Xpsm425	1	48:51	68:36**
Xpsm347.1	1	49:43	70:36**
Xpsm360	1	50:35	66:33**
Xpsm607.1	1	49:47	63:41**
Xpsm227	2	41:64*	44:60
Xpsm286	2	39:63*	46:60
Xpsm176	2	39:63*	–
Xpsm25	2	37:64**	52:54
Xpsm662	2	40:65*	52:52
Xpsm592	2	34:61**	53:51
Xpsm716	4	53.45	63:41*
Xpsm265	4	48:43	62:41*
Xpsm320.2	5	30.65**	10:96**
Xpsm815	5	29:74**	9:95**
Xpsm320.1	5	23:75**	8:98**
Xpsm523	5	24:77**	5:101**
Xpsm651.2	5	25:72**	–
Xpsm735.1	5	21:72**	8:98**
		*Moll*3W♀	*Moll*3W♂
Xpsm492	1	21:19	67:45*
Xpsm515	1	51:45	69:40**
Xpsm425	1	51:45	70:42**
Xpsm360	1	50:44	68:42*
Xpsm347.1	1	50:45	69:42*
Xpsm669	1	51:45	68:43*
Xpsm464	4	53:43	71:38**
Xpsm716	4	55:41	79:31**
Xpsm612	4	57:38	80·32**
Xpsm607.3	4	44:41	76·36**
Xpsm588	6	51:40	98:14**
Xpsm696	6	51:44	93.17**
Xpsm713	6	56:40	89.22**
Xpsm579	6	54:40	89:22**

* Significant at P≤0.05; ** significant at P≤0.01

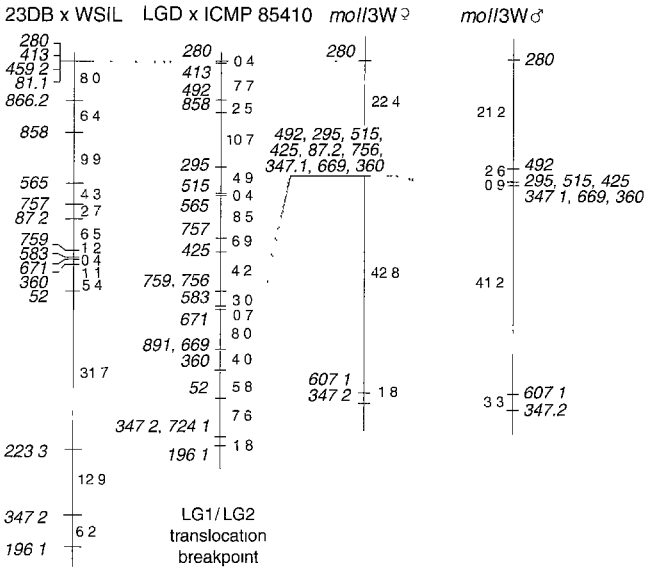

Fig. 2 Comparative linkage maps of Tift 23DB$_1$×WSIL, LGD-1-B-10 ICMP 85410, *moll*3W♀ and *moll*3W♂ on linkage group 1, indicating the presence of a chromosome inversion between the wild and cultivated species. The inversion is between *Xpsm492* and *Xpsm360*, as indicated by the limited recombination in *moll*3W♂

Of the 38 loci mapped in *viol*3W♂, 12 exhibited a skewed distribution from the expected 1:1 allelic ratios. These loci were located on linkage groups 1, 4 and 5 (Table 1). Those located on groups 1 and 4 were skewed in the direction of IP 6271, the cultivated male parent, and the average ratio between alleles of IP 6271 (male) and IPW 2 (the female) was 1.7:1. The loci on group 5 showed the strongest allelic ratio distortion so far encountered in this species, where the average allelic ratio in favour of the alleles from the "wild" parent was 1:12.

P. glaucum×*P. mollissimum populations*

None of the 64 loci assayed in *moll*3W♀ exhibited significant distortion from the expected allelic ratios. However, 14 of the 36 loci mapped in *moll*3W♂ deviated significantly from the expected 1:1 ratios. At all these loci the allelic ratios were skewed in favour of IP 12070, the cultivated female parent, and were located on three linkage groups, 1 (1.6:1), 4 (2.2:1) and 6 (4.9:1) (Table 1).

Comparison of genetic maps derived from intra- and inter-subspecific crosses

Locus orders and linkage groups were in agreement between the inter-subspecific and the previously analysed intraspecific crosses. Total genetic lengths, using the most distal comparable markers, were broadly similar over the intra- and inter-subspecific maps with the *P. violaceum* and *P. mollissimum* maps being on average 86% (208/241 cM)

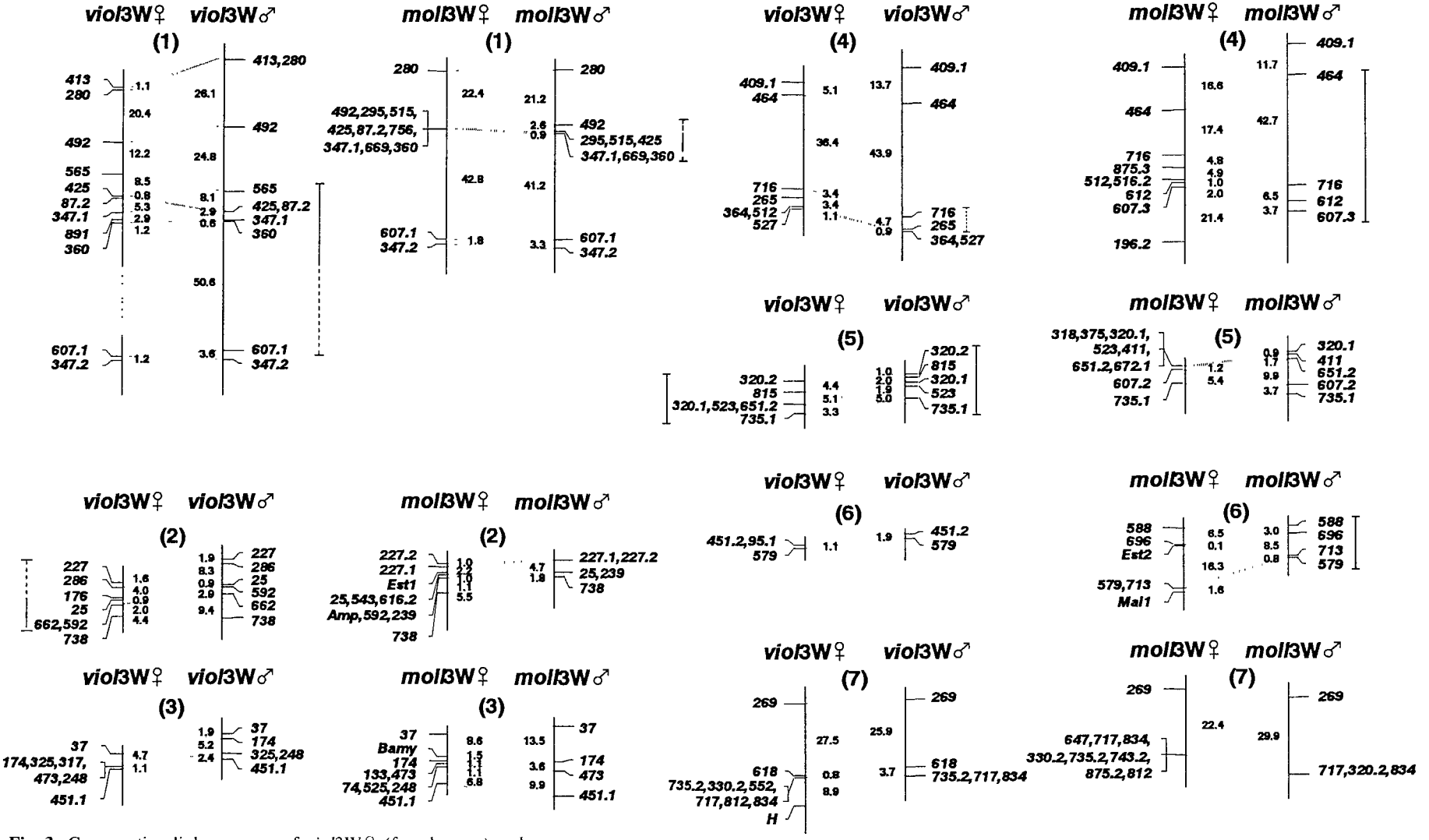

Fig. 3 Comparative linkage maps of *viol*3W♀ (female map) and *viol*3W♂ (male map), and *moll*3W♀ (female map) and *moll*3W♂ (male map). The *bars* alongside the individual chromosome maps indicate the extent of segregation distortion from the expected 1:1 ratios (*solid lines* at $P \leq 0.01$, *dotted lines* $0.01 < P \leq 0.05$); for explanation see text

and 74% (183/246 cM), respectively, of the intervarietal *P. glaucum* map. The additional reduction in length of the *P. mollissimum* maps is almost all accounted for by a probable internal inversion spanning about 40 cM on linkage group 1 (LG1) (Fig. 2). The total intraspecific map lengths are given for LG1 for the Tift $23DB_1 \times$WSIL cross plus LG2-LG7 from the LGD-1-B-10×ICMP 85410 cross. The most appropriate comparison is with the Tift $23DB_1 \times$ WSIL LG1 map since the bottom of the LGD-1-B-10×ICMP 85410 LG1 map is probably forshortened due to a suspected translocation (Liu et al. 1994).

Comparison of genetic maps derived from male and female gametes

The two pairs of reciprocal crosses were examined for differences in recovered male and female recombination (Fig. 3). The trend for the female maps to be shorter by about 10% was not statistically significant. An analysis of all 53 comparable intervals revealed no differences significant at the $P \leq 0.01$ level. Hence, there is no evidence in these crosses for any differences in recombination rates between male and female gametogenesis.

Location of a major gene(s) discriminating cultivated and wild pearl millet

The inflorescence of the *P. violaceum* accession IPW 2 is strikingly different from that of cultivated pearl millet. The main difference is that the spikelets of the wild form are covered by dense and long bristles, a characteristic involved in the "domestication syndrome" described by Pernès et al. (1980). More than 90% of the progeny from *viol*3W♀ could be scored unequivocally as wild or cultivated ear types. All of the "wild" inflorescences also exhibited the shattering habit inherited from IPW 2. The locus controlling these characters, designated *H*, was mapped 9 cM from *Xpsm618* on LG7 (Fig. 3). The fact that not all progeny could be unambiguously grouped based on bristle characters supported the arguments that these characters are likely controlled by several closely linked genes (A. Sarr, personal communication).

Discussion

Segregation distortion

It is well-known that some loci in a genome often segregate in a non-random fashion (reviewed by Lyttle (1991)). Such distortions can be caused by genes affecting gametic or hybrid fitness, such as *Sd* genes in *Drosophila* (Temin and Marthas 1984) and "Cuckoo", or gametocidal genes, in *Aegilops* spp (Endo 1982; Miller 1982). Some of these latter genes may prove to be valuable in breeding practice (King et al. 1991). In pearl millet, plasmotype may also influence pollen selection. In our experiments the effect of cytoplasm was excluded in the *P. mollissimum* reciprocal crosses, while in the *P. violaceum* reciprocals, *viol*3W♀ is in wild cytoplasm and *viol*3W♂ is in cultivated cytoplasm. Six of the seven regions of segregation distortion follow the same pattern as noted earlier by Robert et al. (1991), namely a tendency to maintain wild-wild and cultivated-cultivated nuclear-cytoplasmic allelic associations. Thus, LGs 1 and 4 in the *viol*3W♂ and LGs 1, 4 and 6 in *moll*3W♂ all show cultivated allele-cultivated cytoplasm associations, and LG2 in *viol*3W♀ shows a wild-wild association (Table 1). The preponderance of these effects through the pollen is as expected, but the lack of correspondence between the map location of the effects (Fig. 3) either over reciprocals or over crosses meant that, in this experiment, no further conclusions concerning the genetics of segregation could be revealed.

In LG5 in the *P. violaceum* crosses, both male and female crosses showed distortion in favour of the wild alleles (Table 1), very extreme (1:12) in the male three-way cross. This phenomenon is reminiscent of the gametocidal chromosomes found in certain *Aegilops* species, e.g. chromosome $4S^s$ from *Aegilops sharonensis* (Miller 1982).

Linkage maps derived from wide crosses

To date, analysis of DNA markers is still labour-intensive and expensive. Thus, it is attractive, and often necessary, to maximize the polymorphism available in a given species by using single wide crosses for map construction. For example, inter-subspecific crosses have been used for rice (McCouch et al. 1988), oats (O'Donoughue et al. 1992), tomato and potato (Tanksley et al. 1992). Similarly, very wide crosses between a common wheat and an artificially synthesised hexaploid wheat have been used to generate the major mapping population (Devos et al. 1992; Van Deynze et al. 1995). However, maps generated from such crosses, rather than crosses based on adapted varieties, have inherent limitations. Inter-subspecific or wide crosses are likely to show less recombination resulting in shorter maps compared to those generated from intraspecific crosses. Similarly, any divergence in chromosome structure, such as inversions discriminating the two parental genomes, will not be visible, although large inversions might be reflected by the convergence of many markers at the same point on the map.

It was not surprising that the orders of genetic markers were very similar between maps derived from intra- and inter-subspecific crosses. Highly conserved marker loci orders have been found between even less related species, for example, the extreme co-linearity observed between the A, B and D genomes of hexaploid wheat (Chao et al. 1989; Devos et al. 1992), and that between wheat, rye and barley (Gale and Miller 1987; Wang et al. 1992; Devos et al. 1993). There is convincing evidence of the presence of an inversion on linkage group 1 in *P. mollissimum* (Fig. 2). From the view point of utilising *P. mollissimum* in plant breeding, it is important to know whether this inversion is

specific to the accession used in this study or general to the species. There is evidence (V. Poncet and A. Sarr, personal communication) that in another *P. mollissimum* ×*P. glaucum* cross the recombination rates were dramatically reduced in the region of the putative inversion on linkage group 1.

Difference in recombination frequency between male and female gametes

Contrary to the case in tomato (de Vicente and Tanksley 1991), there is no evidence of significant differences in recombination rate between the male and female. This is in agreement with the results obtained from analyses of intraspecific pearl millet crosses (Busso et al. 1995) where little difference was found between recombination rates in male and female gametes.

Feasibility of developing single chromosome substitution/recombination lines in *Pennisetum*

Single intervarietal or inter-subspecific chromosome substitution and recombination lines can be important tools for genetic analyses. Genetic effects of individual chromosomes can be investigated in a uniform genetic background. Such genetic stocks have been used in wheat for locating major genes (Law and Jenkins 1970) and for identifying genes controlling quantitative traits (Worland and Law 1986). The most common approach of creating these genetic stocks is through monosomic stocks (Sears 1953; Law 1966). This is limited to polyploid species such as hexaploid wheat where the redundancy offered by polyploidy allows such species the ability to tolerate the loss of chromosomes. This approach is not feasible for diploid species like pearl millet where the loss of any single chromosome is likely to be fatal.

Compared with other major crop species, the linkage map obtained for pearl millet is small even when intraspecific crosses were employed (Liu et al. 1994). As expected, the low recombination frequency was even more pronounced in the inter-subspecific crosses. For example, the total length of linkage group 2 was less than 10 cM in all four inter-subspecific crosses, and in no case was more than one crossing-over event in this linkage group observed in each gamete. This indicated that whole chromosome reassortment, rather than chromosome recombination, is very common in these crosses. Thus, it should be quite possible to select single chromosome substitution lines from the progeny of such crosses.

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