Theor Appl Genet (2000) 100:190–198 © Springer-Verlag 2000

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Comparative mapping reveals a complex relationship between the pearl millet genome and those of foxtail millet and rice

Received: 10 February 1999 / Accepted: 6 July 1999

Abstract Comparative genetic maps were constructed of the pearl millet genome with foxtail millet and used to describe the homoeology between the genomes of pearl millet, foxtail millet and rice. Despite the close taxonomic relationship of pearl and foxtail millet, their genomes were highly, rearranged. A comparison of the millet and rice genomes indicated that most of these rearrangements were likely to have taken place in pearl millet. Two duplications were identified in pearl millet. A duplication between the distal segments of linkage groups 1 and 4 corresponds to the ancient duplication previously identified between rice chromosome arms 11S and 12S and foxtail millet chromosomes VII and VIII. The other putative duplication, also between regions of linkage groups 1 and 4, is likely to be species-specific. The exploitation of the comparative maps in pearl millet research is discussed.

Key words Colinearity · Comparative maps · Foxtail millet · Grasses · *Oryza* · Pearl millet · *Pennisetum glaucum* · Rice · *Setaria*

Introduction

Over the past few years, a lot of effort has gone into establishing the extent of synteny between genomes of different species. The grass family is probably the best characterised, with good comparative genetic maps showing the interrelationship between the genomes of rice, foxtail millet, sugar cane, sorghum, maize, wheat and oats (for overview see Devos and Gale 1997). Pearl millet, *Pennisetum glaucum* (L.) R. Br. (2n=2x=14), is an important food crop from the Indian and African continents. It belongs to the subfamily Panicoideae, which includes the tribes Paniceae with pearl millet and foxtail millet, Maydeae with maize and Andropogoneae with sorghum and sugar cane. When the genomes of each of these crops are described in function of their homoeology to rice, it is clear that marker orders are highly conserved over large chromosome segments. The gross chromosomal rearrangements that have taken place in the Panicoideae genomes relative to rice can be classified as either species-specific or as characterising the taxonomic group. Examples of the latter are the insertion of rice chromosome 10 into rice 3, and rice 9 into rice 7 to form homoeologous Panicoideae chromosomes (Devos and Gale 1997).

Pearl millet research can benefit greatly from the application of knowledge gained from the integration of its genome into the grass consensus map. Currently, genetic maps are available covering the seven pearl millet chromosomes (Liu et al. 1994; Devos et al. 1995b). However, these maps are short, and comparative data may give an indication of the extent of genome coverage provided by the pearl millet maps. Heterologous probes will also provide a resource to, if necessary, extend the maps and saturate regions with low marker density.

Trait analysis in pearl millet is focussed on downy mildew resistance (Jones et al. 1995), traits related to domestication (Poncet et al. 1998) and drought tolerance (C. Howarth, personal communication). Especially for the latter trait, comparative maps may provide valuable information if the genes underlying drought stress are conserved across the grass species. A number of chromosomal regions associated with tolerance to drought resistance have been identified in rice (Champoux et al. 1995; Ray et al. 1996; Lilley et al. 1996), maize (Lebreton et al. 1995; Ribaut et al. 1997; Tuberosa et al. 1998) and barley (Teulat et al. 1998). In order to be able to exploit the knowledge already available in other grass crops in pearl millet research, we constructed a comparative pearl millet (2n=2x=14; C=2.4 pg) – foxtail millet (2n=2x=18; C=0.45 pg) – rice (2n=2x=24; C=0.4 pg) map.

Communicated by J. Dvorak

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Materials and methods

Plant material

Two pearl millet F_2 populations, derived from crosses between the inbred lines LGD-1-B-10 and ICMP 85410 (Liu et al. 1994), and 81B and ICMP 451 (C.T. Hash, unpublished), and a foxtail millet population from an interspecific cross *Setaria italica* (L.) P. Beauv. accession B100× *S. viridis* (L.) P. Beauv. acc. A10 (Wang et al. 1998) were used for mapping.

Restriction fragment length polymorphism (RFLP) probes

Probes previously mapped in wheat (prefix PSR, AK, MSU, WIA), maize (UMC, NPI, PHP, Bnl), rice (RGC, RGL, RGR, RZ) and pearl millet (PSM, UGT, HHU) were used for cross-mapping. Their map locations were obtained from the following sources; Kurata et al. (1994), Gale et al. (1995), Devos et al. (1998), MaizeDB (http://www.agron.missouri.edu/), the Japanese Rice Genome Project (RGP) database (http://www.staff.or.jp/) and RiceGenes (http//ars-genome.cornell.edu/cgi-bin/WebAce/webace?/db=ricegenes).

RFLP analyses

DNA inserts were labelled and hybridized as described in Devos et al. (1992). Genetic maps were constructed using the programme MAPMAKER v. 3.0 (Whitehead Institute for Biomedical Research, Cambridge, USA), and marker orders were manually checked for critical cross-overs. Integration of the two pearl millet maps was carried out by eye and based on the presence of common markers and relative genetic distances.

Results

Pearl millet linkage group 1

Linkage group (LG) 1 is homoeologous, from end to end, with a segment of foxtail millet (FM) chromosome VIII corresponding to the long arm of rice 11, a cluster of markers corresponding to, probably, the centromeric region of foxtail millet chromosome VI, a large segment of FM III corresponding to rice 5 and a proximal segment of rice 12S, and the duplicated segments of FM VII and VIII. The latter segments correspond to the rice 11S/12S duplication (Nagamura et al. 1995; Devos et al. 1998) (Fig. 1). Five probes that map to the bottom of LG 1, PSM607, RGC920, PSM724, PSM196 and PSM837, detect additional loci at the bottom of LG 4. The loci *Xrgc920.1* and *Xpsm196.2* were mapped on LG 4 in the 81B×ICMP 451 cross (Fig. 1), while *Xpsm607.3*, *Xpsm724.2* and *Xpsm837.2* were mapped on LG 4 in three further crosses (Liu et al. 1996; K.M. Devos, unpublished results). Although the order of these markers could not be established unambiguously, their presence on both LG 1 and LG 4 indicates that the region, corresponding to the 11S/12S duplication in rice is also duplicated in pearl millet. A further 5 probes mapping to the top of LG 1, PSM81, PSM866, RGC2, RGC950 and PSM515, also detect loci in the same order on LG 4 (Fig. 1; Devos et al. 1995; Poncet et al. 1998) and may be indicative of a second inter-chromosomal duplication.

Pearl millet LGs 2, 3 and 5

Pearl millet linkage group 2 is homoeologous with segments, probably corresponding to entire chromosome arms, of FM IX, FM IV and FM I. Linkage group 3 is homoeologous with the remaining segment of FM I and a segment of FM VII, and LG 5 with a small segment of FM VII (relationship based on 1 marker point only) and the remaining segments of FM IV and FM IX (Fig. 1). There is some ambiguity about the precise relationship of the interstitial cluster, comprising the loci *Xrgc621* and *Xrgc777*, on pearl millet LG 3 with foxtail millet and rice. These loci map to the long arm of chromosome 2 in rice and to chromosome VII in foxtail millet and represent a region of disrupted colinearity between rice 2L and FM I (Fig. 1). The pearl millet comparative data provide no evidence whether the rearrangement, leading to the disruption of colinearity between rice 2L and FM I, is also present in pearl millet.

Two probes that map to foxtail millet chromosome I, PSM708 and RGR2510, detected linked loci in the 81B×ICMP451 cross, but did not link to any of the pearl millet linkage groups in that cross. In the cross LGD-1-B-10×ICMP 85410, however, *Xpsm708.2* mapped 32 cM distal to *Xpsm738*. The location of *Xpsm708* and *Xrgr2510* at the bottom of pearl millet LG 2 fits well with the homoeologous relationship of that region with foxtail millet chromosome I and rice chromosome arm 2S.

Pearl millet LG 4

This linkage group is homoeologous with a segment of FM III, probably most of FM VI and the duplicated regions of FM VII and FM VIII. In rice, this corresponds to a region of chromosome arm 12L, chromosome 8 and the 11S/12S duplicated regions.

Pearl millet LG 6

Linkage group 6 is largely homoeologous to foxtail millet chromosome V and rice chromosome 1. The two most distal markers, *Xpsm870* and *Xhhu33*, mapped to foxtail millet chromosomes I and VI, respectively. However, PSM870 detects two copies in both pearl and foxtail millet, only one of which was polymorphic. The probe HHU33 is single copy in pearl millet, but detects three fragments in foxtail millet, only one of which was polymorphic in our mapping population. It is thus possible that the *Xpsm870* and *Xhhu33* loci in pearl millet and foxtail millet are not homoeologous. Alternatively, colinearity may be disrupted in these distal regions.

Pearl millet LG 7

This linkage group is homoeologous to FM II and rice 7S-9-7L. The latter structural arrangement was shown to be typical for all Panicoideae species examined to date

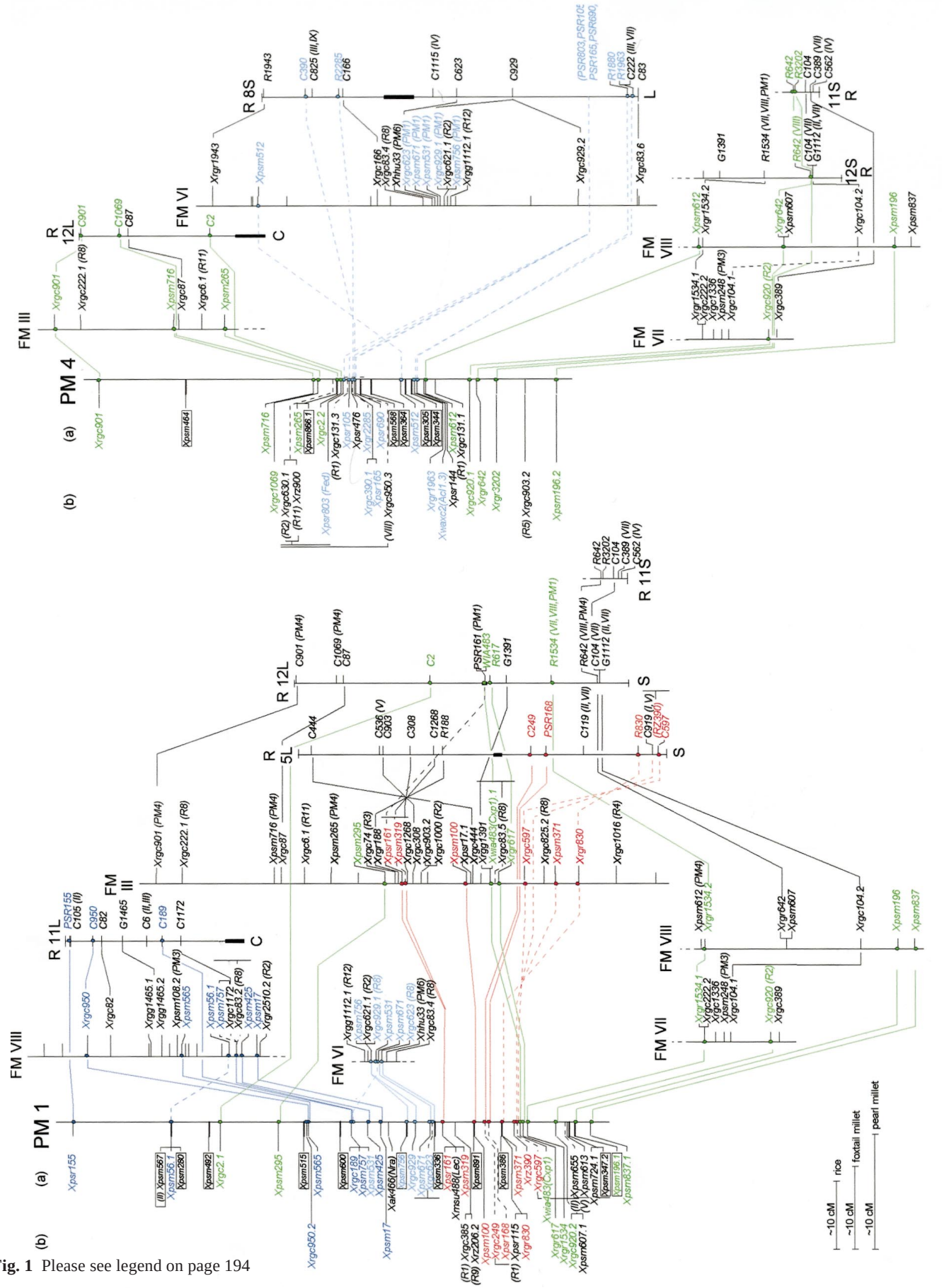
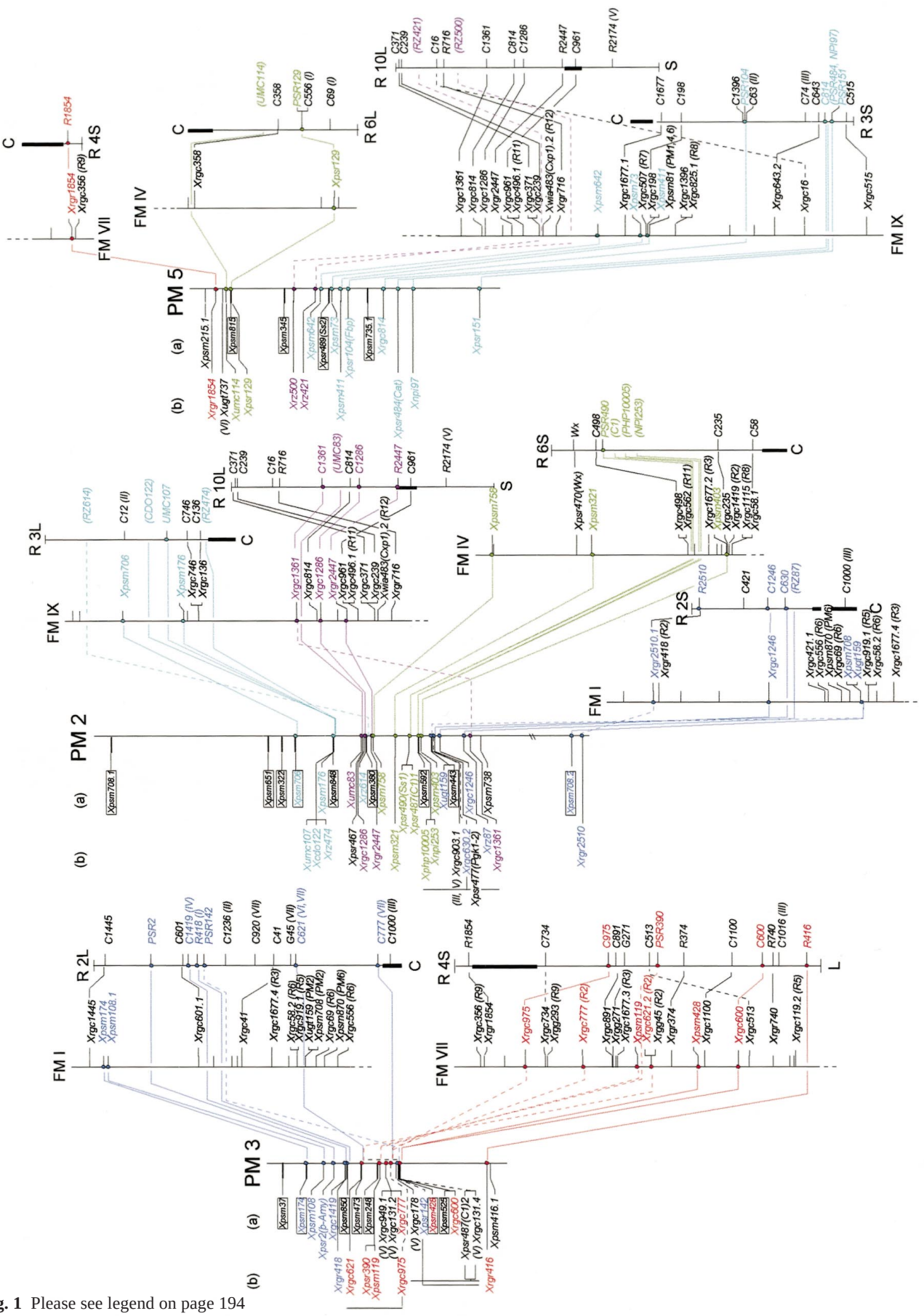


Fig. 1 Please see legend on page 194



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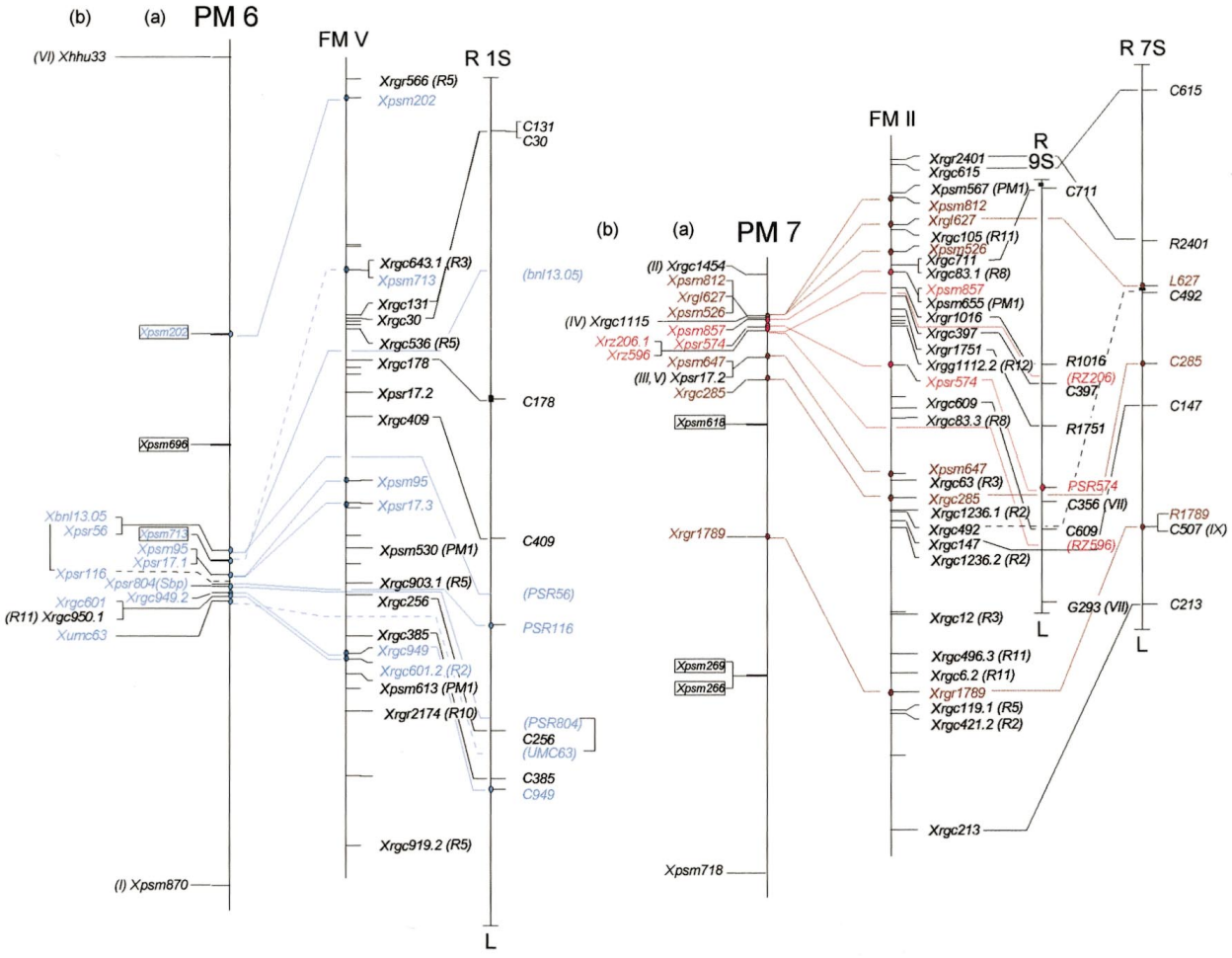

Fig. 1 Comparative genetic maps of pearl millet, foxtail millet and rice. The pearl millet genetic map is a consensus map. Loci mapped in the LGD-1-B-10×ICMP 85410 and 81B×ICMP 451 cross are in columns (*a*) and (*b*). Markers within the individual maps that could not be placed unambiguously are indicated with *dotted* (- - -) *lines*, and the extent of their possible location is indicated with *vertical bars. Boxed markers* in column (*a*) are common to both maps. Please note that, with the exception of *Xpsr708.2* and *Xrgr2510* in the cross 81B×ICMP451, all markers in the individual maps were linked with a LOD≥3. However, the consensus map contains only those markers relevant to the comparative analysis. Homoeologous relationships between markers are indicated with *full lines* (–) when colinearity is maintained and *dotted lines* (- - -) when colinearity is disrupted, with the *different colours* corresponding to the 12 rice chromosomes. Chromosomal locations of markers that map to non-homoeologous positions are given *in parenthesis*; *R, PM* followed by a number designate rice and pearl millet locations, respectively; foxtail millet locations are given in *roman numbers*. Loci on the rice map *in parenthesis* were obtained from RiceGenes and represent integrated positions on the RGP map. *S, L* and *C* indicate short and long arms and centromeric regions, respectively; centromeric regions on the rice map are also indicated with *black rectangles*

(Devos and Gale 1997). The most distal pearl millet markers could not be mapped in our foxtail millet population due to lack of polymorphism.

Discussion

A pearl millet comparative map was constructed using rice, wheat, maize and other probes previously mapped in one or more grass species. The use of two pearl millet populations increased the number of probes that could be mapped. The resulting maps were highly colinear, and a consensus map was generated based on the presence of a common set of markers (boxed markers in Fig. 1). Within a common marker interval, however, the relative order of loci derived from different maps could not be established unambiguously. For these markers, orders were based on genetic distances relative to the common markers and on the order of homoeoloci in related species. To further refine the comparative maps, especially for regions of the *Pennisetum* genome that displayed low levels of cross-hybridization and/or polymorphisms for the heterologous probes tested, we mapped pearl millet probes from these regions onto the foxtail millet widecross population (Devos et al. 1998). The pearl millet genetic map was compared primarily with foxtail millet,

the crop within the grass family that is taxonomically most closely related to pearl millet. However, as the relationship between the genomes of rice and foxtail millet had previously been established (Devos et al. 1998), this comparison could be extended to rice and other grass crops. The pearl millet – foxtail millet – rice comparative maps are presented in Fig. 1.

Extent of colinearity

The pearl millet genome is differentiated from the rice and foxtail millet genomes by a large number of gross structural chromosomal rearrangements. A comparison of the organisation of the genomes of rice, foxtail millet, sugar cane, sorghum, pearl millet, maize, wheat and oat showed that most of these rearrangements were present only in pearl millet and must thus have been of relatively recent origin. Other rearrangements could be identified that were likely to have occurred earlier in evolution. For example, all species belonging to the Panicoideae subfamily analysed so far, have three chromosomal rearrangements relative to rice in common, i.e. the insertion of rice chromosome 10, which itself is rearranged, into rice 3, and the insertion of rice 9 into rice 7 to form Panicoideae chromosomes. Despite the highly rearranged nature of the pearl millet genome relative to rice, homoeology to the rice configuration 3S-10La-(10S)-10Lb-3L is still apparent in pearl millet. The homoeology of rice chromosomes 5 and 12, on the other hand, in the structural organisation of pearl millet LG 1 and foxtail millet chromosome III was not shown in any of the other Panicoideae chromosomes. This rearrangement may thus be typical for the Paniceae tribe. The colinear relationship between the bottom of LG 1 in pearl millet, and chromosomes 5 and 12S of rice also suggests that the inversion, spanned by *Xrgc597* and *Xrgr830* and which characterises foxtail millet relative to rice, has taken place after the divergence of pearl and foxtail millet.

Nevertheless, it is clear that the number of gross structural rearrangements relative to rice is greater in pearl millet than in any of the other grass genomes analysed to date. The fact that some species accumulate and fix rearrangements more readily than others has been reported within the Triticeae tribe and was observed for self-pollinating as well as outbreeding species (Zhang et al. 1998). Comparative mapping between arabidopsis and *Brassica nigra* also showed an exceptionally high rate of chromosomal rearrangements in the *Brassicaceae* family (Lagercrantz 1998). Lande (1979) stipulated that the presence of chromosomal rearrangements in the heterozygote condition reduces fertility and suggested that the fixation of reciprocal translocations requires small population sizes and has probably been aided in plants by a high degree of inbreeding. Pearl millet is an outbreeding species, and too little is known about the population structure to infer whether this factor has indeed played a role in the fixation of the chromosomal rearrangements in pearl millet.

Inter-chromosomal duplications

Chromosomal duplications appear to have taken place in most plant species. In the small rice genome, high-density genetic maps have revealed the presence of a duplication between the short arms of chromosomes 11 and 12 (Nagamura et al. 1995), and DNA sequencing uncovered a tandem duplication of the *a1* gene (Chen et al. 1998). Both duplications are likely to predate the divergence of the Panicoideae and Oryzoideae subfamilies (Devos et al. 1998; Chen et al. 1998). A comparative analysis of the genetic maps of pearl millet, foxtail millet and rice clearly showed the presence in pearl millet of duplicated segments on LGs 1 and 4 corresponding to the rice 11S/12S duplication. The presence of this duplication in rice, foxtail millet and pearl millet supports the hypothesis that it is of ancient origin. No reports are available to date on the presence of this duplication in other Panicoideae crops such as maize, sorghum and sugar cane; however, this is probably due to insufficient comparative data for these species in the critical chromosome regions.

The markers PSM81, PSM866, RGC2, RGC950 and PSM515 may identify a second duplication between LGs 1 and 4. This rearrangement is likely to be of more recent origin as no evidence for its presence was found in rice.

Estimation of genome coverage

The first pearl millet map published had a genetic length of only 303 cM (Liu et al. 1994). This was originally thought to be due to low levels of recombination. The subsequent identification of more distally located markers suggested, however, that the pearl millet map was incomplete. It appears that, in the pearl millet crosses examined, recombination is extremely localised in the distal chromosome regions. Uneven distribution of recombination has also been observed in wheat (Devos et al. 1995a) and to a limited extent in rice (Harushima et al. 1998). Gill et al. (1996) suggested that recombination takes mainly place in gene-rich regions. Establishment of a possible correlation between recombination and gene-density in pearl millet, however, will have to await the results of physical mapping. To estimate the genome coverage of the current map, we surveyed whether the distal pearl millet regions corresponded to telomeric regions on rice chromosomes. The two most distal markers on pearl millet LG 1, *Xpsr155* and *Xpsm837*, mapped, or could be extrapolated to map, to the distal regions of the long and short arms of rice chromosome 11, respectively. It is therefore likely that LG 1, which has a length of about 90 cM, completely covers a pearl millet chromosome. Other pearl millet linkage groups that are expected to represent nearly complete chromosome coverage are LG 3, which carries distal markers of rice chromosome arms 2L and 4L, LG 4 with distal markers of rice 12 and LG 5 with distal markers of rice 4S and 3S. This would indicate that recombination is indeed low in some pearl millet linkage groups, such as LGs 3 and 5, which span

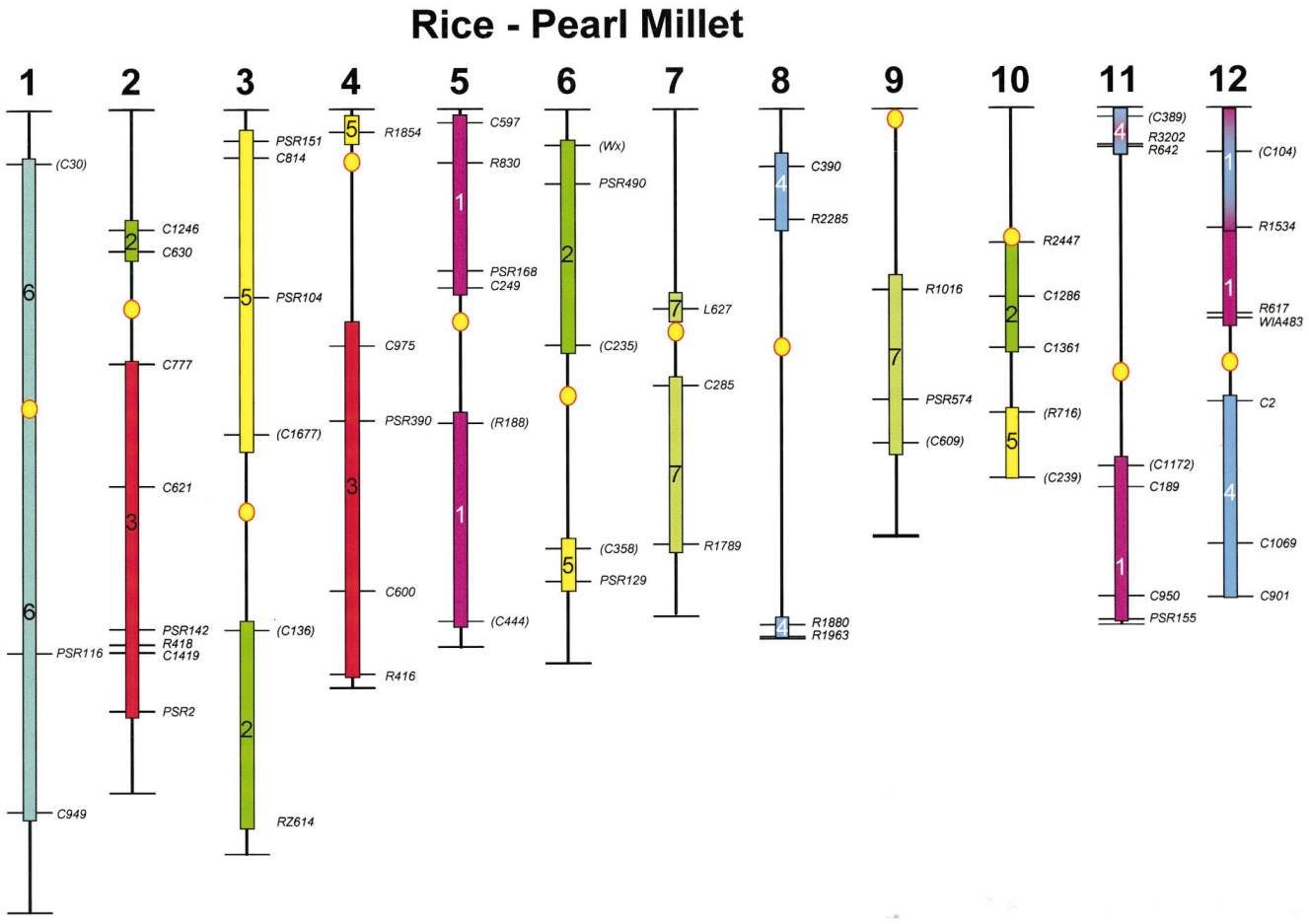

Fig. 2 Comparative alignment of the seven pearl millet chromosomes onto the RGP rice map. With the exception of RZ614 only markers previously mapped on the RGP map are shown. Markers in *brackets* have not been mapped in pearl millet, but indicate, based on the pearl millet – foxtail millet – rice comparative maps, the approximate regions to where the rice – pearl millet homoeology extends. The *absence* of *coloured bars* indicates regions of the rice genome devoid of comparative pearl millet data. *Yellow circles* indicate the position of centromeres

36 cM and 49 cM, respectively. It is however still possible, on the other hand, that the pearl millet maps are incomplete and that synteny is disrupted in the distal regions. The extent of coverage of the rice map in function of the pearl millet genome is shown in Fig. 2. This overview of the regions of the rice genome for which homoeology with pearl millet has been established demonstrates that breaks in synteny between rice and pearl millet tend to correspond to centromeric regions in rice. This has also been observed for maize and wheat relative to rice and led to the hypothesis that cereal centromeres are sites of breakage and fusion (Moore et al. 1997).

Exploitation of the comparative maps

The integration of the pearl millet genetic maps in the grass consensus map will allow the exploitation of information from all grass crops. The use of comparative genetic maps may make it possible to predict the location in pearl millet of genes underlying adaptative traits previously mapped in other crops, such as plant height, flowering time, seed dormancy, etc. Several genes controlling plant height have been identified in pearl millet. Study of the endogenous gibberellin acid (GA) levels suggested that the recessive dwarfing genes *d1*, *d2* and *d4* may be similar to the rye *ct1*and *ct2* dwarfing genes (Devi et al. 1994), which map to the centromeric region of rye chromosome 7R and the long arm of 5R, respectively (Plaschke et al. 1993, 1995). These regions are homoeologous to segments of pearl millet LG 4 and LG 2, respectively. Although none of the dwarfing genes have, as yet, been mapped in pearl millet, preliminary data indicate that a gene affecting plant height, which may correspond to *d2*, is located on LG 4 (K.M. Devos, J. Wilson, unpublished).

Similarly, major quantitative trait loci (QTL) for photoperiod-dependent flowering have been mapped in rice on the short arm of chromosome 6 and the long arm of chromosome 7 (Yano et al. 1997). The latter gene is likely to be homoeologous to the *Ppd*-genes on the short arms of the wheat and barley group 2 chromosomes which control photoperiod sensitivity (Laurie 1997). Assuming that the positions of genes controlling day-length response have remained conserved in grass species dur-

ing evolution, one would expect to find photoperiod-dependent flowering time QTL homoeologous to *Hd1* and *Hd2* to be located on pearl millet linkage groups 2 and 7, respectively.

Conclusions

The pearl millet genome is distinguished from the rice genome by a large number of gross structural rearrangements, some of which characterise the Panicoideae species, such as the rice 10 into rice 3, and rice 9 into rice 7 arrangement, while others are species-specific. The close taxonomic relatedness between pearl millet and foxtail millet – the former with a highly rearranged genome relative to rice, the latter displaying a simpler genomic relationship – indicates that some species accumulate and fix rearrangements more readily than others. The pearl millet genome carries at least one, and probably two duplications between linkage groups 1 and 4. These duplications are likely to be independent events. One corresponds to the duplication found between the short arms of rice chromosomes 11 and 12 and must have occurred before the divergence of the Panicoideae and Oryzoideae subfamilies. The other may be specific to pearl millet. The knowledge of the relationship between the pearl millet genome and that of other grass species will be exploited in gene isolation studies, currently underway to clone genes underlying quantitative trait loci for downy mildew resistance.

Acknowledgements We thank T. Sasaki, S. McCouch, B. Burr, E. Coe, T. Helentjaris, A. Kleinhofs, P. Westhoff, G. Fincher and N. Raikhel for providing the heterologous probes. This document is an output from a project funded by the UK Departement For International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID. The senior author acknowledges funding from the Biotechnology and Biological Sciences Research Council (BBSRC) through a David Phillips Research Fellowship.

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