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Comparative genetic maps of foxtail millet (*Setaria italica*) and rice (*Oryza sativa*)

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Abstract A foxtail millet-rice comparative genetic map was constructed using mapped rice RFLP markers and wheat genomic and cDNA clones with known map position in rice. About 74% and 37% of the cDNA and genomic clones, respectively, were transferable to foxtail millet, confirming that conservation at the DNA level is greatest in genic regions. A high degree of conserved colinearity was observed between the two genomes. Five entire foxtail millet chromosomes appear to be colinear with five entire rice chromosomes. The remaining four foxtail millet linkage groups each show colinearity with segments of two rice chromosomes. The rearrangements of rice chromosomes 3 and 10 to form foxtail millet chromosome IX, and 7 and 9 to form chromosome II are very similar to those required to form maize chromosomes 1 and 7 and sorghum linkage groups C and B, indicating *Setaria*'s clear taxonomic position within the subfamily of the Panicoideae.

Key words Colinearity · Comparative maps · Foxtail millet (*Setaria italica*) · Rice (*Oryza sativa*)

Introduction

Foxtail millet (*Setaria italica* (L.) P. Beauv.) is an important food crop in India, China and Japan, and is also grown in Australia, North Africa and South America for hay and silage (Wanous 1990). It is a self-pollinating species with nine pairs of chromosomes, a haploid DNA content of 0.82 pg (Sivaraman and Ranjekar 1984) with, for grass genomes, a low proportion of repetitive DNA. The first RFLP-based genetic map of the foxtail millet genome was published just recently (Wang et al. 1997).

It is well known that, in the grasses, conservation of gene orders extends beyond species and even tribes (Chao et al. 1988; Whitkus et al. 1992; Ahn and Tanksley 1993; Devos et al. 1993, 1994; Grivet et al. 1994; Kurata et al. 1994a; Pereira et al. 1994; Moore et al. 1995; Paterson et al. 1995). Establishment of the relationship between the genomes of different species not only provides researchers with large pools of available markers and a tool for trans-genomic gene identification and isolation, but will, via the consensus maps, allow us to enhance our knowledge of gene action and metabolic and physiological pathways. Foxtail millet and other species for which little is known at the genetic level will benefit greatly from the information already available in other grasses. Furthermore, integration of the foxtail millet genetic map with those of other grass species will also provide data on the evolution of grass genomes. In the study reported here the foxtail millet genome was compared with that of rice, allowing its integration into the comparative grass genetic map (Moore et al. 1995).

Materials and methods

Plant material

Genetic mapping of loci detected with rice probes in foxtail millet was carried out in 127 F_2 progenies from an interspecific cross *S. italica* accession B100 × *S. viridis* acc. A10 (Wang et al. 1997).

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RFLP probes

Rice cDNA (RGC, RGR), *Pst*I genomic (RGG) and *Not*I-linking clones (RGL) were provided by the Japanese Rice Genome Mapping Project (JRGP) (Kurata et al. 1994b). Foxtail millet (PSF) and pearl millet clones (PSM) were from the libraries described by Wang et al. (1997) and Liu et al. (1994). Anonymous wheat cDNA and genomic clones (PSR) from libraries at the John Innes Centre (JIC) and two known function clones identifying the waxy locus, *Xpsr470*(*Wx*) (Rhode et al. 1988), and carboxypeptidase locus, *Xwia483*(*Cxp1*) (Doan and Fincher 1988), and previously mapped on rice (Kurata et al. 1994b) were also employed.

RFLP procedures

All methods of DNA extraction, gel electrophoresis, Southern blotting, DNA labelling and hybridization are as described in Devos et al. (1992). Genetic maps were constructed using MAPMAKER 3.0 (Whitehead Institute for Biomedical Research, Cambridge, USA). Linkage groups were established at LOD $\geq$ 3. Most likely orders of loci were determined using three-point and multipoint analyses and manually verified on the basis of critical recombination events. Recombination fractions were converted to genetic distances using the Kosambi function.

Results

Transferability of rice probes to foxtail millet

Forty-three rice genomic and 189 rice cDNA probes covering the 12 rice chromosomes were tested for their ability to cross-hybridize to and to detect polymorphism between *S. italica* accession B100 and *S. viridis* acc. A10, the parents of the interspecific mapping population. Of the 43 genomic clones, 27 (63%) failed to give scorable hybridization patterns, 9 (21%) detected monomorphic fragments, and 7 (16%) detected polymorphic fragments that could be mapped. In contrast, 141 (75%) of the rice cDNAs were transferable to foxtail millet and the loci detected with 104 (54%) could be mapped. Five wheat cDNA clones previously used for mapping in rice were also used in this study.

Genetic maps

Of the rice probes that were polymorphic in our mapping population 38 detected single-copy loci in foxtail millet. The remainder detected between 2 and 4 loci. In total, 144 foxtail millet loci, identified with 111 rice and five wheat probes, were incorporated (Fig. 1) in the foxtail millet genetic map reported by Wang et al. (1997). The current map contains 257 loci and spans 1050 cM.

Alignment of the maps of foxtail millet and rice shows that foxtail millet chromosome I corresponds with rice chromosome 2, II with 7 and 9, III with rice chromosome 5 and a large part of 12, IV with 6, V with 1, VI with 8, VII with 4 and the distal part of the short arm of 12, VIII with 11 and IX with 3 and 10 (Fig. 2).

Discussion

Transferability of probes

The comparative genetic maps were constructed using both cDNA and genomic clones. However, the genomic clones were generated from *Pst*I-digested total genomic rice DNA and were, thus, likely to be derived from undermethylated regions of the genome, which are, in turn, likely to be associated with genes. About 37% of the rice genomic clones revealed scorable patterns when hybridized to digested foxtail millet DNA. The remainder either failed to hybridize or displayed high-background smears. In contrast, 74% of the rice cDNA clones were transferable to foxtail millet. In hexaploid bread wheat it was shown that about 50% of *Pst*I genomic clones display a hybridization behaviour similar to cDNAs and detect sequences across the three wheat genomes and in related Triticeae species (Gale et al. 1995). If, by analogy, about half of the rice *Pst*I genomic clones are from genic regions with a transferability level of 74%, a figure of 37% cross-hybridization would indicate that few of the remaining rice *Pst*I intergenic sequences are conserved in foxtail millet. This would confirm that intergenomic conservation, in the main, extends only to the genic, and not the intergenic regions.

Comparative genetic maps

The majority of the loci detected by the probes clearly indicate a high degree of colinearity between the 12 rice and nine foxtail millet chromosomes. Of the 116 mapped probes 27 (23%) detected loci in foxtail millet and rice that did not support a precise syntenic relationship. However, all but one of these detected at least two fragments in the foxtail millet genome, and thus the non-correspondence may simply indicate that non-syntenic duplicated loci were mapped in these cases.

The relationship between foxtail millet chromosomes IV, V, VI and VIII and rice chromosomes 6, 1, 8 and 11, respectively, appears to be simple and complete. For these chromosomes and within the limits afforded by the locations of the DNA probes used in this study, marker orders are probably completely conserved over

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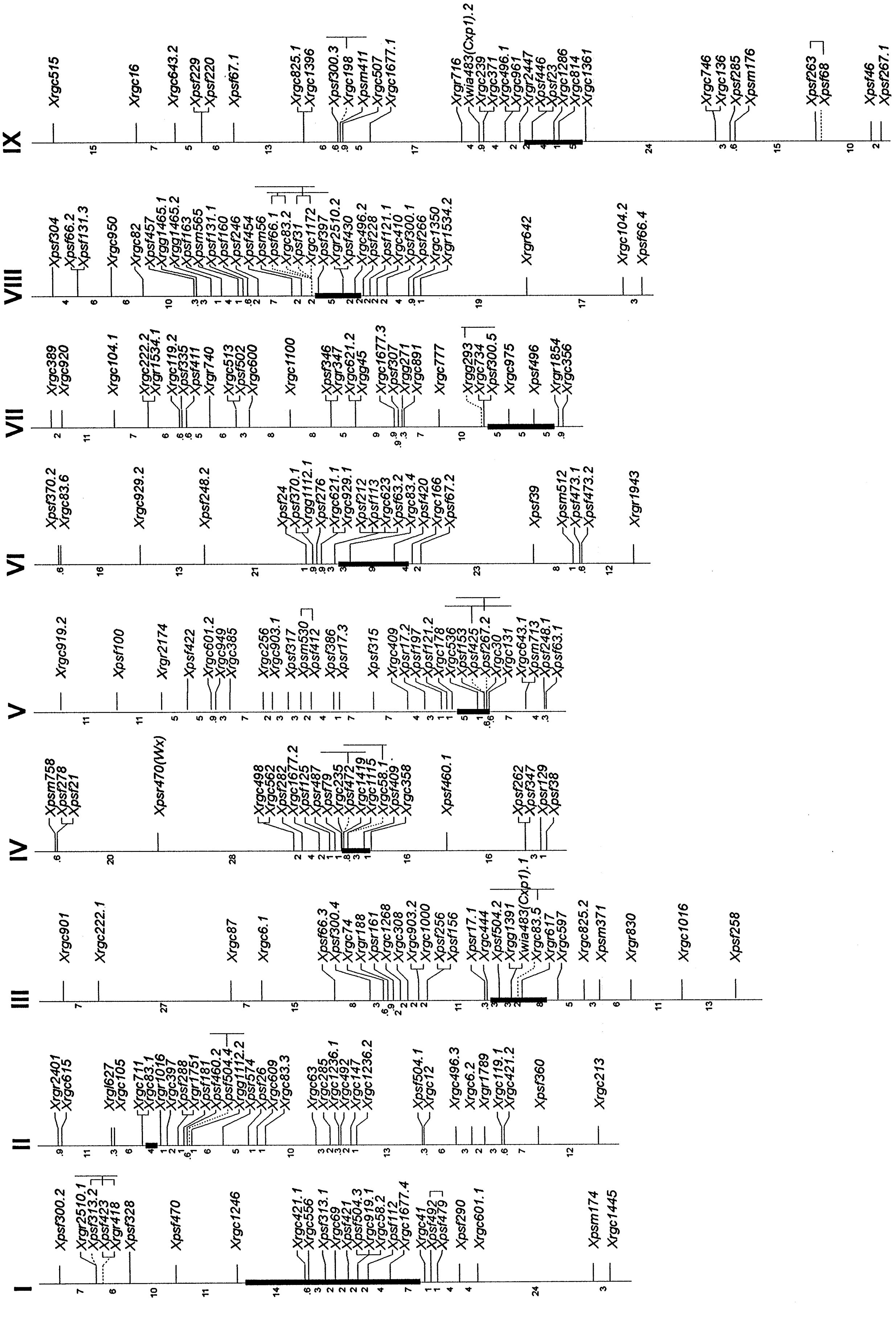
Fig. 1 Genetic map of the foxtail millet genome in a *S. italica* × *S. viridis* cross. Loci mapped with probes obtained from John Innes Centre are indicated with *psf* (foxtail millet), *psm* (pearl millet) and *psr* (wheat). Rice clones were obtained from JRGP, Tsukuba, Japan (*rgc*, *rgg*, *rgr* and *rgl*). Predicted centromere locations are indicated with *black blocks*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Xpsf423
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Xpsf328
Xpsf470
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Xrgc421.1
Xrgc556
Xpsf313.1
Xrgc69
Xpsf421
Xpsf504.3
Xrgc919.1
Xrgc58.2
Xpsf112
Xrgc1677.4
Xrgc41
Xpsf492
Xpsf479
Xpsf290
Xrgc601.1
Xpsm174
Xrgc1445
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II
Xrgr2401
Xrgc615
Xrgl627
Xrgc105
Xrgc711
Xrgc83.1
Xrgr1016
Xrgc397
Xpsf288
Xrgr1751
Xpsf181
Xpsf460.2
Xpsf504.4
Xrgg1112.2
Xpsf574
Xpsf26
Xrgc609
Xrgc83.3
Xrgc63
Xrgc285
Xrgc1236.1
Xrgc492
Xrgc147
Xrgc1236.2
Xpsf504.1
Xrgc12
Xrgc496.3
Xrgc6.2
Xrgr1789
Xrgc119.1
Xrgc421.2
Xpsf360
Xrgc213
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III
Xrgc901
Xrgc222.1
Xrgc87
Xrgc6.1
Xpsf66.3
Xpsf300.4
Xrgc74
Xrgr188
Xpsr161
Xrgc1268
Xrgc308
Xrgc903.2
Xrgc1000
Xpsf256
Xpsf156
Xpsr17.1
Xrgc444
Xpsf504.2
Xrgg1391
Xwia483(Cxp1).1
Xrgc83.5
Xrgr617
Xrgc597
Xrgc825.2
Xpsm371
Xrgr830
Xrgc1016
Xpsf258
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IV
Xpsm758
Xpsf278
Xpsf21
Xpsr470(Wx)
Xrgc498
Xrgc562
Xpsf282
Xrgc1677.2
Xpsf125
Xpsr487
Xpsf79
Xrgc235
Xpsf472
Xrgc1419
Xrgc1115
Xrgc58.1
Xpsf409
Xrgc358
Xpsf460.1
Xpsf262
Xpsf347
Xpsr129
Xpsf38
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V
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Xpsf100
Xrgr2174
Xpsf422
Xrgc601.2
Xrgc949
Xrgc385
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Xrgc903.1
Xpsf317
Xpsm530
Xpsf412
Xpsf386
Xpsr17.3
Xpsf315
Xrgc409
Xpsr17.2
Xpsf197
Xpsf121.2
Xrgc178
Xrgc536
Xpsf153
Xpsf425
Xpsf267.2
Xrgc30
Xrgc131
Xrgc643.1
Xpsm713
Xpsf248.1
Xpsf63.1
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VI
Xpsf370.2
Xrgc83.6
Xrgc929.2
Xpsf248.2
Xpsf24
Xpsf370.1
Xrgg1112.1
Xpsf276
Xrgc621.1
Xrgc929.1
Xpsf212
Xpsf113
Xrgc623
Xpsf63.2
Xrgc83.4
Xpsf420
Xrgc166
Xpsf67.2
Xpsf39
Xpsm512
Xpsf473.1
Xpsf473.2
Xrgr1943
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VII
Xrgc389
Xrgc920
Xrgc104.1
Xrgc222.2
Xrgr1534.1
Xrgc119.2
Xpsf335
Xpsf411
Xrgr740
Xrgc513
Xpsf502
Xrgc600
Xrgc1100
Xpsf346
Xrgr347
Xrgc621.2
Xrgg45
Xrgc1677.3
Xpsf307
Xrgg271
Xrgc891
Xrgc777
Xrgg293
Xrgc734
Xpsf300.5
Xrgc975
Xpsf496
Xrgr1854
Xrgc356
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VIII
Xpsf304
Xpsf66.2
Xpsf131.3
Xrgc950
Xrgc82
Xpsf457
Xrgg1465.1
Xrgg1465.2
Xpsf163
Xpsm565
Xpsf131.1
Xpsf160
Xpsf246
Xpsf454
Xpsm56
Xpsf66.1
Xrgc83.2
Xpsf31
Xrgc1172
Xpsf397
Xrgr2510.2
Xpsf430
Xrgc496.2
Xpsf228
Xpsf121.1
Xrgc410
Xpsf300.1
Xpsf266
Xrgc1350
Xrgr1534.2
Xrgr642
Xrgc104.2
Xpsf66.4
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IX
Xrgc515
Xrgc16
Xrgc643.2
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Xpsf220
Xpsf67.1
Xrgc825.1
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Xpsf300.3
Xrgc198
Xpsm411
Xrgc507
Xrgc1677.1
Xrgr716
Xwia483(Cxp1).2
Xrgc239
Xrgc371
Xrgc496.1
Xrgc961
Xrgr2447
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Xpsf23
Xrgc1286
Xrgc814
Xrgc1361
Xrgc746
Xrgc136
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Xpsm176
Xpsf263
Xpsf68
Xpsf46
Xpsf267.1
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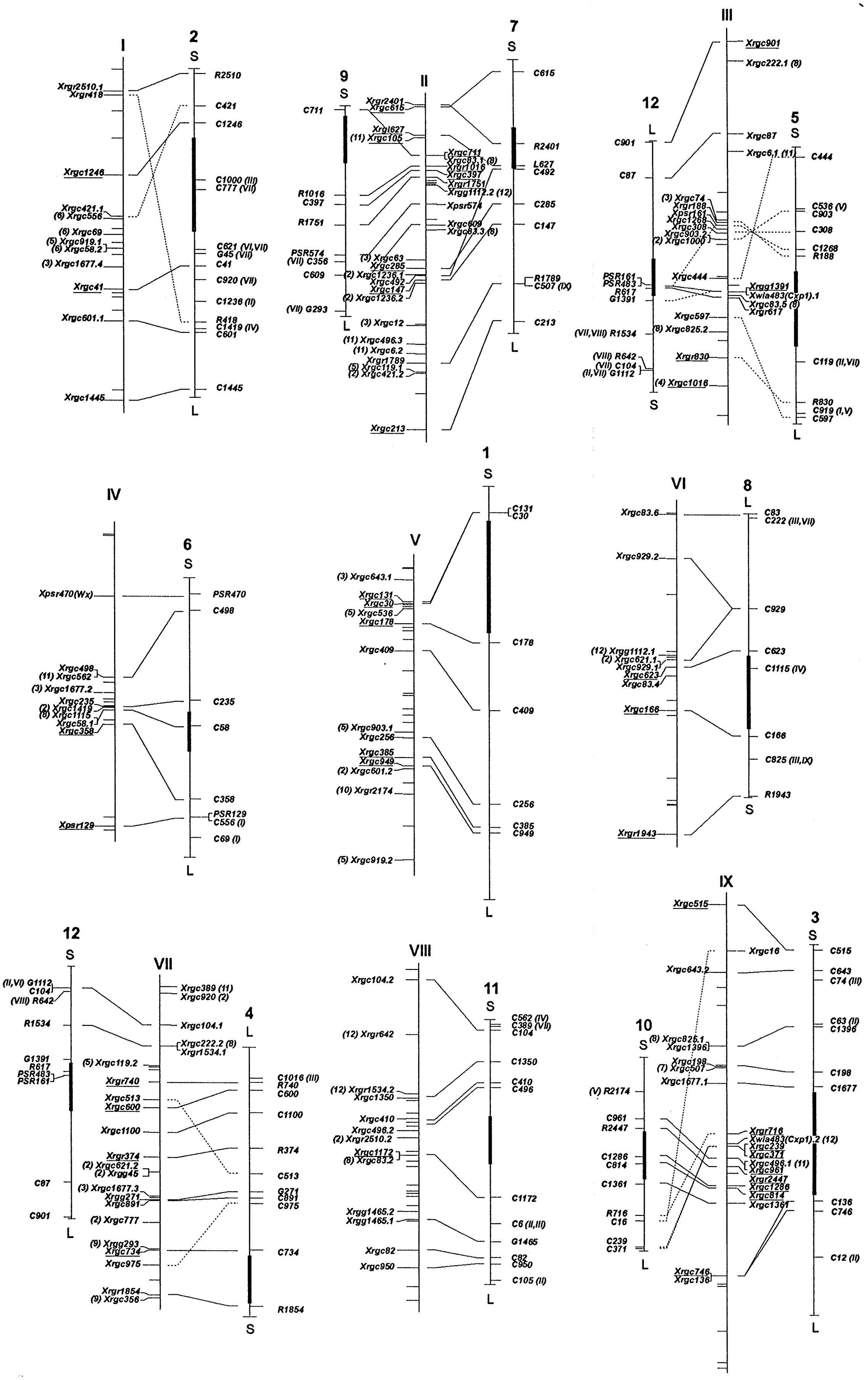
I
2
S
L
R2510
C421
C1246
C1000 (III)
C777 (VII)
C621 (VI,VII)
G45 (VII)
C41
C920 (VII)
C1236 (II)
R418
C1419 (IV)
C601
C1445
Xrgr2510.1
Xrgr418
Xrgc1246
Xrgc421.1
(6) Xrgc556
(6) Xrgc69
(5) Xrgc919.1
(6) Xrgc58.2
(3) Xrgc1677.4
Xrgc41
Xrgc601.1
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II
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C711
R1016
C397
R1751
PSR574
(VII) C356
C609
(VII) G293
Xrgr2401
Xrgc615
Xrgl627
(11) Xrgc105
Xrgc711
Xrgc83.1 (8)
Xrgr1016
Xrgc397
Xrgr1751
Xrgg1112.2 (12)
Xpsr574
Xrgc609
Xrgc83.3 (8)
(3) Xrgc63
Xrgc285
(2) Xrgc1236.1
Xrgc492
Xrgc147
(2) Xrgc1236.2
(3) Xrgc12
(11) Xrgc496.3
(11) Xrgc6.2
Xrgr1789
(5) Xrgc119.1
(2) Xrgc421.2
Xrgc213
C615
R2401
L627
C492
C285
C147
R1789
C507 (IX)
C213
III
12
5
C901
C87
(3) Xrgc74
Xrgr188
Xpsr161
Xrgc1268
Xrgc308
Xrgc903.2
(2) Xrgc1000
Xrgc444
PSR161
PSR483
R617
G1391
(VII,VIII) R1534
(VIII) R642
(VII) C104
(II,VII) G1112
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Xrgc222.1 (8)
Xrgc87
Xrgc6.1 (11)
Xrgg1391
Xwla483(Cxp1).1
Xrgc83.5 (8)
Xrgr617
Xrgc597
(8) Xrgc825.2
Xrgr830
(4) Xrgc1016
C444
C536 (V)
C903
C308
C1268
R188
C119 (II,VII)
R830
C919 (I,V)
C597
IV
6
Xpsr470(Wx)
Xrgc498
(11) Xrgc562
(3) Xrgc1677.2
Xrgc235
(2) Xrgc1419
(8) Xrgc1115
Xrgc58.1
Xrgc358
Xpsr129
PSR470
C498
C235
C58
C358
PSR129
C556 (I)
C69 (I)
V
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Xrgc949
(2) Xrgc601.2
(10) Xrgr2174
(5) Xrgc919.2
C131
C30
C178
C409
C256
C385
C949
VI
8
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Xrgc929.2
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Xrgc929.1
Xrgc623
Xrgc83.4
Xrgc166
Xrgr1943
C83
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C929
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C825 (III,IX)
R1943
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VII
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C104
(VIII) R642
R1534
G1391
R617
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C87
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Xrgc975
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R740
C600
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R374
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G271
C891
C975
C734
R1854
VIII
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(12) Xrgr642
(12) Xrgr1534.2
Xrgc1350
Xrgc410
Xrgc496.2
(2) Xrgr2510.2
Xrgc1172
(8) Xrgc83.2
Xrgg1465.2
Xrgg1465.1
Xrgc82
Xrgc950
C562 (IV)
C389 (VII)
C104
C1350
C410
C496
C1172
C6 (II,III)
G1465
C82
C950
C105 (II)
IX
3
10
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Xrgc643.2
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(7) Xrgc507
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Xwla483(Cxp1).2 (12)
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Xrgr2447
Xrgc1286
Xrgc814
Xrgc1361
Xrgc746
Xrgc136
C515
C643
C74 (III)
C63 (II)
C1396
C198
C1677
C136
C746
C12 (II)
(V) R2174
C961
R2447
C1286
C814
C1361
R716
C16
C239
C371

the entire linkage groups. Foxtail millet chromosome I is homoeologous mainly to rice chromosome 2, but this relationship may be incomplete due to the insertion of a small segment with homoeology to the long arm of rice 6.

The interspersion of segments of rice chromosomes 5 and 12, such as observed here, corresponding to foxtail millet chromosome III, has not previously been observed in the grasses. However, an interchromosomal duplication between segments of rice chromosomes 1 and 5 may confound this relationship. This putative duplication spans the region defined by the loci *Ald* (aldolase), *W170*, *C191*, *Arf* (ADP-ribosylation factor), *Oc* (oryzacystatin), *L172* and *C2782* (Kishimoto et al. 1994; Kurata et al. 1994b). As the duplicated segments on rice chromosomes 1 and 5 correspond to chromosomal regions on foxtail millet linkage groups V and III, respectively (Fig. 2), it is likely that the duplication preceded the divergence of the rice and foxtail millet genomes. Two loci, *Xrgc903* and *Xpsr17*, that could be indicative of this ancient duplication, were found in the corresponding regions of the foxtail millet map. In maize, the duplications on rice chromosomes 1 and 5 also correspond to two different duplicated regions on chromosomes 3 and 8, and 6 and 8, respectively (after Ahn and Tanksley 1993), again suggesting the ancient nature of the rice duplication.

An interchromosomal duplication has also been observed that includes the distal part of the short arms of rice chromosomes 11 and 12 (Nagamura et al. 1995). Two loci from this region on chromosome 12, *C104* and *R1534*, detect duplicated loci on foxtail millet chromosomes VII and VIII. Two further loci from the corresponding regions on rice chromosome 11, *C389*, and 12, *R642*, map to the top of foxtail millet chromosomes VII and VIII, respectively. As the regions that are duplicated in rice chromosome arms 11S and 12S also appear to be duplicated in foxtail millet chromosomes VII and VIII, one can speculate that this duplication also occurred before the divergence of rice and *Setaria*. We therefore expect it to be present in other members of the Panicoideae subfamily.

Foxtail millet linkage group IX corresponds, from top to bottom, to the short arm of rice chromosome 3, rice chromosome 10 and the long arm of rice chromosome 3 (Kurata et al. 1994b). A similar composition was observed for maize chromosome 1 (Ahn and Tanksley 1993) and sorghum linkage group C (Paterson et al. 1995). Maize chromosome 1 differs from foxtail millet chromosome IX and sorghum linkage group C by the presence of a segment with homoeology to rice 8 and an inversion of part of the segment with homoeology to rice 10. The adjacent positions of the short arm of rice chromosome 3 and rice chromosome 10, in an orientation similar to that of foxtail millet group IX, was also found in maize chromosome 5. A highly similar chromosome composition was also observed between foxtail millet linkage group II, sorghum B and maize 7. All are colinear, from top to bottom, with a segment of rice chromosome 7, rice chromosome 9 and the remaining segment of rice chromosome 7. The structural conservation of these chromosomes indicates that maize chromosomes 1 and 7, rather than their duplicates 5 and 2, represent the most original chromosomes in the genome.

Centromeres

Recently, Singh et al. (1996) determined the centromere positions on the genetic map of rice. As these maps have been aligned with the JRGP linkage maps (McCouch et al. 1995), approximate centromere positions are also known in the JRGP maps. A comparison of the linkage maps and centromere positions of rice with those of wheat has shown that colinearity extends to the centromere positions (Gale et al. 1996). In foxtail millet, no genetic stocks are available to determine the arm locations of markers. However, the comparative rice – foxtail millet maps suggest putative locations for centromeres on all foxtail millet chromosomes. The centromere of foxtail millet chromosome IX, which, in terms of rice linkage segments, is composed of rice chromosome 10 inserted in the centromeric region of rice chromosome 3, is expected to show homoeology with that of rice chromosome 10. The centromeres on foxtail millet chromosome II and rice chromosome 9 would be expected to be syntenous. Similarly, the centromere of foxtail millet III is likely to correspond to that of either rice chromosomes 5 or 12.

The transfer of these possible centromeric locations to the full foxtail millet map (Fig. 1) lends further weight to their assignment, since these regions coincide with clusters of markers, particularly on chromosomes I, IV, V, VI and IX. These locations now remain to be verified either by the development of tertiary trisomics, ongoing from the trisomic set developed at Hebei Academy, or by the use of centromeric probes as are available in wheat (Aragon-Alcaide et al. 1996) or by the locations of indicator microsatellites as developed by Tanksley et al. (Grandillo and Tanksley 1996) in tomato.

◄

Fig. 2 Comparison of the genetic maps of foxtail millet and rice. Single-copy loci in the foxtail millet genome are *underlined*. The chromosomal location of the loci that are at variance with the colinear relationship are indicated in *brackets*. Centromeric regions of the rice chromosomes are identified by *black blocks*

Conclusions

The alignment of the little studied foxtail millet with rice, and thus with all the major cereals, should presage rapid development of the agronomic genetics of the crop. Just as the locations of the centromeres have been predicted above, predictions can now be made for a number of key genes controlling adaptation such as flowering time, dwarfism, dormancy control and shattering, as shown by Lin et al. (1995) between wheat, rice, maize and sorghum. The map and the markers described above will initially provide diagnostics with which breeders can incorporate these traits where the detailed character analysis already carried out in other crops will provide information which will be immediately transferable to foxtail millet.

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