Relationship Between Chromosome 9 of Maize and Wheat Homeologous Group 7 Chromosomes

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ABSTRACT

Comparison of the genetic map of maize chromosome *9* with maps of wheat chromosomes has revealed a high degree of colinearity between maize chromosome *9* and the group *4* and *7* chromosomes of wheat. The order of DNA markers on the short arm and a proximal region of the long arm of the genetic map of maize chromosome *9* is highly conserved with the marker order on the short arm and proximal region of the long arm of the genetic maps of the wheat homeologous group *7* chromosomes. A major part of the long arm of the genetic map of maize chromosome *9* is homeologous with a short segment in the proximal region of the long arm of the genetic map of the wheat group *4* chromosomes. Evidence is also presented that maize chromosome *9* has diverged from the wheat group *7* chromosomes by both a pericentric and a paracentric inversion. The paracentric inversion is probably unique to maize among the major cereal genomes.

COMPARATIVE mapping studies have already demonstrated the existence of extensive colinearity between markers on the genomes of species belonging to the same tribe. Within the Triticeae, a few chromosomal rearrangements distinguish the genomes of wheat, barley and rye, but colinearity is conserved within each of the translocated regions (DEVOS *et al.* 1993a,b; LAURIE *et al.* 1993). In a similar study, carried out within the Andropogonae, it was demonstrated that the 3.5-fold greater DNA content of the maize genome compared to the sorghum genome was due mainly to differences in the amount of repetitive DNA and had no relevance to the gene content or gene order (HULBERT *et al.* 1990, WHITKUS *et al.* 1992; BERHAN *et al.* 1993). Recently, it was shown by AHN and TANKSLEY (1993) and AHN *et al.* (1993) that homeology also exists between regions of the genomes of species belonging to different *Poaceae* tribes such as wheat ($2n = 6x = 42$, $C = 1.7 \times 10^{10}$ bp), rice ($2n = 24$, $C = 4 \times 10^8$ bp) and maize ($2n = 20$, $C = 3 \times 10^9$ bp). In a more detailed comparative mapping study, KURATA *et al.* (1994) not only reinforced the concept of homeology between the genomes of wheat and rice, but further demonstrated the existence of extensive colinearity between markers in these two species, thereby presenting wheat geneticists with comparative chromosome walking in rice as a possible tool for the isolation of homeologous genes in wheat. The colinearity between the Poaceae genomes will allow the integration of much of the available genetic, biochemical, morphological and possibly disease resistance data in one "basic" genome, thereby providing researchers with a vast pool of genetic and agronomic information, which may be transferred between species (MOORE *et al.* 1993). In this study, we present a detailed analysis of the homeologous relationships of maize chromosome *9* with wheat chromosomes in homeologous groups *4* and *7*.

MATERIALS AND METHODS

Genetic stocks: Nullisomic-tetrasomic (NT) (SEARS 1954) lines of the cultivar Chinese Spring (CS) were used to determine the wheat chromosome locations of sequences with homology to maize restriction fragment length polymorphism (RFLP) probes. The wheat mapping population consisted of 120 F_2 or bulked F_3 progenies from a CS × Synthetic (IPSR1190903) cross, the rye mapping population consisted of 128 F_2 plants, or their F_3 derivatives, from a cross between the inbred lines Ds2 × RxL10 (MASOJC and GALE 1991), and the maize population consisted of 56 immortal F_2 individuals from a cross between Tx303 and CO159 (GARDINER *et al.* 1993).

DNA markers: Thirty-three maize genomic clones, previously used to map RFLP loci on maize chromosome *9*, obtained from the collection at the University of Missouri, Columbia, Dr. David Grant at Pioneer Hi-Bred International Inc. and Dr. Ben Burr at Brookhaven National Laboratory, were hybridized to membranes containing *Eco*RI-, *Eco*RV-, *Dra*I- and *Hin*dIII-digested DNA from 21 NT lines, and from the wheat cultivars CS and Synthetic, and the rye inbred lines Ds2 and RxL10. Eighteen wheat homeologous group *7* probes, 15 cDNA and three genomic clones, were used to screen for polymorphism in maize. Polymorphic wheat and rye loci, detected by maize probes, and polymorphic maize loci, detected by wheat probes, were respectively added to the existing wheat (GALE *et al.* 1994) and rye (DEVOS *et al.* 1993a), and maize maps (GARDINER *et al.* 1993).

RFLP techniques: All techniques of DNA extraction, restriction-enzyme digestion, gel electrophoresis, Southern transfer, probe labeling and hybridization were as described by DEVOS *et al.* (1992). The stringency of the final posthybridization washes varied between 1 × SSC/0.5% sodium dodecyl

TABLE 1

Chromosomal locations and copy numbers in maize and wheat of DNA fragments that hybridized to maize probes that detect loci on maize chromosome *9*

Probe	Chromosomal location of hybridizing fragments		Copy no.		
	Maize	Wheat[a]	Maize	Wheat[c]	Mapped[b]
Npi253	*4L, 5L, 6L, 9S*	*6A 6B 6D, 7A 7B 7D*	4	1, 1	W, R
Php10005	*9S*	*2A 2B 2D, 7A, 7B 7D*	1	2, 1	R
Umc113	*6L, 9S*	*7A 7B 7D*	2	1	—
C1*	*9S*	*7D*	1	M	—
Umc207 (*sh1*)	*9S*	*7A 7B 7D*	1	2	W
Umc105	*9S*	*7A 7B 7D*	1	M	R
Umc 81*	*9*	*1B, 5A 5B 5D, 7A 7B 7D*	1	1, 2, 1	—
Npi416*	*6L, 9*	*7A*	2	1	—
Npi454	*9L*	*7A 7B 7D*	≥2	2	W
Umc114	*9L*	*6A 6B 6D, 7A 7B 7D*	1	1, 1	W, R
Umc190 (*sus1*)*	*9L*	*2B 2D, 7A 4A 7D*	1	1, 1	W
Npi293*	*1L, 5L, 9L*	*1A 1B 1D*	3	M	—
Npi427	*1S, 9L*	*4A 4B 4D*	2	1	R
Bn15.09	*9L*	*4A 4B 4D*	1	1	W, R
Npi403	*1S, 9L*	*4A 4B 4D*	2	1	W
Npi209	*1S, 9L*	*4A 4B 4D*	2	1	R
Npi97*	*1S, 9L*	*1A 1B, 4B 4D*	2	1, 1	—

[a] Chromosomal location as derived from the CS NT lines. * indicates probes for which not all of the hybridizing fragments could be assigned to chromosomes.
[b] Loci mapped in wheat (W), rye (R), or both (W,R). Monomorphic probes are indicated with a dash (—).
[c] Copy number per wheat homoeologous group. M indicates probes detecting multicopy loci.

sulfate (SDS) and 0.2 × SSC/0.5% SDS depending on the strength of the hybridization signal.

RESULTS

Maize clones as probes for wheat loci: Analysis of the Southern blots of wheat DNA probed with 33 maize probes showed that 17 maize clones gave detectable signals in wheat, while the remainder either produced smear-hybridization patterns or failed to hybridize at all. The chromosomal locations and copy numbers of wheat fragments which hybridized to these 17 maize clones are listed in Table 1. To maximize the number of mapped loci, maize probes were screened for variation not only in wheat, but also in rye. Probes that failed to show any polymorphism between CS and Synthetic, the parents of our main wheat mapping population, but showed variation between Ds2 and RxL10, the parents of our rye mapping population, were mapped in rye. The precise knowledge of the relationship between the wheat and rye genomes (Devos *et al.* 1993a) allowed us to infer their map positions in wheat. Six of the 17 probes detected monomorphic loci, four detected polymorphism only in wheat, four only in rye, and three both in wheat and rye (Table 1). The relative map position of the *XBz* (bronze) locus was inferred from its position on a barley map (Kleinhofs *et al.* 1993). A consensus wheat map, which includes mapping data obtained in the wheat crosses CS × Synthetic and Hobbit "S" × Hobbit "S" (VPM1 *7D*) (Chao *et al.* 1989) and the rye cross Ds2 × RxL10 (Devos *et al.* 1993a), is shown in Figure 1.

Wheat clones as probes for maize loci: Eighteen wheat group *7* probes were used to screen for polymorphism in maize. All 15 wheat cDNA-sequences cross-hybridized well with maize, while the three genomic sequences gave faint or no hybridization signals under the high stringency hybridization and washing conditions used. The latter is not surprising as the three genomic clones tested had previously been classified as "non-homeologous," *i.e.*, their sequences were not conserved among different Triticeae genomes. In most cases the copy number of the cDNA-sequences was comparable in wheat and maize, taking into account that maize is likely to be an ancient tetraploid (Table 2). In maize, because of either lack of polymorphism or the complexity of the banding patterns, only eight loci identified by wheat probes could be mapped. These include one *psr129* locus on maize chromosome *9* (Figure 1), three α-amylase loci on maize chromosomes *2*, *5* and *7*, one *psr150* locus on maize chromosome *1* and one locus on maize chromosome *6* detected by each of the wheat clones PSR108, PSR119 and PSR121. A consensus map of maize chromosome *9*, which include data from published maps (B. Burr, personal communication; Matz *et al.* 1994) and data obtained in the maize cross Tx303 × CO159, is presented in Figure 1.

DISCUSSION

The comparative maps: Nullisomic-tetrasomic analysis in wheat of 17 maize chromosome *9* probes clearly demonstrates a high degree of homeology between markers on the short arm and the proximal part of the

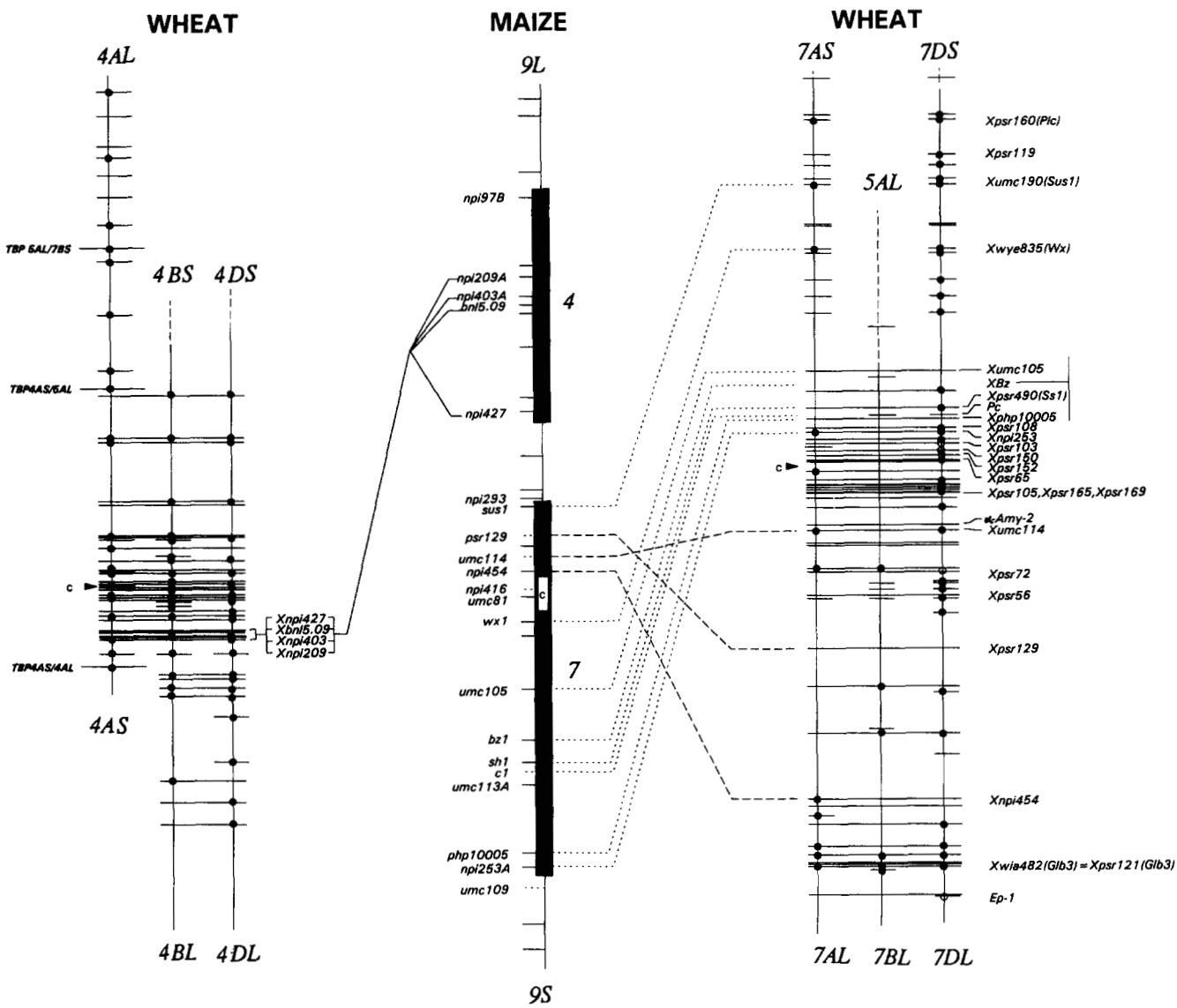

FIGURE 1.—A comparison of the genetic map of maize chromosome *9* with the maps of the wheat homeologous group *4* and *7* chromosomes. Loci mapped in the Tx303 × CO159 cross have been included in the maize consensus map (B. BURR, personal communication). The wheat consensus map comprises loci mapped in the wheat cross CS × Synthetic (loci indicated by ●), in the wheat cross Hobbit "S" × Hobbit "S" (VPMI *7D*) (loci indicated by ○), and in the rye cross DS2 × RxL10. Homeologous regions in the maize and wheat genome, as determined by aneuploid mapping, are indicated by blocks. Homeoloci in wheat and maize are indicated by dotted lines. c indicates the centromere region.

long arm of the linkage map of maize chromosome *9*, and the wheat homeologous group *7* chromosomes, while a major segment of the linkage map of the long arm of maize chromosome *9* shows homeology with a short linkage interval in the homeologous group *4* chromosomes of wheat (Table 1 and Figure 1). In total, loci detected with eight maize probes were placed on the consensus map of the wheat homeologous group *7* chromosomes and four on the consensus map of the group *4* chromosomes. One wheat group *7* probe, PSR129, was used to map a maize chromosome *9* locus. One further locus, *wx* in maize and *Xwye835(Wx)* in wheat, detected by a waxy sequence, which had previously been mapped in both wheat and maize, was also included in the analysis. The comparative maps show that, despite the 6-fold higher DNA content of wheat compared to maize and the evolutionary separation of the genomes for as much as 60 million years (WOLFE *et al.* 1989), a high degree of colinearity remains between maize chromosome *9* and the wheat group *7* chromosomes (Figure 1). A proximal segment of the long arm of the linkage map of maize chromosome *9*, including the loci *psr129* and *umc114*, is homeologous with the proximal part of the long arm of the linkage map of the wheat homeologous group *7* chromosomes, while the gene order on the short arm of maize chromosome *9* is the same, albeit inverted, as that on the short arm of the wheat homeologous group *7* chromosomes (Figure 1). Markers on a large segment of

TABLE 2

Chromosomal location in wheat and copy numbers in wheat and maize of DNA fragments that hybridized to wheat homeologous group 7 probes

Probe	Type of probe[a]	Chromosomal location of hybridizing fragments in wheat	Copy no.	
			Wheat[b]	Maize[c]
PSR56	C	*3AL 3BL 3DL, 7AL 7BL 7DL*	1, 1	4
PSR65	C	*7AS 7BS 7DS*	1	Smear
PSR72	C	*7AL 7BL 7DL*	2	3
PSR103	C	*7AS 7BS 7DS*	1	5
PSR105	C	*7AL 7BL 7DL*	2	2
PSR108	C	*2AS 2BS 2DS, 7AS 7BS 7DS*	1, 1	3
PSR119	C	*7AS 4AL 7DS*	1	5
PSR121	C	*1AL 1BL 1DL, 7AL 7BL 7DL*	1, 1	3
PSR129	C	*7AL 7BL 7DL*	1	2
PSR150	C	*2AS 2BS 2DS, 5AL 5BL 5DL, 7AS 7BS 7DS*	1, 1, 1	4
PSR152	C	*7AS 7BS 7DS*	1	2
PSR160	C	*7AS 4AL 7DS*	1	2
PSR165	C	*7AL 7BL 7DL*	1	8
PSR169	C	*7AL 7BL 7DL*	1	Smear
α-amylase-2	C	*5AL 5BL 5DL, 6AL 6BL 6DL, 7AL 7BL 7DL*	1, 1, 1	3
PSR350	G	*7BL 7DL*	1	—
PSR389	G	*7AL 7BL 7DL*	3	—
PSR392	G	*7AS 4AL 7DS*	2	—

[a] C indicates cDNA, G indicates a genomic DNA clone
[b] Copy number per wheat homoeologous group
[c] Determined as number of hybridizing fragments, excluding those with light intensity. — indicates no or weak hybridization signal

the long arm of the genetic map of maize chromosome *9* map in the proximal regions of the long arms of the linkage map of the wheat homeologous group *4* chromosomes. The relative order of these maize markers in wheat could not be established, however, due to the low recombination frequency in the centromeric regions of wheat chromosomes (Figure 1).

Most or all of the short arm and a segment of the long arm of maize chromosome *9* and most of wheat chromosome *7*, including both centromeres, have clearly originated from the same ancestral chromosome. Based on the available cytological and comparative mapping data, it is possible to speculate about the evolution of that chromosome. A comparison between the wheat and rice genomes indicates that wheat chromosome *7* is colinear with rice chromosome *6* and that no major translocations or inversions have occurred since the divergence of these two species (KURATA *et al.* 1994). Furthermore, the maize and rice comparative maps of AHN and TANKSLEY (1993) reveal that most of the short arm of maize chromosome *9* is colinear, but inverted, with rice chromosome *6*, while the proximal part of the long arm of the linkage map shows direct colinearity with rice chromosome *6*. A similar paracentric inversion also separates the maize and sorghum genomes (BERHAN *et al.* 1993). To place this inversion event on an evolutionary time scale, a comparative RFLP map was established (C. A. BLAKEY, personal communication) between this segment of maize chromosome *9* and its homeologous chromosome in Tripsacum, a close relative of maize. The marker order *wx* (distal)-*umc105-bz1-sh1-umc113-umc109-umc81-umc114* (proximal) corresponds well with the general marker order on the genetic map of wheat, *Xwye835(Wx)* (distal)-*Xumc105-Xpsr490(Ss1)-Xphp10005-Xnpi253-Xumc114* (proximal), while in maize these loci are ordered, from distal to proximal, *umc109-npi253-php10005-umc113-sh1-bz1-umc105-wx-umc81-umc114* (Figure 1). The inversion breakpoint that separates maize and Tripsacum can therefore be assigned to the interval *wx-umc81*. Because the Tripsacum sequence is like wheat, it is likely that the inversion took place after the differentiation of the *Tripsacum* and *Zea* genera. In order to explain the current gene order on maize chromosome *9* compared to the wheat group *7* chromosomes, the paracentric inversion described above must have been preceded by a pericentric inversion of the segment probably spanned, on the wheat map, by *Xwye835(Wx)* and *Xnpi454* (Figure 2). As the linear order of the distal markers of rice chromosome *6* and wheat chromosomes *7* [*Xpsr160, Xwye835(Wx), Xpsr490(Ss1)*] is the same (KURATA *et al.* 1994), this inversion must have taken place after the divergence of maize and rice from their common ancestor. Assuming that this hypothesis is correct, the relative position on the maize map of *npi454* (Figure 1) would indicate that either the wheat and maize loci mapped with this probe are nonhomeologous, or that further rearrangements have taken place in the centromere region of maize chromosome *9*.

The wheat/maize comparative maps are almost entirely based on mapping using maize probes in wheat. The difficulty in obtaining detectable signals with maize RFLP probes in the large wheat genome is trifling com-

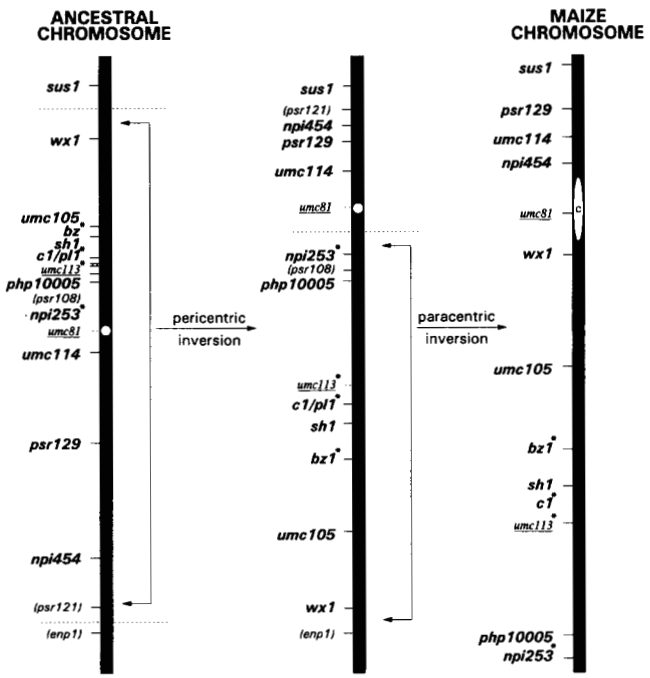

FIGURE 2.—Model for the evolution of maize chromosome *9* from an ancestral chromosome assumed to have a similar structure to the wheat group *7* chromosomes. Markers in bold have been mapped both on the homeologous group *7* chromosomes of wheat and maize chromosome *9*; underlined markers have been mapped only on maize chromosome *9*; markers in parentheses ( ) have been mapped on the wheat group *7* chromosomes and maize chromosome *6*; asterisk (*) indicates markers that have been mapped on maize chromosomes *6* and *9*.

pared to the problems, caused by the many duplications and rearrangements within the maize genome, in determining homeologous relationships from the mapping of wheat clones in maize. In maize, the wheat homeologous group *7* probes PSR108, PSR119 and PSR121 all detect linked loci on the long arm of chromosome *6* (not shown), and therefore do not appear to provide support for the homeologous relationship between the wheat group *7* chromosomes and maize chromosome *9*. However, a segment of the long arm of maize chromosome *6* is duplicated with a segment of the short arm of chromosome *9* (T. HELENTJARIS, personal communication), and it is possible that duplicated loci are present on chromosome *9* but that these were either not polymorphic, and thus could not be mapped, or that their sequences have diverged or been deleted since the polyploidization of maize. Furthermore, the genetic map of maize chromosome *6* (COE and NEUFFER 1993) carries loci for *bz1* (bronze), *pl1* (purple plant, a regulatory gene with a high degree of sequence homology to *c1*, CONE and BURR 1988), *umc113*, and *npi253*. These were closely linked to the loci detected by PSR108, PSR119 and PSR121, and mapped both on maize chromosomes *6* and *9*, and on the wheat group *7* chromosomes (Figure 1). The maize locus, *pl1* (or *c1*), is likely to be homeologous to the wheat morphological marker, *Pc* (purple culm), which maps on the short arm of the wheat homeologous group *7* chromosomes (CHAO *et al.* 1989). A further locus, *enp1* (endopeptidase), present on maize chromosome *6* but not on maize chromosome *9*, is located on the long arms of the homeologous group *7* chromosomes in wheat. One can speculate that the duplicated regions of maize chromosome *6* and *9* have evolved from the same ancestral chromosome. The relative order of the markers on maize chromosome *6* (*enp1–bz1–pl1–umc113–npi253–psr121*), would then indicate that, in relation to the wheat group *7* chromosomes and rice chromosome *6*, maize chromosome *6* has undergone the pericentric inversion but not the paracentric inversion shown in Figure 2. This would indicate that the pericentric inversion took place after the divergence of the wheat, rice and maize genomes from their common ancestor, but before the duplication or polyploidization of the maize genome, while the paracentric inversion took place later in the evolution, as illustrated in Figure 2.

Centromeres: The availability of ditelosomic lines allows the map interval containing the wheat centromeres to be identified. In maize, approximate positions of the centromeres have been obtained by hybridization of the RFLP probes to the B/A translocation lines with breakpoints very close to the centromeric region (WEBER and HELENTJARIS 1989). On maize chromosome *9* the centromere is located close to *umc81*. As the conservation of colinearity between wheat and maize is likely to extend to the centromeres, comparative mapping could provide a method to locate the centromeres. This is demonstrated on maize chromosome *9* where, based on the centromere position on the wheat group *7* chromosomes and taking into account the subsequent evolution of that chromosome (Figure 2), the centromere may be placed in the interval *umc114-wx*.

However, there was no apparent transfer of centromeres between the wheat group *7* chromosomes and the homeologous segment of maize chromosome *6*, which is encompassed entirely by the long arm. From the hypothetical model presented in Figure 2, one would have predicted the presence of a centromere in the interval *psr121–npi253*, however, the marker order on chromosome *6* is *centromere–enp1–bz1–pl1–umc113–npi253–psr121* (B. BURR, personal communication; MATZ *et al.* 1994). The loss of centromere regions due to chromosomal rearrangements cannot be excluded.

Sucrose synthase loci: Two non-allelic sucrose synthase loci, *sh1* and *sus1*, have been mapped on maize chromosome *9*. In wheat, sucrose synthase loci have been mapped on the homeologous group *7* [*Xpsr490(Ss1)*] and group *2* chromosomes [*Xpsr489(Ss2)*], and it was suggested that *Xpsr490(Ss1)*, a locus detected by the clone pST8, was homeologous with *sh1* and *Xpsr489(Ss2)*, a locus detected by pST3, was homeologous with *sus1* (MARTINEZ DE ILARDUYA

et al. 1993). A comparison of the chromosomal locations of loci and hybridization patterns obtained in wheat with the maize sucrose synthase clones umc207 (*sh1*) and umc190 (*sus1*), and the wheat sucrose synthase clones pST8 and pST3 (Table 1), confirmed the relationship between *Xpsr490(Ss1)* and *sh1*, but indicated that the loci *Xpsr489(Ss2)* in wheat and *sus1* in maize are independent. Thus, it appears that at least three sucrose synthase genes are present in wheat, one on the short arm of the homeologous group *2* chromosomes [*Xpsr489(Ss2)*], and two more which are identified by *Xumc190(Sus1)* and *Xpsr490(Ss1)* on the short arms of the homeologous group *7* chromosomes.

CONCLUSIONS

It was possible to construct a model for the evolution of maize chromosome *9* using the comparative maps of the wheat group *7* chromosomes, maize chromosome *9* and rice chromosome *6*. Extending the comparative maize/wheat mapping exercise to all maize chromosomes will help to elucidate the complex interchromosomal relationships in maize. More importantly, when applied to a range of species within the Poaceae, comparative maps may give us an insight in the structure of the primeval Poaceae genome. Practical implications of the integration of all grass maps into one "basic" map include identifying vast pools of markers for genetic research and plant breeding in any cereal crop species, and, of particular importance in large genome species such as maize and wheat, the potential to develop gene isolation strategies employing small genomes, such as that of rice, for comparative chromosome walking.

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