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The 'inner circle' of the cereal genomes

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Early marker-based macrocolinearity studies between the grass genomes led to arranging their chromosomes into concentric 'crop circles' of synteny blocks that initially consisted of 30 rice-independent linkage groups representing the ancestral cereal genome structure. Recently, increased marker density and genome sequencing of several cereal genomes allowed the characterization of intragenomic duplications and their integration with intergenomic colinearity data to identify paleo-duplications and propose a model for the evolution of the grass genomes from a common ancestor. On the basis of these data an 'inner circle' comprising five ancestral chromosomes was defined providing a new reference for the grass chromosomes and new insights into their ancestral relationships and origin, as well as an efficient tool to design cross-genome markers for genetic studies.

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Introduction

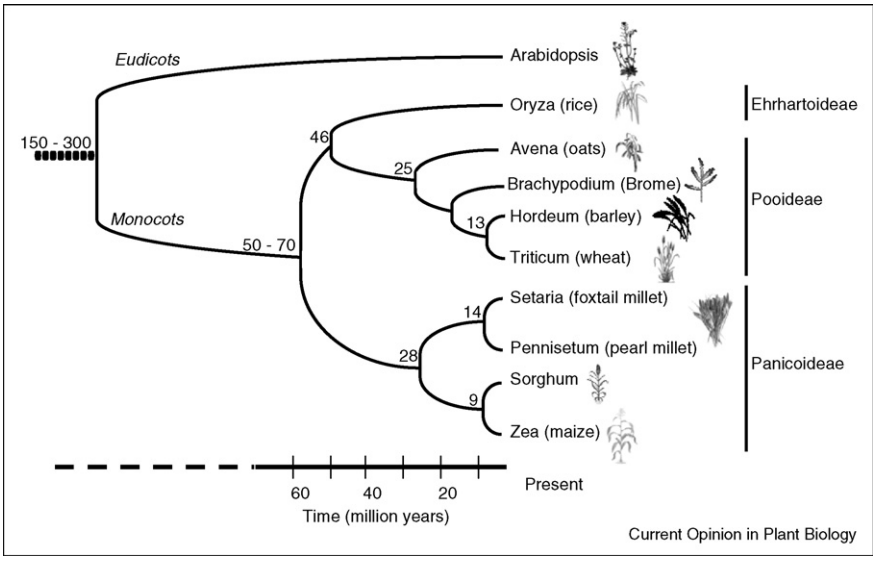
The five socio-economically most important cereal crop species are members of the grass (Poaceae) family and belong to three major sub-families, that is, the Panicoideae (sorghum, maize), the Ehrhartoideae (rice) and the Pooideae (wheat, barley), cf Figure 1, that diverged from a common ancestor 50–70 million years ago, hereafter MYA (for reviews [1,2]). Comparative genomics studies in grasses have provided insights into the evolutionary forces that have shaped the actual species from a common cereal ancestor and also supported the development of genomic tools such as conserved orthologous sequences (COS) markers (for reference see [3]). Recently, the availability of high-density resources (e.g. genome sequences and large collections of mapped ESTs) and of improved methods of analysis (e.g. sequence alignment tools, statistical tests) helped to refine the relationships between the cereals genomes opening up new perspectives for the reconstruction of an 'ancestral cereal genome'.

Cereal genome macrocolinearity studies suggest a 30 linkage blocks ancestor

Early marker-based comparative genetic mapping based on restriction fragment length polymorphism (RFLP) markers indicated that despite large differences in ploidy level, chromosome number and haploid DNA content, the linear order of markers remained largely conserved between grass species over 50–70 MY of divergent evolution. Alignments between the grass chromosomes were visualized as concentric 'crop circles' that provided a convenient representation of the relationships between orthologous chromosomal segments of the rice, sorghum, maize and Triticeae (wheat and barley) genomes [4]. Grasses were considered as a single genetic system built from 30 rice-independent linkage blocks (Figure 2, A1–A30) that putatively reflected the ancestral grass genome chromosome structure [4–6]. However, these results obtained with low copy RFLP markers and low resolution genetic maps did not allow the detection of whole genome duplication events and a clear differentiation between orthologous and paralogous gene families. The deduced level of synteny between grasses was thus largely overestimated owing to artificial redundancy created by undetected intra-genome duplications (reviewed in [3,7]).

Recently, the sequencing of the rice and sorghum genomes [8,9] as well as the development of a high-density anchored physical map of the maize inbred B73 [10•] provided invaluable tools to compare these three grass genomes. In parallel, the development of large mapped EST collections from the Triticeae allowed *in silico* genome-wide macrocolinearity analyses with these genomes (for review see [6]). Comparative genome analyses were first performed between the rice genome, used as a reference and the individual wheat [11–14], sorghum [15,16], barley [17,18] and maize [19] genomes. The increased resolution of these analyses revealed additional chromosomal rearrangements within the 30 original ancestral linkage blocks and led eventually to a revision of the 'concentric crop circles' representation [20]. The evolutionary models that can be deduced from *in silico* genome comparisons rely on the capacity to evaluate with

Figure 1



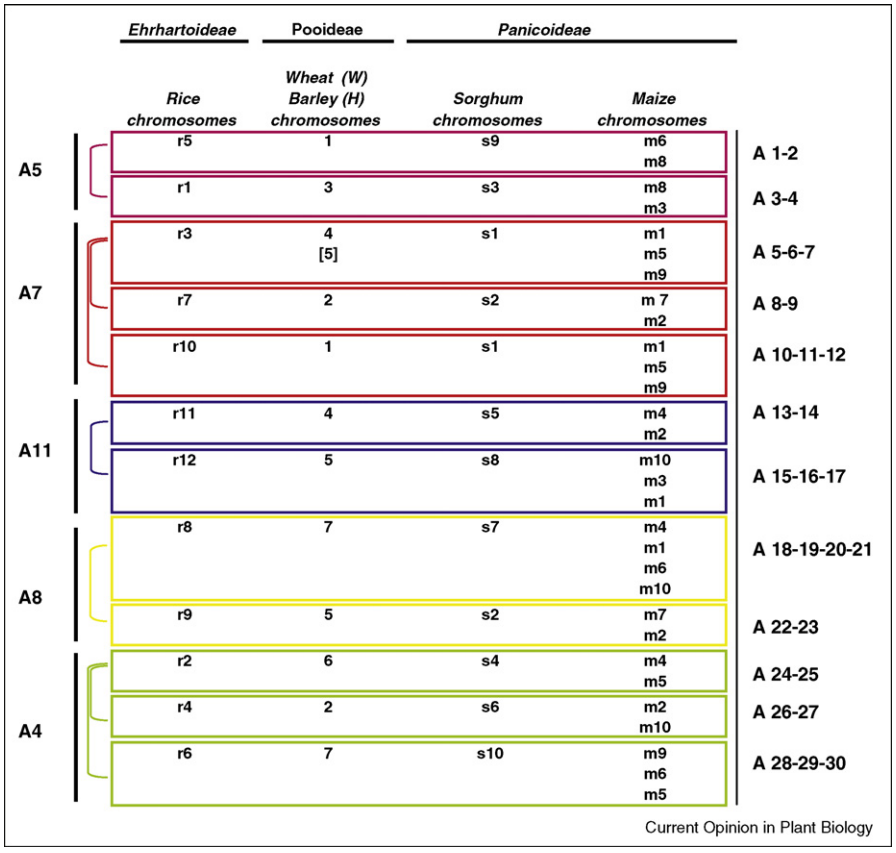
Phylogenetic relationships between cereals. Divergence times from a common ancestor are indicated on the branches of the phylogenetic tree (in millions years).

confidence whether two or more genes found in the same order on two chromosomal segments are truly orthologous. So far most of the studies were based on default sequence alignment parameters and were not systematically validated statistically. Very recently, improved sequence alignment criteria and systematic statistical analyses were applied to the latest genome sequences and EST releases of rice, wheat, barley, sorghum and maize to reassess the colinearity between their chromosomes [21•]. The results showed that within 50–70 MY of evolution ~70% of the genes retained conserved structural motifs, ~40% remained conserved as single copies, while only ~20 remained orthologous. For example, comparisons between the 42654 rice genes and 5003 non-redundant mapped wheat ESTs contigs revealed that 1180 orthologous gene pairs, covering 83.1% and 90.4% of the rice and wheat genomes, respectively, are conserved. A similar comparison between the rice genome sequence and 1411 mapped maize ESTs contigs showed 656 conserved orthologous pairs (Figure 3). Interestingly, 27.2% and 21.8% of these were not found in the expected orthologous position based on the rice gene order, indicating previously unreported rearrangements (inversions, translocations, deletions) in orthologous regions between rice and wheat and between rice and maize, respectively. In addition to genome wide analyses, microcolinearity studies performed at target loci between rice, maize, wheat, barley and sorghum [22,23,24•,25–28] provided additional evidence for orthologous gene shuffling before and after speciation in each species independently, probably to prevent pairing of non-homologous chromosomes.

Cereal paleo-duplications suggest an 'inner crop circle' with five chromosomes

Comparative genomics studies have shown that genome or segmental duplications have been a driving force during the evolution of plant species [29]. Evidence for intragenomic duplications were first provided by RFLP mapping in maize where a large number of probes hybridized systematically to two distinct loci [30,31]. Further comparative analyses with sorghum showed a 2:1 relationship between maize and sorghum loci for 85 DNA probes [32], suggesting that the duplication observed in maize originated from a specific tetraploidization event. Duplications were also detected by comparative mapping of chromosomes 1 and 5 [33] as well as chromosomes 11 and 12 [34] in rice but no evidence was found for a 2:1 relationship at the genome level with another grass species and therefore whole genome duplication was not suggested at that time. The duplicated nature of the grass genomes became obvious after the release of the rice genome sequence drafts in 2002 and the first comparisons at the sequence level with large collections of mapped ESTs from other cereal genomes. Two methods were used for the identification and characterization of genome duplications within the grass genomes. The most robust and direct approach called 'Intra-genome Duplication' (ID) consists in aligning a given genome sequence on itself. ID approach was undertaken in rice and Yu *et al.* [35] found evidence for 10 chromosome to chromosome duplication relationships (corresponding to 18 pairs of individual duplicated segments) involving a large number of genes and representing 65% of the *Oryza sativa* ssp *japonica* and *indica* genome drafts that refined

Figure 2

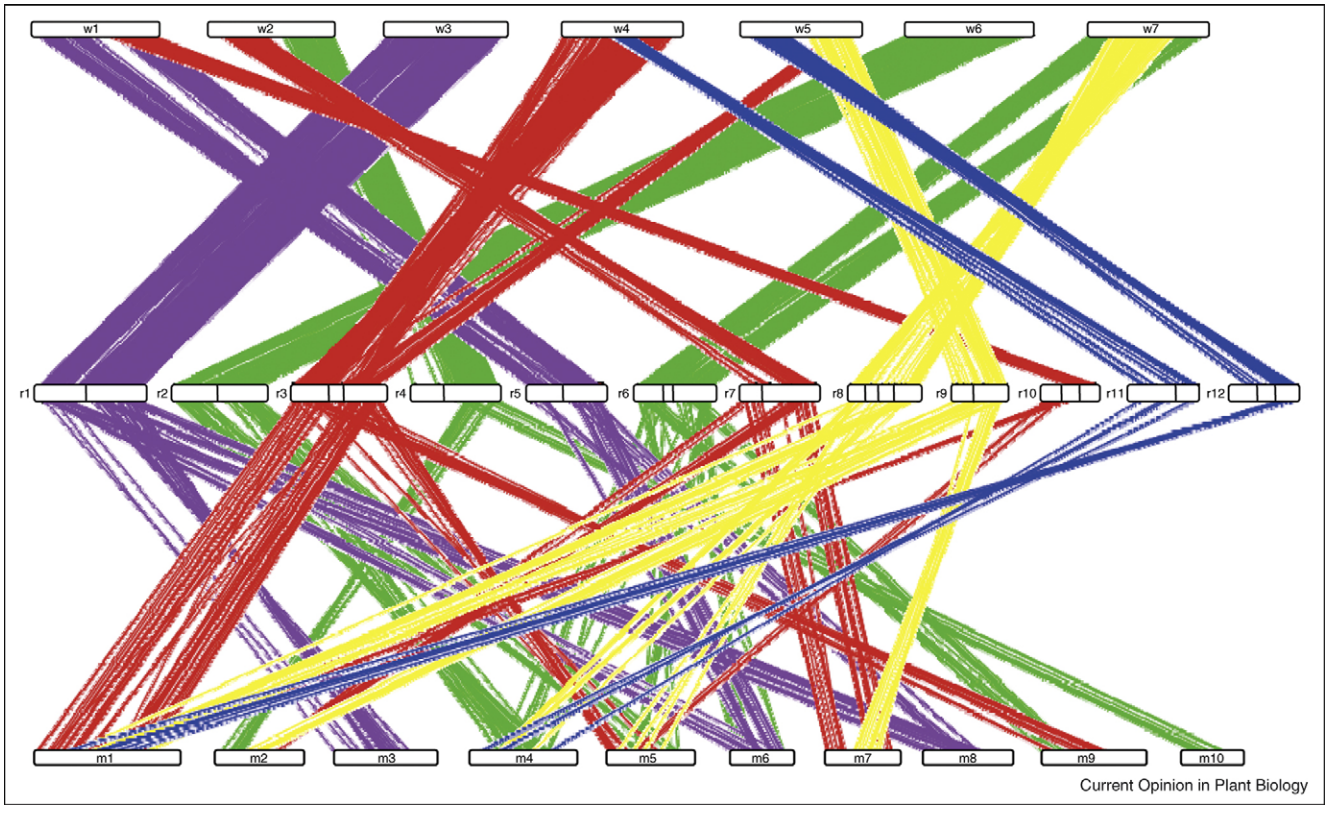


Colinearity between the Ehrhartoideae (rice), Pooideae (wheat, barley) and Panicoideae (sorghum, maize) chromosomes (updated from Salse *et al.* [21•]). Rice, wheat, barley, sorghum, maize orthologous chromosomes are displayed within 12 boxes that refer to the 12 rice chromosomes used as a reference. The 30 ancestral linkage blocks (A1–A30) originally identified by RFLP analysis are shown at the right end side of the figure in regard to the corresponding defined rice/maize/barley/wheat/sorghum syntenic blocks. Blocks with the same colour (purple, red, blue, yellow, green) and linked by brackets at the left end side correspond to chromosomes sharing one of the seven paleo-duplications identified at orthologous position in the five species. The five ancestral grass chromosome groups identified by the synteny and shared paleo-duplications analyses are shown on the far left of the figure.

and extended previous ID analyses [8,36–38]. Moreover, nucleotide substitution analyses led the authors to suggest a whole genome duplication (WGD) of the rice genome between 53 and 94 MYA (i.e. before the divergence of the cereal genomes) and a recent (7.7 MYA) segmental duplication between chromosomes 11 and 12 as well as numerous individual gene duplications [39]. Recently intragenomic duplications of the rice genome were refined and 29 duplications covering 72% (267 Mb) of the rice genome including the 10 major blocks published by Yu *et al.* [35] were characterized [21•]. The ID approach can be applied also to un-sequenced genomes as demonstrated recently for wheat in which intra-specific sequence comparisons using 6426 mapped wheat ESTs led to the identification and characterization of 10 duplication blocks covering 67.5% of the genome [21•].

A second indirect approach called 'Double Synteny' (DS) has been largely used to detect intragenomic duplications. It is based on the detection of regions showing a high proportion of gene matches on two different chromosomes within a genome and corresponding to two syntenic regions in another genome. DS was used to detect interchromosomal duplications in cereal genomes using synteny with the rice duplicates. Using a DS approach, Paterson *et al.* [16] provided evidence for the existence of six duplications in sorghum that corresponded to the rice r1-r5, r2-r4, r2-r6, r3-r7, r8-r9 and r11-r12 duplications previously identified. In barley, Stein *et al.* [17] assigned 475 EST markers to syntenic linkage groups of rice and performed dot-plot comparisons between the barley and rice chromosomes. Duplications on chromosomes 2H and 6H were analysed in more details and the results showed that the rice duplication r4-r2 is conserved in barley between chromosomes 2H-6H [17]. In maize, Wei *et al.* [10] provided evidence for nine duplications in maize that correspond to the duplications between the r1-r5, r2-r4, r2-r6, r3-r7, r3-r10, r3-r12, r8-r4, r8-r9 and r11-r12 chromosomes previously characterized in rice. The 'dual synteny' approach was also used by

Figure 3



Cereal (rice, maize, wheat) synteny. Graphical representation of the synteny between wheat (seven chromosomes from w1 to w7 at the top), rice (12 chromosomes from r1 to r12 at the centre) and maize (10 chromosomes from m1 to m10 at the bottom). Vertical lines represent orthologous pairs identified between rice and wheat [21•] or rice and maize [19]. The 30 previously defined ancestral linkage blocks are indicated into the 12 rice chromosome. The five colours used to represent the orthologous relationships refer to the five ancestral chromosomes (A5 = purple, A7 = red, A11 = blue, A8 = yellow, A4 = green) detailed in the text and in Figure 2.

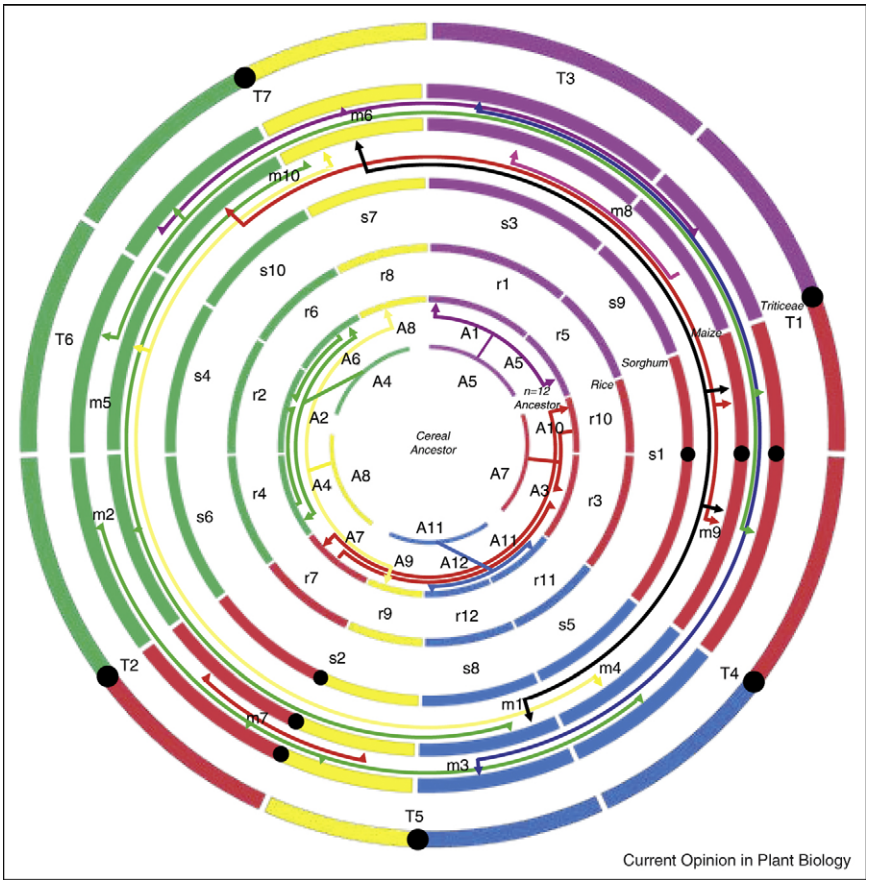
Singh *et al.* [40] on wheat using mapped ESTs and provided evidence for five duplications in the wheat genome that correspond to the previously characterized r1-r5, r2-r4, r2-r6, r8-r9, r11-r12 duplications in rice.

While the DS strategy can help to identify shared duplicated regions between the cereal genomes, it is limited by the ability to detect syntenic relationships that can be eroded by the so called diploidization process following WGD. Diploidization results in disruption of microcolinearity and the observation that genes that are not found at orthologous positions, are nevertheless present in the genomes but at non-orthologous locations [22,25,38]. One copy may have been retained at one locus in the first genome but has been lost in the second genome while the second copy is retained in both species at orthologous positions. By contrast, the ID approach allows a precise and extensive identification of shared and lineage-specific duplications. Independent intra-specific (i.e. paralogs) and inter-specific (i.e. orthologs) comparisons are necessary to infer precisely paralogous or orthologous gene relationships in order to (i) define synteny accurately, as well as (ii) identify a minimal ancestral genome structure. A recent integration of independent analyses of the duplications within and synteny between the four major cereal genomes (wheat, rice, maize, sorghum) led to the identification of seven shared duplications in the four species and the definition of five ancestral chromosomal groups [21•], cf Figure 2. The identification of the seven shared paleo-duplications provided the simplest picture of orthologous relationships between the grass genomes and allowed a revision of the 'concentric crop circles' by introducing the ancestral inner circle with five chromosomes.

Cereal genome evolution from a five chromosome ancestor

The characterization of the seven paleo-duplications and the relationships between the different conserved regions allowed us to identify evolutionary events that have shaped the grass genomes since their divergence from a putative ancestor with five chromosomes (A5, A7, A11, A8, A4 on the inner crop circle in Figure 4). After a WGD event (5 + 5 = 10 chromosomes) about 50–70 MYA, the

Figure 4



The 'inner circle' of the cereal genomes. The Triticeae, maize, sorghum and rice chromosomes are represented as concentric circles according to their genome size with the rice genome closest to the ancestral genomes at the centre. The maize genome is depicted with the 20 original chromosomes that arose from the tetraploidization event. The 17 chromosomal translocations that followed this event and resulted in 10 rearranged chromosomes are indicated with coloured arrows. Fusions between chromosomes are symbolized by black dots. The two inner circles represent the $n = 12$ chromosomes intermediate ancestor and the $n = 5$ chromosome ancestral grass genome. The five chromosome colours refer to the five ancestral chromosomes (A5 = purple, A7 = red, A11 = blue, A8 = yellow, A4 = green) and the coloured arrows indicate the relationships between the 12 intermediate and the five ancestral chromosomes after the WGD as detailed in Figure 2.

ancestral genome underwent two interchromosomal translocations and fusions that resulted in a $n = 12$ intermediate ancestor, represented as the second circle ($5 + 5 + 2 = 12$ chromosomes; A1–A12 in Figure 4) and originally defined as the first circle in the previous representations [20].

In this model, rice (third circle from the centre) retained the 12 original chromosome number whereas the other grass genomes have evolved differentially from this ancestral genomic structure. In rice, additional segmental duplications occurred without modifying the basic structure of 12 chromosomes including the recent duplications over ~3 Mb at the terminal ends of chromosomes r11 and r12. The maize and sorghum genomes have evolved from the intermediate 12 chromosomes ancestor through two chromosomal fusions (between A3 and A10 and, A7 and A9, Figure 4) that resulted in an Panicoideae ancestor with $n = 10$ ($5 + 5 + 2 - 2$) chromosomes [10,21•]. Then, maize and sorghum evolved independently from this ancestor. While the sorghum genome structure remained similar to the $n = 10$ chromosome ancestral genome (Figure 4), maize underwent a WGD event, resulting into an intermediate with $n = 20$ chromosomes. This corresponds to the tetraploidization event described in previous studies [41,42] leading to the representation of the maize genome as a double circle (Figure 4). Rapidly following this event, numerous chromosomal fusions led to a genome structure with 10 chromosomes ($n = 10$ ($5 + 5 + 2 - 2$) $\times$ $2 - 10$). At least 17 chromosomal fusions (Figure 4) must have occurred to explain the paralogous relationships that can be observed today between the different maize chromosomes. From the intermediate ancestral genome with 12 chromosomes, the Triticeae ancestor genome underwent five chromosomal fusions (Figure 4) between A5 and A10, A6 and A8, A9

and A12, A3 and A11 and A4 and A7 that resulted in the five chromosomes T1, T7, T5, T4 and T2, respectively, and a basic number of $n = 7$ (5 + 5 + 2 − 5) chromosomes for the wheat and barley genomes.

Thus, with this new version of the concentric circle including the ancestral genome as the inner circle and proposing a reconstruction of the rice, wheat, barley, sorghum and maize colinearity from a ancestor with $n = 5$ chromosomes, it is possible to immediately identify in each of the four genomes the ancestral relationships and the origin (WGD, breakage, fusion) of the different chromosomes.

Conclusion

Whole genome sequencing projects in grasses including sorghum [43], maize (www.genome.arizona.edu), Brachypodium (www.brachypodium.org [44]), foxtail millet (www.jgi.doe.gov) and the perspective of the barley and wheat genome sequences in the next decade (www.barleygenome.org, www.wheatgenome.org) will help to continue refining the degree of colinearity between the grasses as well as the evolutionary pathway that has shaped their genomes within 50–70 million years of speciation. Preliminary and recent large scale sequence comparisons based on microcolinearity studies involving the Brachypodium, maize and sorghum genome sequences [27,45••,46•,47] are consistent with the pattern of paleo-duplications and the evolutionary model from a 5-chromosome inner ancestral cereal circle presented here. With these new resources, comparative genomic studies between cereal genome sequences will deliver additional information about plant genome evolution and will provide efficient tools to navigate from one genome to the other to identify candidate genes and support crop improvement.

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