

Genetic and evolutionary studies in wheat

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Rapid genome evolution in polyploid wheat

Recent studies have shown that allopolyploidy, i.e., interspecific or intergeneric hybridization followed by chromosome doubling, has played a decisive role in the evolution of higher plants and animals. Allopolyploidization has facilitated the development of higher, more complicated eukaryotes, improved their adaptability to a wider range of environments and facilitated their establishment in nature through successful competition with the diploid progenitors. In spite of this important role, little is known about the nature of genomic changes that occurred at the polyploid level facilitating the harmonious coexistence of the different genomes in the same nucleus, changes that led to an improved orchestration of gene expression and chromosome behavior.

To study these changes we produced a variety of hybrids and synthetic wheat allopolyploids. Studying this material and the diploid parents, evidence were obtained that allopolyploidization is associated with a number of rapid cardinal genetic and epigenetic changes. Our studies of newly synthesized wheat allopolyploids showed that these changes comprise: (1) elimination of low-copy, coding and non-coding DNA sequences (Fig. 1); (2) epigenetic changes such as DNA methylation of coding and non-coding DNA and gene silencing; (3) demethylation and possibly activation of low-copy coding sequences; (4) transcriptional activation of retroelements. These nonrandom and highly reproducible changes, occurring in the F1 hybrids or in the first generation(s) of the nascent allopolyploids, might be a response of the wheat genome to the genetic shocks of wide hybridization and chromosome doubling. Elimination of non-coding DNA sequences augments the differentiation of homoeologous chromosomes (partially homologous chromosomes of different genomes) at the polyploid level, thus providing the physical basis for the diploid-like meiotic behavior of polyploid wheat. Changes in gene structure and expression bring about rapid diploidization that ameliorate the harmonious co-existence of the two or more diploid genomes combined in one allopolyploid nucleus. This may improve the adaptability of the newly formed allopolyploids thus facilitating their rapid and successful establishment in nature as new species. The mechanisms involved in these genetic and

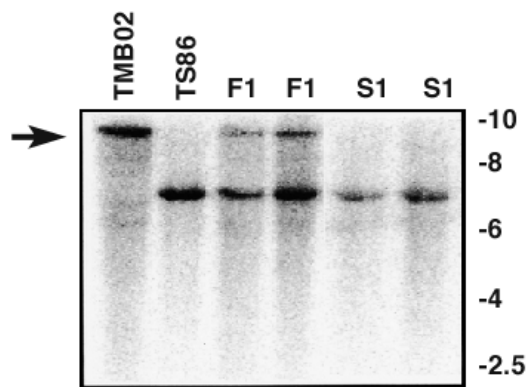


Fig. 1 Hybridization of the chromosome-specific sequence WPG90 to genomic DNA from the F1 hybrid between *Triticum monococcum* ssp. *aegilopoides* (TMB02) and *Aegilops speltoides* (TS86), from the S1 generation of the allotetraploid that derived from this hybrid and from the two parental plants. The arrow indicates the band from genome of TMB02 that disappeared in the S1 generation of the allopolyploid.

epigenetic changes as well as their evolutionary consequences are currently being studied (in collaboration with Avi Levy from our department).

Involvement of polycomb proteins in the initiation of meiotic chromosome pairing

On the basis of specificity the DNA sequences of an allopolyploid organism like wheat, containing two or more different genomes, can be classified into four groups: non-specific (occurring on all the chromosomes), group-specific (occurring on all the homoeologues - partial homologues of the different genomes; these are mainly the coding sequences), genome specific (occurring on several or all chromosomes of one genome), and chromosome-specific (occurring only on one homologous pair). The latter are the sequences that determine homology. Recently we isolated a number of chromosome-specific sequences from allopolyploid wheat and characterized them. Using a series of deletion lines it was found that the chromosome-specific sequences are arranged in clusters in one to several sites on each chromosome arm. These sites are homology-determining regions and therefore, might function as

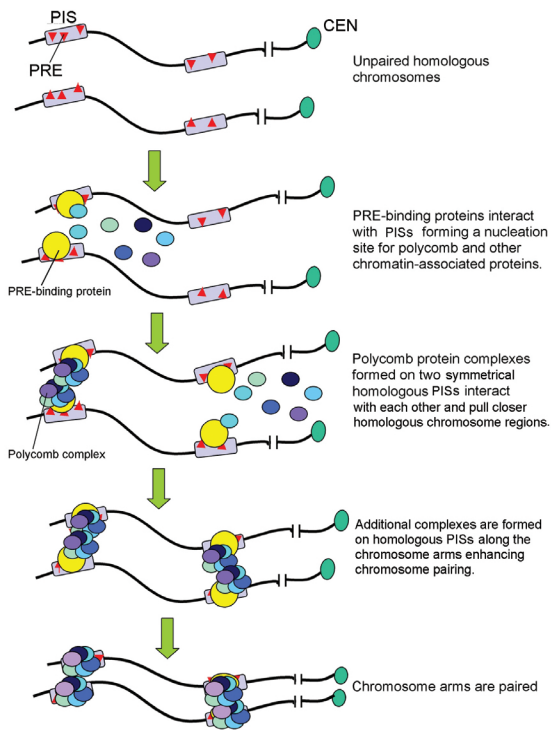


Fig. 2 A model for polycomb response element (PRE)-mediated pairing initiation of homologous chromosomes during meiosis. This model is based on the assumption that chromosome-specific pairing between homologous chromosomes are described in the figure. CEN indicates centromere.

pairing-initiation sites.

The chromosome-specific sequences of wheat possess a high frequency of polycomb-response elements (PREs) with the core motif GCCAT. Band shift assays showed the capacity of such PREs to specifically bind wheat premeiotic proteins. These bindings suggest that polycomb proteins are part of the molecular machinery involved in pairing initiation between homologous chromosomes (Fig. 2). We plan to isolate the PRE-binding proteins and hope that this will lead to a better understanding of the molecular mechanism underlying homologous recognition, and pairing initiation during meiosis (in collaboration with Gideon Grafi from our department).

Selected Publications

Feldman, M., Liu, B., Segal, G., Abbo, S., Levy, A.A., and Vega, J.M. (1997) Rapid elimination of low copy DNA sequences in polyploid wheat: A possible mechanism for differentiation of homoeologous chromosomes. *Genetics* 147, 1381-1387.

Feldman, M. (2001) The origin of Cultivated Wheat. In: *The Wheat Book A History of Wheat Breeding*, A. P. Benjean and W. J. Angus, (Eds.), Lavoisier Publishing, Paris, pp. 3-56.

Ozkan, H., Levy, A. A. and Feldman, M. (2001). Allopolyploidy-induced rapid genome evolution in the wheat (*Aegilops-Triticum*) group. *Plant Cell* 13, 1735-1747.

Shaked, H., Kashkush, K., Ozkan H., Feldman, M. and A. A. Levy. (2001). Sequence elimination and cytosine methylation are rapid and reproducible responses of the genome to wide hybridization and allopolyploidy in wheat. *Plant Cell* 13, 1749-1759.

Ozkan, H., and Feldman, M. (2001). Genotypic variation in tetraploid wheat affecting homoeologous pairing in hybrids with *Aegilops peregrina*. *Genome* (in press).

Kashkush, K., Feldman, M. and Levy, A. A. (2001). Gene loss, silencing, and activation in a newly-synthesized wheat allopolyploid. (Submitted).

Patents

Feldman, M. and Millet, E. (2001). Maintenance of genic male-sterile female lines using a maintainer line with a stable engineered chromosome (application no. 30291).

Feldman, M. and Millet, E. (2001). Method to maintain a genic male-sterile female parental lines for the production of hybrid wheat. (Application no. 30293).

Feldman, M. and Millet, E. (2001). A method for production of low-cost seeds of hybrid wheat. (Application no. 30295).

Acknowledgements

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