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"Compair" wheat: a breeder's variety with the yellow rust resistance of *Aegilops comosa* introduced by homoeologous recombination

Yellow rust (*Puccinia striiformis*) is a hazard to the cultivation of wheat (*Triticum aestivum*) in many temperate regions. The most economic method of limiting losses of yield due to the disease lies in the cultivation of varieties with genetically determined resistance to infection. Most current varieties owe their resistance to the activities of a few major genes which they carry in various combinations. However, new sources of resistance must be sought continually because mutation or somatic recombination in the pathogen can give rise to genetic variants against which particular resistance genes or combination of genes, in current use, cease to be effective.

In the search for new forms of disease resistance for use in wheat improvement, attention has often been turned to related species, some of which display outstanding levels of resistance. For example the wild annual grass *Aegilops comosa* (2n = 14), which is distributed round the Aegean Sea in Greece, Turkey and Crete, has especially good resistance to yellow rust[1]. Like all species in the genus *Aegilops*, *Ae. comosa* is closely related to wheat in an evolutionary sense and *T. aestivum* - *Ae. comosa* hybrids can be produced by hand pollination and hybrid-embryo culture. This communication describes work which resulted in the incorporation of the yellow rust resistance of *Ae. comosa* in wheat by interference with the genetic regulation of meiotic recombination. Such procedures have never previously been employed in crop improvement.

Riley, Chapman & Macer[2] initiated a backcrossing programme from 28-chromosome hybrids derived from the cross *T. aestivum* "Chinese Spring" x *Ae. comosa*, using "Chinese Spring" as the recurrent parent. After the second backcross, selection was practised for resistance to yellow rust. The result of this programme was the isolation of a 44-chromosome addition line that had the 42 chromosome of "Chinese Spring" and the pair of chromosomes of *Ae. comosa* determining rust resistance. It was further shown that this pair of *Aegilops* chromosomes would substitute for chromosomes 2A, 2B and 2D of the wheat complement, but for no other chromosome. The *Aegilops* chromosome determining rust resistance is therefore closely related genetically to the chromosomes of wheat homoeologous group 2. Indeed it can be regarded as homoeologous with these chromosomes, and designated 2M since *Ae. comosa* carries the M genome.

However, in normal circumstances chromosome 2M does not pair and recombine with any wheat chromosome[2]. Consequently the single gene on chromosome 2M that is presumed to be responsible for rust resistance cannot be incorporated in a wheat chromosome without further manipulation. Nevertheless it seemed likely that chromosome 2M would recombine, at meiosis, with its wheat homoeologues if the genetic suppression of homoeologous recombination normally exercised by chromosome 5B were removed[3,4].

To achieve this condition, use was made of another *Aegilops* species, *Ae. speltoides* (2n = 14), which has the property of inhibiting the 5B activity in wheat hybrids[5,6,7]. Thus in *T. aestivum* x *Ae. speltoides* hybrids there is homoeologous chromosome pairing and recombination. In the present work, therefore, the line with chromosome 2M added to the normal complement of "Chinese Spring" was crossed with *Ae. speltoides*. The resulting 29-chromosome hybrids had 21 chromosomes of *T. aestivum*, seven chromosomes of *Ae. speltoides* and chromosome 2M of *Ae. comosa*. Because of the inhibition of the 5B activity, recombination could take place at meiosis in these hybrids between chromosome 2M and its homoeologues in the wheat complement.

A backcrossing programme was initiated from these 29-chromosome hybrids using T. aestivum "Chinese Spring" as the recurrent parent. After the first backcross, selection was practised for rust resistance. In the third backcross generation a 42-chromosome, rust-resistant, plant was isolated that formed 21 bivalents at meiosis. This plant was heterozygous for a dominant rust resistant condition and homozygotes were isolated in its progeny.

A line homozygous for rust resistance was thus established which, when crossed with standard wheat varieties, gives hybrids that form 21 bivalents at meiosis. In the F_2 generation, derived from hybrids between "Chinese Spring" and this rust resistant line, segregation fits the ratio 3 resistant : 1 susceptible, so that the resistance introduced from Ae. comosa is inherited as though determined by the dominant allele at a single locus designated Yr8. The resistant line has been called "Compair" to indicate that it has a pair of genes for yellow rust resistance derived from Ae. comosa.

The study of meiotic pairing configurations in cytologically marked hybrids, and of the disturbance of segregation ratios in the F_2 generations derived from monosomic hybrids, shows that, in the origin of "Compair", homoeologous recombination took place in the long arm of chromosome 2M and the right arm of chromosome 2D. The recombined chromosome, that is homozygous in "Compair", has a distal segment of the right arm of 2D and a proximal segment of the long arm of 2M; while the centromere and the entire short arm are derived from 2M. This is the first example of the introduction of useful alien genetic variation into wheat by genetic interference with the regulation of recombination in the manner originally proposed by Riley & Chapman[3].

The Ae. comosa form of yellow rust resistance, carried by "Compair" is effective against races 2B, 3/55 (Opal-attacking), 8B, 54 and 60; giving 00-0 reactions in every case. Indeed this form of resistance is effective against all variants of the pathogen to which it has so far been exposed.

"Chinese Spring" was the recurrent wheat parent in the breeding programme because its use simplifies cytogenetic procedures and allows a rapid turnover of generations. Of course the incorporation of the alien yellow rust resistance in a genotype which is close to that of "Chinese Spring" means that further work must be done to establish it in an agriculturally acceptable genotype. However, this presents no further cytogenetic problems since the recombined 2M-2D chromosome pairs at meiosis in intervarietal heterozygotes with chromosome 2D and segregates normally, apparently with unimpaired transmission through both pollen and eggs. Consequently "Compair" can be treated as a normal wheat variety in planning breeding programmes and breeders need have no particular concern for chromosome behaviour in the derivatives of hybrids of which it was a parent.

In phenotype "Compair" is close to "Chinese Spring" but with longer spikelets, florets, glumes and grains. These are attributes that may result from the activities of Ae. comosa genes linked to Yr8 - the rust resistance gene. In "Compair" the development of awns is very variable since on the same plant some spikes may have short scurs while others are fully awned.

Seeds of "Compair" will be supplied to all breeders and pathologists who would like to use it.

A full description of the derivation and cytogenetic structure of "Compair" will be published elsewhere.

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