Results using substitution lines for disease studies have been reported by Sears, Loegering and Rodenhiser (1957), Green et al. (1960), and Knott and Shen (1961).

The genetics of resistance of Kenya Farmer to several moderately virulent races of stem rust has been analyzed by studying the reactions of the 21 substitution lines of Kenya Farmer in Chinese. Those lines shown to be carrying a factor for resistance were crossed with Chinese and with each other and segregation studied in F_2 (Sheen and Snyder 1962). Several factors for rust resistance, previously unknown, were located. Also several other relationships were clarified.

Substitution lines of Thatcher, Hope and Timstein were used in studies of earliness, awning, lodging, plant height, kernel weight and yield (Kuspira and Unrau 1957). The number of lines significantly different from Chinese varied with the donor variety. For example, four Thatcher, 10 Hope and 14 Timstein lines had significantly higher yields than Chinese. The protein content of five of the Thatcher substitution lines was significantly higher than that of Chinese.

Monosomics in practical breeding

Since substitution lines can be produced by the use of monosomics or other aneuploids, it becomes possible to transfer a chromosome carrying a desired gene from one variety to another.

To accomplish this, however, the recipient variety, the one to be improved, must be monosomic for the chromosome which is to be replaced by one carrying the desired gene.

Since several transfers may be needed, the best procedure is to introduce the complete monosomic sets into the best commercial varieties. The method of doing this has been described above. A word of caution is needed at this point. The aneuploid used as the recurrent parent must be the exact equivalent of the variety. Enough backcrosses to ensure this are essential. In wheat, agronomic and baking tests might be made to determine if that had been accomplished.

The next steps are then the same as for the production of substitution lines, as outlined above. The monosomics may be used as in Method 2, or Method 3 may be used after establishing nullisomic plus telocentric or nullisomic plus isochromosome stocks. As an example, the steps in transferring a gene (on chromosome 7B (7)) from Kenya Farmer to Thatcher are outlined below, assuming that a stock of Thatcher is available that is nullisomic 7B (7) plus telocentric for one arm of 7B (7).

1. Cross the Thatcher nullisomic + telocentric with Kenya Farmer.
2. Backcross the monosomic from the F_1 in step 1, on the Thatcher nullisomic + telocentric.
3. Repeat the process, using the monosomic as the $\sigma^{\prime}$ parent in each backcross.

At the end of the backcrossing, monosomics from the last backcross progeny are selfed and the disomic progeny selected. These should have 20 pairs of Thatcher chromosomes and should be homozygous for the 7B (7) chromosome from Kenya Farmer. Since this chromosome may have undesirable genes also, it may be advisable not only to self the monosomics in the last backcross progeny but also to cross them with Thatcher. Selection in the following generations from these latter crosses might be successful in combining the desirable genes brought in by the Kenya Farmer chromosome with those

in its Thatcher homologue. If both procedures were used at the end, no delay would occur if the lines from selfing were unsatisfactory.

If two factors on different chromosomes are to be transferred as seems to be the case for resistance to certain races of stem rust, each chromosome can be transferred in separate programs. At the end the two substitution stocks will have to be crossed, and selections for both genes made in the progeny. Since two chromosomes from another variety have been transferred, there is a still greater chance of undesirable effects of genes that came in with the desired ones.

If successive transfer were to be used, incorporation of the second factor would have to be delayed by the transfer of the needed monosomic condition to the first substitution line. This might go on simultaneously with the substitution program.

If the chromosome transferred does not pair with the Thatcher chromosome which is being replaced, the undesirable characters cannot be removed and the desired one retained by crossing over. X-ray treatment has been used to transfer a small segment carrying rust resistance from Aegilops umbellulata to T. vulgare wheat (Sears 1956).

Sears has suggested also that if the chromosome which carries the desired gene is known, the line that is monosomic for that chromosome in the variety to be improved might be crossed with a disease resistant variety and carried to F_2. Then in the F_2 from the monosomic F_1, select the plants with 21 pairs of chromosomes. These must be homozygous for the chromosome from the resistant variety, and for whatever factors it carries (disease resistance if the proper one). In subsequent generations selection could be practiced for the other characters, whether disease epidemics occurred or not. If disease resistance, winter hardiness, or other characters were simply inherited, such a technique might be useful.

In all of this work, information as to which chromosomes carry the desirable genes is essential for the efficient planning of a breeding program using the aneuploids.

Other uses

Aneuploid stocks of allopolyploids will undoubtedly have other special uses. One of these already reported was designed to test for the occurrence of secondary pairing in a situation where chromosomes known to be partially homologous could be identified (Riley 1960). Lines of hexaploid wheat with 20 II and a pair of telocentrics representing chromosomes 3A, 3B and 3D were crossed in all combinations. Each F_1 had two heteromorphic bivalents which also were partial homologs. The number of normal bivalents between them at Metaphase I ranged from 0 to 19, but there was a big excess of figures with none between the two heteromorphic bivalents. This indicates that secondary association does occur in this material.

CHAPTER 8. ALLOPOLYPLOIDY

Monosomics for the 14 chromosomes of T. durum cv. Stewart have been established. Fertility varied from 0.5 to 23.3%, and the percentages of shriveled seed varied form low values up to 57.7% (Mochizuki, 1970).

In Table 115, pp. 240-241, published in 1962, 69 genes for Triticum aestivum (2n = 42) were located to chromosome. Sears (1974), lists 154 loci, of which 114 are placed to chromosome. The placement was accomplished by the substitution method and by monosomic and nullisomic analysis (see also McIntosh, 1973; and Kush, 1973). By using telocentrics or isochromosomes, many of the genes have been located to arm. Sears (1966) reports data from tests using the telocentric for the arm carrying a mutant to determine the distance of the gene from the centromere and also for distances between genes in the same chromosome. He also discusses the cytological tests needed to confirm the crossovers. Sears (1974) includes maps for the 21 chromosomes which are based on distances of the genes from the centromere.