Chromosomal location of the structural genes for the M_r 75,000 γ -secalins in *Secale montanum* Guss: evidence for a translocation involving chromosomes 2R and 6R in cultivated rye (*Secale cereale* L.)

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Analysis of seed proteins from addition and substitution lines of *S. montanum* chromosomes into wheat shows that the structural genes for the M_r 75,000 γ -secalins are located on chromosome 6R^{mon}. Since these genes have been shown recently to be located on chromosome 2R in *S. cereale*, this indicates the presence of a translocation between 2R and 6R in *S. cereale* relative to *S. montanum*.

INTRODUCTION

Translocations are thought to have played an important role in the speciation of *Secale*. The ancient species *S. montanum* differs from the more recently evolved cultivated rye (*S. cereale*) by two translocations involving three pairs of chromosomes (Riley 1955; Stutz, 1957). Van Heemert and Sybenga (1972) identified these chromosomes as I, III and V, which correspond to 7R, 2R and 6R respectively in the revised nomenclature based on homoeology with wheat chromosomes (J. Sybenga, personal communication). We present here further evidence for a translocation between chromosomes 2R and 6R in *S. cereale* by showing that the structural genes for a group of endosperm storage proteins, recently reported to be located on chromosome 2R in *S. cereale* (Shewry *et al.*, 1984a), are present on chromosome 6R^{mon} of *S. montanum*. This finding is discussed in relation to the presence of genes for related proteins on the group 6 chromosomes of wheat.

MATERIALS AND METHODS

The series of Chinese Spring wheat/*Secale montanum* R15 addition and substitution lines were developed at the Plant Breeding Institute, Cambridge, U.K. The Kharkov wheat/*S. montanum* 2D23 addition lines were supplied by Dr J. P. Gustafson, University of Missouri, U.S.A. Total seed proteins were extracted from single seeds as described by Payne *et al.* (1980) and separated by sodium dodecylsulphate polyacrylamide gel electrophoresis (SDS-PAGE).

RESULTS AND DISCUSSION

Four groups of rye storage proteins (secalins) have been purified and characterized (Shewry *et al.*, 1982; Field *et al.*, 1982; Kasarda *et al.*, 1983). The structural genes for two groups, the ω -secalins and M_r 40,000 γ -secalins, are located on the short arm of chromosome 1R in *S. cereale* (Shepherd, 1968;

Bernard *et al.*, 1977; Lawrence and Shepherd, 1981) and for a third group, the high molecular weight (HMW) secalins, on the long arm of the same chromosome (Shewry *et al.*, 1984a; Singh and Shepherd, 1984). These locations are similar to those of the structural genes for the homologous groups of proteins in barley and wheat (see Shewry *et al.*, 1984b).

SDS-PAGE of the 1R^{mon} and ditelocentric 1R^{mon}L addition lines and the (1B) 1R^{mon}L substitution line of *S. montanum* into Chinese Spring wheat (fig. 1, tracks d, h, j) showed the presence of the HMW secalin subunits (arrowed). This indicates that, as in *S. cereale*, the genes for these proteins are located on the long arm of chromosome 1R. The M_r 40,000 γ -secalins and ω -secalins could not be conclusively demonstrated in the 1R^{mon} addition line or in the Chinese Spring/*S. montanum* amphiploid, which may be due to the presence of wheat proteins with similar mobilities.

The fourth group of secalins are related to the M_r 40,000 γ -secalins, but have M_r 's around 75,000. These M_r 75,000 γ -secalins are the quantitatively major group and are encoded by genes on 2RS in *S. cereale* (Shewry *et al.*, 1984a and unpublished results). It was therefore unexpected to find these proteins present in the 6R^{mon} addition line and the (6A) 6R^{mon} and (6D) 6R^{mon} substitution lines (bracketed in fig. 1, tracks g, m, n), but not in the addition and substitution lines involving chromosome 2R^{mon} (fig. 1, tracks e, i, k, l). The M_r 75,000 γ -secalins present in the seed of *S. montanum* R15 (bracketed in fig. 1, track b) migrated slightly more slowly than those in the amphiploid (bracketed in fig. 1, track c) and the addition and substitution lines, indicating that a different genotype may have been used in the original cross. This is not surprising, since *S. montanum* R15 is maintained as an outbreeding population and may have retained some heterozygosity.

We also analysed the four Kharkov wheat/*S. montanum* 2D23 addition lines of Gustafson *et al.* (1976), which are thought to have chromosomes corresponding to 1R, 2R, 5R and 7R of *S. cereale*. We were not able to demonstrate conclusively the presence of secalins in any of these lines (results not shown).

Since *S. montanum* is considered to be an ancient species and an ancestor of *S. cereale*, the results reported here suggest the presence of a translocation between chromosomes 2R and 6R in *S. cereale*. This is consistent with the cytogenetic results of Van Heemert and Sybenga (1972), and is the first biochemical evidence for this event.

Figure 1 SDS-PAGE of total seed proteins from Chinese Spring wheat, R15 *S. montanum* and Chinese Spring/R15 addition and substitution lines. a, Chinese Spring wheat. The brackets indicate, in order of increasing mobility, the HMW subunits, ω -gliadins and S-rich prolamins (α , β , γ -gliadins and low-molecular-weight subunits of glutenin); b, R15 *S. montanum*. The brackets indicate, in order of increasing mobility, the HMW secalins, M_r 75,000 γ -secalins, ω -secalins and M_r 40,000 γ -secalins; c, Chinese Spring/R15 amphiploid; d, 1R^{mon} addition line; e, 2R^{mon} addition line; f, 4R^{mon} addition line; g, 6R^{mon} addition line; h, 1R^{mon}L ditelocentric addition line; i, 2R^{mon}L ditelocentric addition line; j, (1B) 1R^{mon}L substitution line; k, (2B) 2R^{mon} substitution line; l, (2D) 2R^{mon} substitution line; m, (6A) 6R^{mon} substitution line; n, (6D) 6R^{mon} substitution line. The arrows in tracks c, d, h and j indicate the HMW secalins. The brackets in tracks c, g, m and n indicate the M_r 75,000 γ -secalins.

The structural genes for the M_r 75,000 γ -secalins are thought to be derived from those for the M_r 40,000 γ -secalins, which are located on chromosome 1R in *S. cereale*. The presence of loci encoding related proteins in similar positions on the homoeologous chromosomes of barley and wheat (see Shewry *et al.*, 1984b) indicates that this was the situation in the common ancestor of these species. This implies that the genes for the M_r 75,000 γ -secalins have been involved in two successive translocations, from 1R to 6R in an

ancestor of *S. montanum* and from 6R to 2R during the evolution of *S. cereale*.

Related storage proteins (α -type gliadins) are also encoded by genes on the short arms of the group 6 chromosomes of wheat (see Payne *et al.*, 1984), but not barley. It is possible that a single event in the ancestor of wheat and rye resulted in the translocation of storage protein genes from chromosome 1 to 6, and these then diverged to encode the *M*, 75,000 γ -secalins in rye and the α -type gliadins in wheat.

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