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Relationships of *Agropyron intermedium* Chromosomes Determined by Chromosome Pairing and Alcohol Dehydrogenase Isozymes in Common Wheat Background

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Summary. The relationships of *Agropyron intermedium* chromosomes in two wheat-*Agropyron* addition series were determined. Chromosome pairing behaviour revealed that the alien chromosome in lines TAF-2 and L7 of 'Vilmorin'-*A. intermedium* set are homologous to the alien chromosomes in lines P and C of the 'Caribo'-*A. intermedium* set respectively. Localization of alcohol dehydrogenase isozyme genes in 'Vilmorin'-*Agropyron* addition line L4 and in 'Caribo'-*Agropyron* line O indicated relationships with wheat chromosomes of homoeologous group 4.

Key words: Wheat – *Agropyron* – Chromosome pairing – Alcohol dehydrogenase isozymes

Introduction

Improvement of cultivated wheat is enhanced by the transfer of useful characters from its relatives, *Aegilops*, *Agropyron* and *Secale*. A partial amphiploid (2n = 56) with the complete genome of *Triticum aestivum* L. em Thell. cv. 'Vilmorin-27', and seven chromosome pairs from hexaploid *Agropyron intermedium* (Host.) Beauv., was shown to be resistant to wheat stem rust, leaf rust and stripe rust (Cauderon 1958, 1966). Six of the seven possible wheat-*Agropyron* addition lines were further isolated, and genes controlling the resistance were assigned to three addition lines (Cauderon et al. 1973). The *Agropyron* chromosome in addition line TAF-2, which showed resistance to stem rust, is homoeologous to 7D of wheat, and the *Agropyron* chromosome which carries leaf rust resistance in addition line TAF-1 showed homoeologous relationship with 3A (The and Baker 1970). The addition line L7 possessed the same type of stripe rust resistance as the initial wheat-*Agropyron* amphiploid (Cauderon 1966; Cauderon and Rhind 1976).

Studies of another wheat-*Agropyron* addition series involving wheat variety 'Saratovskaya 29' and *A. intermedium* (*A. glaucum*), also revealed that at least three different chromosomes controlled resistance to leaf rust. One of these chromosomes also controlled resistance to stripe rust (Sinigovets 1976). On the other hand, Wienhues (1960, 1963, 1973, 1979a, 1979b) was able to transfer into wheat cultivar 'Heine IV' a single pair of *A. intermedium* chromosomes which carried simultaneously genes for resistance to all the three rusts. This chromosome showed a homoeologous relationship with wheat chromosome 7A (Wienhues, 1971).

Recently, six other addition lines combining the genome of wheat cultivar 'Caribo' and an added chromosome pair of *A. intermedium* has also been isolated (Zeller, unpubl.). Hence, the genetic behaviour of *Agropyron* chromosomes in the wheat background, and a knowledge of the relationship between wheat-*Agropyron* addition series becomes a requisite, for full exploitation of the potential genetic variability. The present study deals with chromosome identification, facilitated by cytological analysis and alcohol dehydrogenase isozyme marker genes.

Materials and Methods

'Vilmorin 27'-*A. intermedium* disomic addition lines were kindly supplied by Y. Cauderon, Versailles, France. The initial hybrid was obtained from a cross of hexaploid wheat cultivar 'Vilmorin 27' and *A. intermedium* (2n = 6x = 42). A stable perennial octaploid line TAF-46, which showed resistance to wheat rusts was first selected. Further systematic selections produced six wheat-*Agropyron* addition lines, with TAF-2 (L1), TAF-1 (L2) and L7 carrying genes for resistance against wheat stem rust, leaf rust and stripe rust respectively. The other addition lines L3, L4 and L5 lacked resistance. L6 was not isolated (Cauderon 1966).

The wheat-*A. intermedium* amphiploid line, TA 139, used for the development of 'Caribo'-*Agropyron* addition lines was kindly supplied by J. E. Giessen, Max Planck Institut für

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Züchtungsforschung, Köln, Germany. A winter wheat cultivar 'Heine IV' was involved in the initial cross. TA 139 was also an octaploid with the complete genome of hexaploid wheat, and an added genome of *A. intermedium*. This amphiploid line was crossed with the high yielding winter wheat cultivar 'Caribo', and monosomic additions were selected from the segregating progenies. Further backcrossing to 'Caribo' were made for five more generations and systematic selection for monosomic addition lines were carried out. These lines were eventually selfed to produce disomic addition lines. Morphologically discernible lines were isolated, and the homology of other lines were verified by meiotic chromosome pairing behaviour. Six addition lines (2n = 44) C, F, G, L, O and P were finally isolated.

'Vilmorin 27'-*Agropyron* addition lines TAF-1, TAF-2 and L7, which showed rust resistance, were crossed with 'Caribo'-*Agropyron* addition lines C, F, G, O and P. Addition line L produced necrotic spots on leaves in disomic additions and was not used in the cross. Chromosome pairing behaviour of the F1 hybrids was studied. Somatic chromosome numbers were verified using the Feulgen method. Pollen mother cells (PMC) from plants with 44 chromosomes were studied from fixed anthers, stained with Feulgen and counter-stained with 1% Aceto-carmine. In addition, the 'Caribo'-*Agropyron* addition line P was crossed with 'Caribo' monosomic 7D. From the progeny of the double monosomic (20″ + 2′) F1, a plant with a meiotic configuration of 21 bivalents possessing also the characteristic red coleoptile was selected. This plant was test crossed with 'Chinese Spring' wheat line ditelo 7DS. Chromosome pairing behaviour in the F1 PMC's was examined using the same methods as described above.

Alcohol dehydrogenase (ADH) isozyme was used as a biochemical marker gene to study the relationships of *Agropyron* chromosomes in 'Vilmorin 27' and 'Caribo' addition lines. Five mature grains were soaked in water for 16 h before being macerated in 0.1 M Tris-HCl buffer, pH 7.5, containing 0.01 M-KCl, 0.005 M EDTA and 0.004 M 2-mercaptoethanol (Carlson 1972), maintaining a ratio of 0.3 ml buffer per kernel. The macerated tissue was centrifuged at 17,000 g for 20 min in a SS-34 rotor in a Sorvall RC 2-B refrigerated centrifuge maintained at 4 °C. An aliquot of 100 µl of supernatant was used for polyacrylamide gel electrophoresis, at 6–8 °C following the method described by Davis (1964). Gels were stained for ADH as described by Hart (1970).

Wheat cultivars 'Vilmorin 27' and 'Caribo', *A. intermedium*, the wheat-*Agropyron* partial amphiploid line TAF-46, 'Vilmorin 27'-*Agropyron* addition lines TAF-1, TAF-2, L3, L4, L5, L7, 'Caribo'-*Agropyron* addition lines C, F, G, L and O were analysed. Four replicate extractions and electrophoreses were carried out.

Results and Discussion

From among the cross combinations of five 'Caribo'-*Agropyron* addition lines and 'Vilmorin 27'-*Agropyron* addition lines and 'Vilmorin 27'-*Agropyron* addition lines TAF-1, TAF-2 and L7, two F1 hybrids formed 22 bivalents at metaphase I of meiosis. 'Caribo'-*Agropyron* addition line P showed 22″ with TAF-2, the addition line which carries the gene for stem rust resistance. Similarly, the F1 hybrid between 'Caribo'-*Agropyron* addition line C and the stripe rust resistant line 'Vilmorin 27'-*Agropyron* addition line L7 possessed a 22″ configuration. F1 hybrids from the other crosses produced a maximum chromosome configuration of 21″ + 2′ (Table 1). One or two quadrivalents were observed occasionally in the hybrids from crosses between the additions. These quadrivalents probably arose from the pairing between structurally different 'Vilmorin 27' and 'Caribo' wheat chromosomes. As reporated earlier by Wienhues (1960), Cauderon (1966), and Dvořák and Knott (1974), an added pair of *Agropyron* chromosomes regularly formed bivalents in disomic additions of *A. intermedium* and *A. elongatum* chromosomes to *T. aestivum*.

Table 1. Chromosome pairing configurations in F1 hybrids between 'Caribo'-*A. intermedium* and 'Vilmorin 27'-*A. intermedium* addition lines

Vilmorin additions	Caribo additions				
	C	F	G	O	P
TAF-2 (L1)	21″ + 2′	21″ + 2′	21″ + 2′	21″ + 2′	22″
TAF-1 (L2)	21″ + 2′	21″ + 2′	21″ + 2′	21″ + 2′	21″ + 2′
L7	22″	21″ + 2′	–	–	21″ + 2′

From the chromosome pairing behaviour, it may be assumed that the *Agropyron* chromosomes in addition lines 'Caribo' P and C are homologous with the *Agropyron* chromosomes in 'Vilmorin 27'-*Agropyron* addition lines TAF-2 and L7 respectively. In the present study, the *Agropyron* chromosome in 'Caribo'-*Agropyron* addition line P also substituted for wheat chromosome 7D. As seen in Fig. 1, the F1 hybrid between 'Chinese Spring' ditelo 7DS and the 'Caribo'-*Agropyron* substitution line, involving the *Agropyron* chromosome from addition line P showed $18'' + 1^{IV} + 1' + t'$, with the telocentric chromosome 7DS and the *Agropyron* chromosome remaining unpaired. The and Baker (1970) also showed that the *Agropyron* chromosome in TAF-2 spontaneously substituted for wheat chromosome 7D. Moreover, the 'Caribo'-*Agropyron* addition P, 'Caribo'-*Agropyron* substitution P and 'Vilmorin 27'-*Agropyron* addition line TAF-2 expressed red coleoptile colour in the seedling stage. The *Agropyron elongatum* chromosome designated 7E by Dvořák (1980), which compensated for wheat chromosomes of homoeologous group 7 was also associated with a red coleoptile colour. These findings are indications of a homoeologous relationship between the alien chromosome in 'Caribo'-*Agropyron* addition line P and the wheat chromosomes of group 7.

Distinct alcohol dehydrogenase (ADH) zymogram phenotypes were observed between wheat, *Agropyron* and wheat-*Agropyron* amphiploid (Fig. 2). Wheat cultivars 'Vilmorin 27' and 'Caribo' both expressed three isozyme bands, with the two more cathodic bands

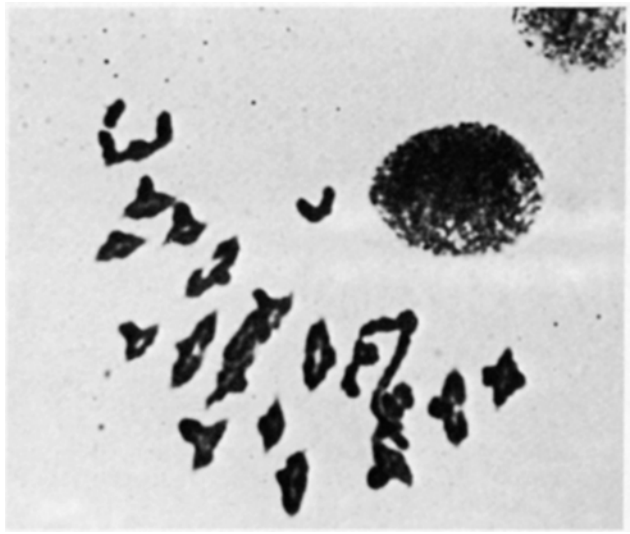

Fig. 1. Metaphase I in PMC's of F1 hybrid between 'Chinese Spring' ditelo 7DS and 'Caribo'-*A. intermedium* substitution line, showing the unpaired *Agropyron* chromosome and telocentric 7DS ($18'' + 1^{IV} + 1' + t'$)

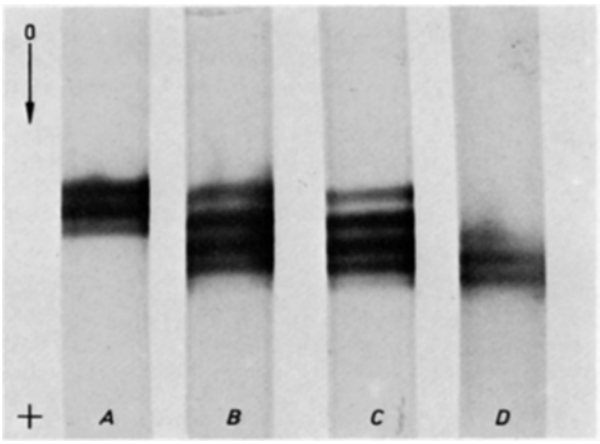

Fig. 2. Zymogram phenotypes of alcohol dehydrogenase isozymes, *A* wheat cultivars 'Vilmorin 27' and 'Caribo', 'Vilmorin 27'-*A. intermedium* addition lines TAF-1, TAF-2, L3, L5, L7, 'Caribo'-*A. intermedium* addition lines, C, F, G, L; *B* 'Vilmorin 27'-*A. intermedium* amphiploid TAF-46; *C* 'Vilmorin 27'-*A. intermedium* addition line L4, 'Caribo'-*A. intermedium* addition line O; *D A. intermedium* 6×

staining more intensively than the anodic band (Fig. 2, A). The hexaploid *A. intermedium* also produced three isozyme bands, but these differed in mobilities from the wheat isozymes (Fig. 2, D). The wheat-*Agropyron* partial amphiploid line TAF-46 expressed five isozyme bands (Fig. 2, B). 'Vilmorin 27'-*Agropyron* addition line L4 and the 'Caribo'-*Agropyron* addition line O also expressed five isozyme bands. These bands exhibited similar mobilities and staining intensities as the wheat-*Agropyron* amphiploid TAF-46 zymogram phenotype (Fig. 2, C). The relative staining intensities and the number of the isozyme bands are similar to ADH isozyme zymogram phenotypes reported earlier for wheat-rye (Tang and Hart 1975), and wheat-barley (Hart et al. 1980) addition lines.

Several biochemical findings indicated that ADH isozymes have a dimeric subunit structure (Hart 1971; Langston et al. 1979). In the 'Chinese Spring'-'Imperial' wheat-rye addition line 'CR', which carried the rye ADH gene, Tang and Hart (1975) have shown that one rye and three wheat ADH subunits randomly dimerized to produce the ten possible dimeric forms which were expressed as five isozymes. The similar findings for ADH zymogram phenotypes of wheat-*Agropyron* addition lines in the present study with a wheat-rye addition line may be an indication that the added *Agropyron* chromosome pair produced only one dimeric ADH subunit. As *A. intermedium* is a hexaploid, and as it also expressed three isozyme bands similar in number to hexaploid *T. aestivum,* it is most likely that ADH isozymes in *A. intermedium* are also controlled by triplicate homoeologous genes. It appears probable that only one pair of homeoallelic genes was included in the initial synthesis of the wheat-*Agropyron* partial amphiploid.

Nevertheless, these results indicate that the ADH isozyme genes are allelic in 'Vilmorin 27'-*Agropyron* addition line L4 and in 'Caribo'-*Agropyron* addition line O. A triplicate set of homoeologous alcohol dehydrogenase structural genes have been located in the chromosome arms 4Aα, 4BL and 4DS of wheat cultivar 'Chinese Spring' (Hart 1970, 1973). On the basis of β-amylase isozymes, 'Vilmorin 27'-*Agropyron* addition line L4 was found to be related to the wheat chromosomes of group 4 (Joudrier and Cauderon 1976; Cauderon et al. 1978). The present findings that ADH isozyme genes are located on addition line L4 constituted further evidence of a homoeologous relationship with the wheat chromosomes of the same group. Similarly, the homoeology of the added alien chromosome in the 'Caribo'-*Agropyron* addition line O to wheat chromosomes of group 4 is also indicated.

Agropyron species have long been used to increase genetic variation in cultivated wheat. Genes for resistance against wheat rusts (Cauderon 1966; Cauderon et al. 1973; Knott 1961, 1968; Knott and Dvořák 1976; Sinigovets 1976; Wienhues 1960, 1973), leaf blotch (Gough and Tuleen 1979), wheat streak mosaic virus (Larson and Atkinson 1970; Wang et al. 1980), wheat curl mite (Larson and Atkinson 1972), genes for higher protein content (Pienaar 1981; Soliman et al. 1980), genes for salt-tolerance (Pienaar 1981), and genes for frost resistance (Sinigovets et al. 1979) have been transferred from *A. elongatum, A. intermedium* and *A. distichum.*

The initial step of alien gene transfer into wheat is by first producing a wheat-alien amphiploid. The detection of desirable alien characters in the amphiploid leads to the isolation of wheat-alien disomic addition lines. Characteristic genes on the added alien chromosomes are further incorporated into the wheat genome, either by substitution of whole chromosome or by translocation of the chromosome segment carrying the alien gene. Transfer of alien genes into wheat is facilitated by homoeologous chromosome pairing between wheat and the alien chromosome (Chueca and Cauderon 1977; Dvořák 1979; Sears 1973; Wang et al. 1980). Homoeology between individually added alien chromosome pairs and wheat chromosomes has been determined by genetic compensation of the alien chromosomes for wheat chromosomes (Johnson 1966; Johnson and Kimber 1967; Dvořák 1980). However, the procedure involves tedious and elaborate amount of cytological work. Morphological characters such as anthocyanin colouration of seeds, aleurone, glumes and coleoptile could be used as markers for homoeologous relationships. On the other hand, biochemical markers such as isozymes are also available for identification of chromosomes. At present at least 57 isozyme structural genes are known in hexaploid wheat, and one or more of these genes have been located in 18 of the 21 chromosome pairs of the species (for a review, see Hart 1979).

Isozyme phenotypes used as indications of homoeology between wheat and alien chromosomes, may facilitate the transfer of genes syntenic with isozyme structural genes. If a desirable agronomic character from an alien chromosome is found to be linked with an alien isozyme gene, the success of gene transfer would be accomplished by the hybridization between the wheat-alien addition line and the wheat aneuploid lines monosomic for the homoeologous chromosomes expressing the same isozymes. The substitution line could be selected from the selfed progeny of the F1 hybrid, or from a backcross progeny with the wheat-alien addition line.

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