

CHROMOSOMAL POLYMORPHISM BY RECIPROCAL TRANSLOCATIONS IN A NATURAL POPULATION OF CULTIVATED RYE, *SECALE CEREALE* L.: A PRELIMINARY NOTE

by

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This paper is dedicated to Prof. S. Rivas Goday on his 70th birthday.

INTRODUCTION

It is generally accepted that differences between karyotypes of related species have been originated by chromosomal rearrangements or numerical changes. At the present time cytotaxonomic differences represent the remains of ancestral chromosomal polymorphisms. WHITE (1965) named *karyotypic orthoselection* the evolutionary cytogenetical phenomenon which refers to the fact that in certain taxonomic groups a natural tendency to produce changes in chromosomal complement exists, taking place by reiteration of the same cytogenetical mechanism. For example, paracentric inversions in the genus *Drosophila* (DOBZHANSKY, 1941) and the Robertsonian translocations in *Acrididae* (ROBERTSON, 1916) or *Rodentia* (MATTHEY, 1958) can be mentioned.

On the basis of the karyotypic orthoselection concept, it is postulated that both in intraspecific and interspecific chromosomal polymorphism similar cytogenetical mechanisms (inversions or translocations) are involved. Such mechanisms having played an important role in the speciation process of the taxonomic group considered.

As a rule, the above postulate is proposed in direct terms; that is, interspecific chromosomal polymorphism is inferred from the previously demonstrated intraspecific one. As a consequence, the reciprocal corollary is usually accepted; namely, intraspecific polymorphism can be inferred from the known interspecific one.

Sistematics of the genus *Secale* L. has been reviewed by a number of authors (VAVILOV, 1926; ANTROPOV and ANTROPOV, 1936; SCHIEMANN, 1948; ROSHEVITZ, 1947; NÜRNBERG-KRÜGER, 1960; JAIN 1960; KHUSH and STEBBINS, 1961; KHUSH, 1962, 1963a, 1963b; STUTZ, 1972; KRANZ, 1973) both from the botanical and cytogenetical aspects.

From the cytotaxonomical point of view, the first evidences of interspecific chromosomal polymorphism by reciprocal translocations in the genus *Secale* were given by RILEY (1955), PRICE (1955), STUTZ (1957), NÜRNBERG-KRÜGER (1960), and KRANZ (1961). Later, KHUSH (*l. c.*) stated the cytogenetical relationships between the different *Secale* species (all of them having $2n = 2x = 14$ chromosomes) as follows: *Secale montanum*, *S. africanum*, and *S. silvestre* differ from each other by one small translocation. *S. vavilovii* differs from *S. montanum*, *S. africanum*, and *S. silvestre* by one and the same large translocation, but an additional small translocation difference is present between *S. vavilovii* and *S. africanum* and between *S. vavilovii* and *S. silvestre*. Cultivated rye, *S. cereale*, differs from all these wild species by two translocations, but, in addition, another small translocation may differentiate *S. cereale* and *S. silvestre*. According to the above data, the critical meiotic configurations observed at first metaphase would be:

Interspecific ybrid		Configuration at metaphase I
<i>S. silvestre</i>	× <i>S. montanum</i>	1 IV + 5 II
<i>S. silvestre</i>	× <i>S. africanum</i>	1 IV + 5 II
<i>S. montanum</i>	× <i>S. africanum</i>	1 IV + 5 II
<i>S. vavilovii</i>	× <i>S. montanum</i>	1 IV + 5 II
<i>S. vavilovii</i>	× <i>S. africanum</i>	2 IV + 3 II
<i>S. vavilovii</i>	× <i>S. silvestre</i>	2 IV + 3 II
<i>S. cereale</i>	× <i>S. silvestre</i>	1 VIII + 3 II
<i>S. cereale</i>	× <i>S. vavilovii</i>	1 VI + 4 II
<i>S. cereale</i>	× <i>S. mantanum</i>	1 VI + 4 II
<i>S. cereale</i>	× <i>S. africanum</i>	1 VI + 4 II

Since reciprocal translocations seem to constitute an evolutionary cytogenetical trend involved in the speciation of the genus *Secale*, one can accept the reciprocal corollary; that is, it has to exist an intraspecific polymorphism for the same chromosomal rearrangements.

In this present work some preliminary data on chromosomal poly-



Fig. 1.—Heterozygote plant for reciprocal translocation in *Secale cereale* L. cultivar Ailés. Metaphase I showing 1 IV + 5 II; the quadrivalent shows an adjacent co-orientation.

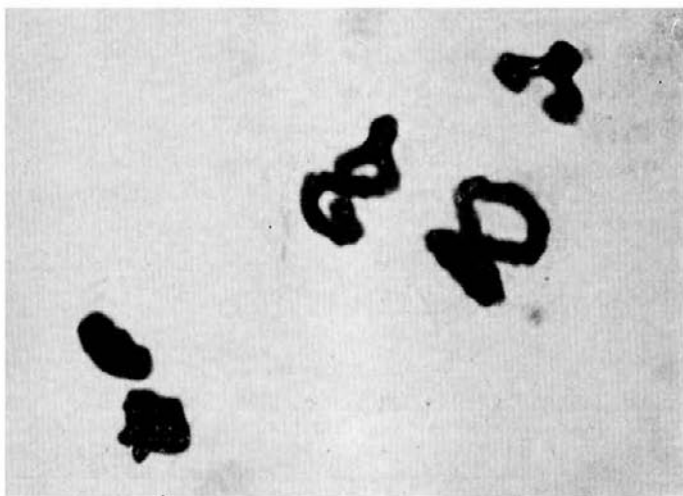


Fig. 2.—Double heterozygote plant for two different reciprocal translocations in *Secale cereale* L. cultivar Ailés. Metaphase I showing 2 IV + 8 II; both quadrivalents show alternate co-orientation.

morphism by reciprocal translocations in cultivated rye, *Secale cereale* L., are presented.

MATERIAL AND METHODS

The material analyzed was a sample of *Secale cereale* collected in the locality of Ailés (Zaragoza, Spain) where is cultivated without interruption for many years. In the following it will be named as cultivar Ailés.

Chromosomal polymorphism among individuals of the natural population was determined by the observation of the meiotic configuration at first metaphase of pollen mother cells (PMCs). The occurrence of quadrivalents was interpreted as structural heterozygosity of the plant analyzed (figure 1).

Anthers were fixed in acetic alcohol 1:3 and PMCs stained with fuchsin after the hydrolisis in 1N HCl at 60° C for 12 minutes. PMCs were squashed in a drop of 45 % acetic acid. Meiotic observations were made on permanent slides mounted in Sandeural.

RESULTS

On making a routine chromosomal control in 1972-73 on a small sample of cultivar Ailés supplied by L. M. Villena, Estación Experimental de Aula Dei, C. S. I. C., Zaragoza, Spain, the presence of structural heterozygotes for reciprocal translocations was observed in such a proportion which advised to enlarge the cytological control. So, in 1973-74 and 1974-75 two samples of cultivar Ailés were sown. Both corresponding to the parental and filial populations, respectively. The results obtained are listed below:

Chromosome constitution

	Homozygotes 7 II	Heterozygotes 1 IV + 5 II	Double heterozygotes 2 IV + 3 II	Total
Parental population 1973-74	58 78.38 %	15 20.27 %	1 1.35 %	74 100 %
Filial population 1974-75	45 78.95 %	12 21.05 %	— —	57 100 %

On the other hand, the offspring harvested from one heterozygote plant of the parental population by open pollination was as follows:

Chromosome constitution

Homozygotes 7 II	Heterozygotes 1 IV + 5 II	Double heterozygotes 2 IV + 3 II
3	1	2

DISCUSSION

The existence of chromosomal polymorphism by reciprocal translocations in natural populations of cultivated rye, *Secale cereale*, was pointed out by MÜNTZING and PRAKKEN (1941) by analyzing two samples of the Swedish cultivars «Stålråg» and «Östgöta Gråråg». The frequency of structural heterozygotes found was less than 4 % (out of 167 plants, five showed 1 IV + 5 II and one 2 IV + 3 II at first metaphase). Perhaps this was the reason why they gave no evolutionary importance to the finding; in fact they only commented that «the species *S. cereale* is not cytologically stable (p. 303). Later on, AKDIK and MÜNTZING (1949) described again new cases of translocation heterozygosity in a very small sample of a cultivar from Ecuador.

Intraspecific chromosomal polymorphism by reciprocal translocations has been also found in *Secale kuprijanovii* (HRISHI and MÜNTZING, 1960). The high frequency of structural heterozygosity found (out of 13 plants, 11 showed 1 IV + 5 II) suggested a great selective value of heterozygotes. In spite of these results, HRISHI et al. (1969) observed a strong reduction of the heterozygote frequencies on their offspring after open pollination. Thus, adaptative implications must be cautiously taken in this case.

The above mentioned investigations and this present preliminary report seem to demonstrate that the reciprocal corollary of karyotypic orthoselection applies to the genus *Secale* and, in particular, to cultivated rye, *S. cereale*: since interspecific polymorphism was known for a long time, it had to be possible to find intraspecific polymorphism.

The most striking fact of the cultivar Ailés is the rather high per-

centage (21 %) of structural heterozygotes observed both in the parental population (1973-74) and in its offspring (1974-75). FORD (1940) defined the polymorphism as the occurrence in the same environment of two or more distinct forms of the same species in such proportions that the rarer cannot be maintained in the population only by recurrent mutation. It is logical to think that the chromosomal rearrangements detected in Ailés populations cannot be attributed to recurrent rearrangements but to a true chromosomal polymorphism. The repetition of the same high frequency (21 %) of structural heterozygotes in the two successive generations may suggest (but not demonstrate) that Ailés population is in equilibrium. On the other hand, the occurrence of two different translocations (see the Results and figure 2) makes more difficult the cytogenetical analysis of population equilibrium. The use of translocation tester sets (SYBENGA and WOLTERS, 1972) or chromosome banding techniques (VOSA, 1974; SYBENGA, personal communication) can be very useful in order to identify the structural homozygotes.

The maintenance of a high level (21 %) of structural heterozygosity in a population of cultivated rye can suggest an adaptative significance. The selective value of structural heterozygotes mainly depends on two factors: firstly, a positive factor widely demonstrated in many organisms; namely, the adaptative value conferred by structural heterozygosity *per se*. Secondly, a negative factor: the loss of fertility originated by the formation of inviable gametes in heterozygote individuals.

With respect to the first point, REES (1961) demonstrated in *S. cereale* that structural heterozygotes for interchange had selective advantage over homozygotes.

With regard to the fertility of interchange heterozygotes, THOMPSON (1956) demonstrated that the frequency of alternate co-orientation of interchange configurations in rye was genotypically controlled. Likewise, REES and SUN (1965) demonstrated a reverse correlation between chiasma frequency and alternate co-orientation; therefore, genotypes with a high chiasma frequency co-orientate in zig-zag with a low proportion. Genotypical control of chiasma frequency variation was demonstrated by SUN and REES (1964) by a diallel cross.

Using the same material as Thompson (*l. c.*); that is, rye inbred lines, LAWRENCE (1958) increased the alternate co-orientation frequency of interchange heterozygotes by about 10 per cent from F_3 to F_4 . This increase resulted indirectly from selection within families for high

self-fertility. Since cultivar Ailés has been cultivated without interruption for many years, it is logical to think that on selecting for the character «yield» (in fact it is closely related to fertility) a correlated response for the character «alternate co-orientation» might have occurred, as pointed by LAWRENCE (1963).

On his hand, SUN and REES (1967) pointed out that the selection for high and low frequencies of alternate co-orientation of quadrivalents at first metaphase was effective in giving rise to distinct lines showing relatively high and low zig-zag co-orientation. They also found that the variation in alternate co-orientation frequency is negatively correlated with chiasma frequency, thus corroborating previous results (REES and SUN, 1965).

In further investigations we will analyze the cytogenetical mechanisms which maintain the chromosomal polymorphism in the cultivar Ailés and identify the chromosomes involved in the rearrangements.

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R E S U M E N

Se analiza la estructura citogenética de una población natural de centeno cultivado, *Secale cereale* L. cultivar Ailés, en sendas muestras de dos generaciones consecutivas. El porcentaje de heterocigosis estructural es de un 21 por 100, existiendo, por lo menos, dos translocaciones diferentes en la población original. Se discuten las observaciones realizadas bajo la perspectiva de la ortoselección cariotípica.

S U M M A R Y

Two samples belonging to two successive generations of a natural population of cultivated rye, *Secale cereale* L. cultivar Ailés, were cytologically analyzed. Chromosomal polymorphism by reciprocal translocations has been detected. In both generations a 21 per cent of

structural heterozygotes was found. The intraspecific chromosomal polymorphism is discussed as an expression of the karyotypic orthoselection phenomenon.

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