

Substitution of rye chromosome 5R for its three wheat homoeologues*

BY L. M. BIELIG† AND C. J. DRISCOLL

*School of Botany, University of New South Wales, Kensington,
N.S.W., Australia*

(Received 14 July 1970)

SUMMARY

Chromosome 5R of *Secale cereale* var. Imperial has been substituted for chromosomes 5A, 5B and 5D of hexaploid wheat. There is evidence of compensation, in terms of vigour, in all substitution lines. Chromosome 5R rectifies the male sterility of nullisomics 5A and 5D; however, it is unable to circumvent the meiotic irregularity and male sterility of 5B-deficient stocks. Another instance of wheat-rye chromosome pairing, in the absence of chromosome 5B, is reported. The data reported here demonstrate that the long arm of 5R is the more essential arm and indicate that chromosome 5R is homoeologously related to the group 5 chromosomes of wheat.

1. INTRODUCTION

'Alien' chromosomes, from other genera in the sub-tribe Triticinae, can be substituted for their homoeologues in hexaploid wheat. The specificity of alien substitution has been established by Riley (1963), Johnson (1966) and Riley, Chapman & Macer (1966). Each of these investigators found that selected alien chromosomes would substitute for the chromosomes of only one homoeologous group in wheat. Jenkins (1966) and Wienhues (1966) reported the substitution of a single alien chromosome for the wheat chromosomes of several different homoeologous groups. However, these substitutions were not cytologically verified; consequently the concept of specific substituting ability is more widely held than that of general substituting ability.

Kattermann (1937), O'Mara (1946) and Smith (1963) have shown that the rye chromosome which bears the marker gene for pubescent peduncle ('hairy neck', *H_p*) is genetically related to chromosome 5A of wheat. Hence, this chromosome is designated '5R'. Bielig & Driscoll (1970) substituted chromosome 5R^L for 5B. The substitution line exhibited irregular meiotic pairing which included wheat-rye chromosome pairing. The research reported on in this paper involves further substitutions in this series, namely, substitution of chromosome 5R or a 5R mis-division product for chromosomes 5A, 5B and 5D, respectively. The genetic compensation observed in each of these substitution lines substantiates the view

* This study is part of a project supported by a Rural Credits Development Fund Grant, Reserve Bank of Australia.

† Supported by a Wheat Industry Research Council Post-Doctoral Fellowship.

that this rye chromosome is a member of homoeologous group 5. Furthermore, it is established that the entire chromosome 5R is unable to restrict pairing to homologous chromosomes.

2. MATERIALS AND METHODS

Monosomic and telocentric lines used were of the variety Chinese Spring. The rye addition lines involved the addition of a single chromosome of *Secale cereale* var. Imperial to Chinese Spring. All these stocks were provided by courtesy of Dr E. R. Sears, U.S.D.A., Missouri.

Monosomic 5A was pollinated by the monotelocentric addition line involving the long arm of 5R ($21''W + t'5R^L$). This is the arm which bears the gene for hairy neck. Monosomic 5B was pollinated by the disomic addition line ($21''W + 1''5R$). Monoisomic 5D was pollinated by the monotelocentric addition line ($21''W + t'5R^L$) and by the monosomic addition line ($21''W + 1''5R$). Consequently, four different F_1 populations were scrutinized. All F_1 individuals having pubescent peduncles were cytologically examined. Individuals simultaneously monosomic for a wheat chromosome (i.e. 5A, 5B or 5D) and monosomic for the alien chromosome were allowed to self-pollinate. Substitution individuals were subsequently isolated by cytological examination of F_2 individuals which exhibited the hairy neck trait. Chromosome 5R shows a dosage effect and F_2 plants were classified as either heavily pubescent ($H_p H_p$) or lightly pubescent ($H_p -$).

The putative 5A and 5D substitution lines were crossed to ditelocentrics 5A and 5D respectively. Failure of the wheat telocentric to pair in the resulting hybrids indicates that the required chromosome had been replaced.

The degree of compensation affected by the alien chromosome was determined by a comparison, in terms of vigour and fertility, between the substitution line, the corresponding nullisomic, and euploid Chinese Spring.

(i) *Morphology of chromosome 5R*

Chromosome 5R is heterobrachial, the subterminal centromere being one-quarter of the way along the chromosome. The entire monosome has a distinctive median constriction, which is seen in the long arm telocentric as a constriction one-third of the way from the centromere.

3. RESULTS AND DISCUSSION

(i) *Substitution for chromosome 5A*

As a result of strong selection for euploid pollen, only one of the 17 F_1 individuals examined was hairy necked. This plant had $20'' + 1' + t'$; the telocentric was cytologically recognizable as the long arm of chromosome 5R. Twenty-five F_2 progeny were examined morphologically; four were heavily pubescent and six were lightly pubescent. One of the former was found to be a ditelocentric substitution; this plant was crossed to ditelocentric 5A. All the resulting hairy necked hybrids possessed $20'' + t'5A + t'5R^L$, indicating correct substitution.

The 5R^L(5A) substitution line is extremely vigorous; tillering is more profuse than in Chinese Spring; leaves and culms are slightly narrower than in Chinese Spring, but wider than in nullisomic - 5A. Like nullisomic - 5A, the substitution plants are taller than Chinese Spring and the spike is speltoid. This indicates that chromosome 5R lacks the Q gene, or has a less powerful Q gene than chromosome 5A of Chinese Spring. This is consistent with Muramatsu's (1968) observation that 5R^L has a duplicate of the spelta gene, q.

The substitution line, with a mean seed set of 1.2 grains per spikelet, is 70.6% as fertile as Chinese Spring. Although some tip-sterility is evident, the fact that the presence of 5R^L can circumvent the male sterility of nullisomic - 5A indicates that a genetic relationship exists between chromosomes 5A and 5R^L. Furthermore, the long arm of chromosome 5R is probably the more essential arm of this chromosome, because alone it compensates well for deficiency of 5A.

(ii) Substitution for chromosome 5B

Of the ten F_1 's which resulted from crossing monosomic 5B by the disomic alien addition line, only five had a pubescent peduncle. Thus, chromosome 5R was only transmitted through 50% of the pollen; this high rate of loss indicates that strong selection operates in favour of euploid pollen which is formed as a result of asynapsis of the rye chromosomes. Four of the hairy-necked F_1 's were of the critical type, namely 20' + 1' 5B + 1' 5R. One hundred F_2 progeny were examined morphologically. Thirty-one were hairy necked, while 69 had glabrous peduncles. Twenty-eight of the 31 were lightly pubescent (*H_p* -), while three were heavily pubescent (*H_p* *H_p*). Two substitution individuals were isolated. One was a monosomic 5R (5B) substitution, the other was a heteromorphic disomic substitution, which involved the entire 5R chromosome and a telocentric for the short arm of 5R, i.e. 5R/5R^S (5B).

Bielig & Driscoll (1970) established that the long arm of chromosome 5R is unable to restrict meiotic pairing to homologous chromosomes. However, the effect of the short arm of 5R was unknown. Consequently, the pairing behaviours of the two newly isolated substitution lines were examined in detail. The results are shown in Table 1; for purposes of comparison the pairing behaviours of the 5R^L (5B) substitution and nullisomic 5B, previously reported, are also shown.

Owing to the difficulty in obtaining well-spread cells in 5B-deficient material, few cells could be scored precisely. However, it is apparent that the level of pairing was similar in the monosomic and heteromorphic disomic substitution stocks. As seen in Table 1, the frequencies of univalents, bivalents, trivalents and quadrivalents were comparable in all four 5B-deficient lines. Quinquevalents and sexivalents were observed in all three substitutions, although not always in cells which could be scored precisely.

Since all the substitutions exhibited the complex pairing behaviour characteristic of nullisomic - 5B, these data show that the entire chromosome 5R has a null effect on homoeologous pairing.

Bielig & Driscoll (1970) have demonstrated that wheat and rye chromosomes

Table 1. *Mean chromosome pairing in the 5R(5B) and 5R/5R^s(5B) substitution lines*

Plant	Cells	5R		Wheat		Trivalents	Quadri- valents	Quinque- valents	Sexi- valents
		unpaired	telocentric	unpaired	univalents				
Monosomic substitution (20 ⁿ + 1'5R)	40	0.98	—	1.40	18.05*	0.18	0.53	0.00	0.00
Heteromorphic disomic substitution (20 ⁿ + t1 ⁿ 5R/5R ^s)	12	0.75	0.75	1.75	17.90	0.41	0.41	0.00	0.00
Monotelocentric substitution (20 ⁿ + t' 5R ^L)†	60	—	0.97	1.38	17.48	0.30	0.60	0.05	0.02
Nullisomic 5B of Chinese Spring†	60	—	—	1.52	18.20	0.07	0.44	0.02	0.00

* One of these bivalents involved 5R, paired with a wheat chromosome.

† Bielig & Driscoll (1970).

are capable of pairing, in the absence of chromosome 5B. In the 5R(5B) substitution individual, the 5R monosome, which is cytologically distinctive, was observed participating in a bivalent. In this bivalent, the long arm of 5R was involved in a chiasma. In order to verify that this was wheat-rye chromosome pairing and not pairing of a wheat chromosome with a spontaneous wheat-rye translocation chromosome, the monosomic substitution individual was crossed to euploid Chinese Spring. The critical F_1 individuals were hairy necked, with a chromosome complement of $20'' + 1'' 5B + 1' 5R$. In 250 cells examined, the 5R monosome remained unpaired, thus verifying another instance of wheat-rye pairing.

The nullisomic-5B individual was dwarfed, with short spikes and extremely narrow leaves and culms. By comparison, the monosomic and heteromorphic disomic substitutions were as vigorous as Chinese Spring, being normal in height, tillering and width of leaves and culms. The spikes of the 5B substitution lines were larger than those of Chinese Spring. As in addition lines involving 5R or $5R^L$, the spikes were extremely lax and emerged laterally from the sheath. There was no obvious phenotypic differences between these two substitutions and the $5R^L(5B)$ substitution described previously (Bielig & Driscoll, 1970). This substantiates the view that the more essential genes are located on the long arm of chromosome 5R.

Although chromosome 5R compensates well for chromosome 5B in vigour, it is unable adequately to rectify the male sterility of 5B-deficient lines. The monosomic and heteromorphic disomic substitutions were respectively 9.4 and 1.1% as fertile as Chinese Spring, grown under comparable glasshouse conditions. Their respective seed sets were 5 grains in 31 spikelets and 1 grain in 50 spikelets.

Table 2. *Transmission of chromosome 5R and its misdivision products, on selfing plants having $20'' + 1' 5D + 1' 5R$ and $20'' + 1' 5D + t' 5R^L$*

F_2 from selfing	Dosage of H_p	No. of individuals	Total transmission of	
			5R entire	5R telocentric or isochromosome
(a) $20'' + 1' 5D + t' 5R^L$	2	0	—	0
	1	5	—	5 (5R ^L telo)
	0	45	—	*
Total		50		5
(b) $20'' + 1' 5D + 1' 5R$	2	3	6	0
	2	1	0	1 (5R ^L iso)
	1	10	10	0
	1	3	0	3 (5R ^L telo)
	1	2	2	2 (5R ^S telo)
	1	1	0	2 (5R ^L and 5R ^S telos)
	0	25	*	*
Total	—	45	18	8

* The plants with glabrous peduncles were not examined cytologically. 5R or 5R^L could not have been present, however 5R^S may have been.

(iii) *Substitution for chromosome 5D*

The two F_1 populations which resulted from crossing monoisomic 5D by the monotelocentric (long) and monosomic additions of chromosome 5R segregated pubescent peduncle: glabrous peduncle in the ratios of 3:18 and 3:23, respectively. Hairy-necked individuals monosomic for 5D and the alien chromosome were allowed to self-pollinate. The F_2 involving $5R^L$ included five individuals with lightly pubescent peduncles ($Hp -$) and 45 with glabrous peduncles. In contrast, the F_2 involving 5R entire included 20 individuals with pubescent peduncles (16 $Hp -$ and 4 $Hp Hp$) and 25 individuals with glabrous peduncles. One monosomic 5R(5D) substitution was isolated, but no telocentric substitution was obtained. Cytological analysis of the two F_2 populations (see Table 2) showed that, in the population involving $5R^L$, the telocentric was transmitted to only five of the 50 individuals examined. However, 5R, or a misdivision product of it, was transmitted to 26 of the 45 individuals which resulted from selfing F_1 's with $20'' + 1'5D + 1'5R$. The marked difference in the transmission rates of 5R entire and the $5R^L$ telocentric indicates that monosomic substitution pollen ($20'' + 1'5R$) competes more strongly against the other types of pollen formed than does telocentric substitution pollen ($20'' + t'5R^L$). The occurrence of eight 5R - misdivision products among the 20 hairy-necked F_2 's in the second population reflects a high rate of misdivision of the 5R univalent.

The one monosomic substitution individual was crossed to ditelocentric 5D. The hairy-necked 42 chromosome F_1 's had $20'' + t'5D + 1'5R$, indicating correct substitution.

Chromosome 5R compensates well for the poor vigour of nullisomic - 5D. As regards tillering, height, spike length and width of leaves and culms, the substitution line is comparable with Chinese Spring. The male sterility of nullisomic 5D is rectified, seed set being 1.1 grains per spikelet or 64.7% that of Chinese Spring. As the substitution line is very late to mature, chromosome 5R must lack the gene(s) for earliness which 5D possesses.

Chromosomes $5R^L$ and 5R entire compensate well, in terms of fertility, for chromosomes 5A and 5D, respectively. These two chromosomes in turn compensate for 5B, because nullisomic 5B tetrasomic 5A and nullisomic 5B tetrasomic 5D are fertile. However, neither $5R^L$ nor 5R compensates for 5B. This apparent anomaly could be explained if it is assumed that the group 5 chromosomes differ quantitatively in their importance in maintaining normal fertility. Chromosomes 5A and 5D may be less essential than 5B but more essential than 5R, so that while $5R^L$ and 5R compensate for 5A and 5D, a higher dosage of 5R may be required, in combination with nullisomy -5B, to restore fertility to normal. However, observations on a number of nullisomic-disomic and nullisomic-tetrasomic combinations involving the group 5 homoeologous and chromosome 5R are required in order to verify such a system.

REFERENCES

- BIELIG, L. M. & DRISCOLL, C. J. (1970). Substitution of rye chromosome 5R^L for chromosome 5B of wheat and its effect on chromosome pairing. *Genetics* **65**, 241–247.
- JENKINS, B. C. (1966). *Secale* additions and substitutions to common wheat. *Proceedings of the 2nd International Wheat Genetics Symposium. Hereditas* (Supplement) **2**, 301–312.
- JOHNSON, R. (1966). The substitution of a chromosome from *Agropyron elongatum* for chromosomes of hexaploid wheat. *Canadian Journal of Genetics and Cytology* **8**, 279–292.
- KATTERMANN, G. (1937). Zur cytologie halmbehaarter Stämme aus Weizenroggenbastardierung. *Züchter* **9**, 196–199.
- MURAMATSU, M. (1968). Studies on translocations between hairy neck chromosome of rye and chromosomes which belong to homoeologous group 5 of common wheat. *Proceedings of the XIIth International Congress of Genetics* **1**, 180.
- O'MARA, J. G. (1946). The substitution of a specific *Secale cereale* chromosome for a specific *Triticum vulgare* chromosome. *Records of the Genetics Society of America* **15**, 62–63.
- RILEY, R. (1963). Cytogenetics and plant breeding. *Proceedings of the XIth International Congress of Genetics* **3**, 681–688.
- RILEY, R., CHAPMAN, V. and MACER, R. C. F. (1966). Homoeology of an *Aegilops* chromosome causing stripe rust resistance. *Canadian Journal of Genetics and Cytology* **8**, 616–630.
- SMITH, J. D. (1963). The effect of chromosome number on competitive ability of hexaploid wheat gametophytes. *Canadian Journal of Genetics and Cytology* **5**, 220–226.
- WIENHUES, A. (1966). Transfer of rust resistance of *Agropyron* to wheat by addition, substitution and translocation. *Proceedings of the 2nd International Wheat Genetics Symposium. Hereditas* (Supplement) **2**, 328–341.