Theor Appl Genet (1987) 73:403–409

The effect of the crossability loci *Kr1* and *Kr2* on fertilization frequency in hexaploid wheat × maize crosses

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Received July 11, 1986; Accepted August 31, 1986
Communicated by R. Riley

Summary. Dominant alleles of the *Kr1* and *Kr2* genes reduce the crossability of hexaploid wheat with many alien species, including rye and *Hordeum bulbosum*, with *Kr1* having the greater effect. However, a cytological study of wheat ovaries fixed 48 h after pollination showed that the wheat genotypes 'Highbury' (*Kr1, Kr2*) and 'Chinese Spring (Hope 5B)' (*Kr1, kr2*) were crossable with 'Seneca 60' maize, fertilization occurring in 14.4 and 30.7% of embryo sacs respectively. The latter figure was similar to the 29.7% fertilization found in 'Chinese Spring' (*kr1, kr2*). Most embryo sacs in which fertilization occurred contained an embryo but lacked an endosperm and where an endosperm was formed it was usually highly aberrant. All three wheat × maize combinations were karyotypically unstable and rapidly eliminated maize chromosomes to produce haploid wheat embryos.

Key words: Wheat – Maize – Crossability genes – Chromosome elimination – Haploids

Introduction

Lein (1943) identified two genes, *Kr1* and *Kr2*, which had major effects on the crossability of hexaploid wheat (*Triticum aestivum*) with rye (*Secale cereale*). Dominant alleles of either gene reduced crossability, with *Kr1* having the greater effect.

Chromosome substitution studies have shown that wheats carrying *Kr1*, located on the long arm of chromosome 5B (Lange and Riley 1973; Sitch et al. 1985), have low seed set when pollinated with rye (Riley and Chapman 1967; Falk and Kasha 1981, 1983) and little or no seed set when pollinated with *H. bulbosum* (Snape et al. 1979; Falk and Kasha 1981, 1983; Sitch et al. 1985). Wheats carrying *Kr2*, located on the long arm of chromosome 5A (Sitch et al. 1985), show a less dramatic reduction in crossability with rye (Riley and Chapman 1967; Falk and Kasha 1981, 1983; Sitch et al. 1985) and remain crossable with *H. bulbosum* (Snape et al. 1979; Falk and Kasha 1981, 1983; Sitch et al. 1985), albeit usually at a reduced frequency. *Kr1* and *Kr2* act independently since their effects are manifest in single chromosome substitution lines and wheats carrying both alleles have extremely low crossability (Lein 1943; Krolow 1970; Falk and Kasha 1983).

The *Kr* genes act by inhibiting alien pollen tube growth at the base of the style and in the transmitting tract of the wheat ovary in both wheat × rye (Lange and Wojciechowska 1976; Jalani and Moss 1980) and wheat × *H. bulbosum* (Snape et al. 1980; Sitch 1984) crosses. Increased dosage of either *Kr1* or *Kr2* reduces crossability (Falk and Kasha 1983) but increased dosage of *kr1* or *kr2* fails to promote crossability (Riley and Chapman 1967; Falk and Kasha 1983). This suggests that *Kr1* and *Kr2* actively inhibit crossability and that *kr1* and *kr2* are null alleles.

The hexaploid wheat 'Chinese Spring' carries the recessive alleles *kr1* and *kr2* and is readily crossed with many alien species including maize (*Zea mays*) where embryos were found in 22% of florets (Laurie and Bennett 1986). Rapid elimination of maize chromosomes produced haploid wheat embryos, and in this respect the two crosses previously investigated resembled that between 'Chinese Spring' and *H. bulbosum* (Barclay 1975). However, in the wheat × maize crosses, endosperm was either not formed or was highly aberrant.

It is of interest to determine the effect of the *Kr* genes on wheat × maize crosses for two reasons. Firstly, haploid production via chromosome elimination in *H. vulgare* × *H. bulbosum* crosses has been widely used in barley breeding programs (Kasha and Reinbergs 1981; Snape 1982) but the exploitation of uniparental chromosome elimination in wheat × *H. bulbosum* crosses for wheat haploid production has been prevented because of the presence of *Kr1* and *Kr2* in many cultivated wheats (Riley and Chapman 1967; Snape et al. 1979; Falk and Kasha 1981, 1983). This problem might be overcome if maize could hybridize with wheats carrying *Kr1*, or *Kr1* and *Kr2*.

Secondly, it would be of great interest to transfer maize DNA, including active transposable elements, into wheat and this would be made considerably easier if karyotypically stable hybrids could be produced. The frequency of hybrid versus haploid production in *H. vulgare* × *H. bulbosum* crosses is known to be influenced by parental genotype (Simpson et al. 1980; Pickering 1983, 1984) and genes which affect the elimination of *H. bulbosum* chromosomes have been assigned to chromosomes 2 and 3 of *H. vulgare* (Ho and Kasha 1975). If maize could be hybridized with wheats carrying *Kr* genes the number of potential wheat parents which could be used in hybridization experiments would be greatly increased and this might improve the likelihood of recovering karyotypically stable hybrids.

Materials and methods

a) Plant stocks

Three genotypes of hexaploid wheat (*Triticum aestivum* L. 2n = 6x = 42 AABBDD) were selected for study.

1) 'Chinese Spring', homozygous for *kr1* and *kr2*.
2) 'Chinese Spring (Hope 5B)', a chromosome substitution line produced by E.R. Sears, University of Missouri, U.S.A. in which the 'Chinese Spring' 5B chromosome has been replaced by 5B from 'Hope', a variety showing low crossability with rye. This substitution line is therefore homozygous for *Kr1* and *kr2*.
3) 'Highbury', a spring wheat cultivar homozygous for *Kr1* and *Kr2*.

These three wheats were used as female parents in crosses with the single-cross F_1 hybrid sweetcorn 'Seneca 60' (*Zea mays* L. 2n = 20) and with the diploid rye cultivar 'Petkus Spring' (*Secale cereale* L. 2n = 14).

b) Pollination methods

Plants were grown in a heated greenhouse under continuous light. Wheat and rye plants were transferred to a 20 °C growth cabinet with continuous light approximately one week prior to anthesis in the leading tiller. For each of ten plants of each wheat cultivar the first spike to emerge was emasculated one to two days prior to anthesis as described by Riley and Chapman (1967). One to two days later, when the stigmas had become feathery, they were pollinated with 'Seneca 60'. Maize pollen was collected by allowing segments of tassel standing in water filled test-tubes to anthese over silver foil. The tassel was tapped to release pollen which was then transferred to the wheat stigmas using a small camel hair brush. Pollinations were made within ten minutes of pollen release. The second spike to emerge was prepared similarly, but was pollinated with 'Petkus Spring' rye. Emerging rye anthers were picked up with fine forceps and the pollen shaken out over the wheat stigma.

c) Light microscopy of embryo sac contents

Ovaries were removed from the ears 24 or 48 h after pollination, fixed in 3 : 1 ethanol/acetic acid and stored at 4 °C. For analysis the ovaries were rinsed in distilled water for 5 min, hydrolysed in 1N HCl at 60 °C for 12 min, rinsed in distilled water and Feulgen stained for 2 h at room temperature. Ovaries were then rinsed in sulphur dioxide water for 10 min and transferred to distilled water. Embryo sac contents were dissected out in distilled water with the aid of a stereo microscope and the remaining tissue was discarded. A cover-slip, supported at one side by a second cover-slip, was placed over the specimen which was then flooded with 45% acetic acid. The unsquashed preparation was examined to determine whether a maize pollen tube had penetrated the micropyle and whether fertilization of either the egg cell or the polar nuclei had occurred. Recognising unfertilized egg cells and polar nuclei was found to be greatly aided by observing the tissue in this unsquashed state. For further analysis, such as the detection of micronuclei, the slide was flooded with 1% acetic orcein and the supporting cover-slip was removed to flatten the specimen. The number of cells in the embryo and endosperm was recorded wherever possible, all stages of mitosis being scored as one cell.

d) Comparisons of fertilization frequency

Analysis of variance was used to test the significance of differences in fertilization frequency after converting the data for percentage fertilization from individual spikes to angles (Snape et al. 1979).

Results

a) The hybrid origin of embryos in wheat × maize crosses

The 4C nuclear DNA contents of 'Chinese Spring' wheat and 'Seneca 60' maize are 69.3 pg and 9.84 pg (Bennett and Smith 1976; Laurie and Bennett 1985, respectively), while relative chromosome size within the respective genomes shows a 1.5 and 2 fold variation (Furuta et al. 1984; Bennett, unpublished). 'Highbury' and 'Chinese Spring (Hope 5B)' are expected to have nuclear DNA contents close to the value for 'Chinese Spring'. Thus the smallest wheat chromosome is expected to be about twice the size of the largest maize chromosome in all three crosses. As in previous work (Laurie and Bennett 1986), zygotes at metaphase obtained from spikes fixed approximately 24 h after pollination contained the expected F_1 combination of 21 large wheat chromosomes and 10 small maize chromosomes, confirming the hybrid origin of the embryos.

b) The frequency of fertilization in wheat × maize crosses

Examination of a total of 615 ovaries fixed 48 h after pollination showed that fertilization occurred in all three wheat genotypes (Table 1). This is illustrated in Fig. 1 which shows the overall percentage of fertilization (i.e. the percentage of embryo sacs per spike with fertilization of the egg cell, polar nuclei or both) for each plant of each genotype in conjunction with that plant's figure for the overall percentage of fertilization with 'Petkus Spring' rye.

For 'Chinese Spring (Hope 5B)' (*Kr1, kr2*) and 'Chinese Spring' (*kr1, kr2*) the results were very similar.

Table 1. Wheat × maize. Number of ovaries examined and frequency of fertilization in ten spikes of each wheat genotype

No. of ovaries	'Highbury' × 'Seneca 60'		'Chinese Spring (Hope 5B)' × 'Seneca 60'		'Chinese Spring' × 'Seneca 60'	
	n	%	*n*	%	*n*	%
Total	194		189		232	
Unfertilized	146	75.3	67	35.4	89	38.4
Unfertilized but with a maize pollen tube within the embryo sac	20	10.3	64	33.9	74	31.9
Containing only an embryo	19	9.8	36	19.0	55	23.7
Containing only an endosperm	0	0.0	7	3.7	4	1.7
Containing an embryo and an endosperm	9	4.6	15	7.9	10	4.3
Total containing an embryo	28	14.4	51	27.0	65	28.0
Total containing an endosperm	9	4.6	22	11.6	14	6.0
Total fertilized	28	14.4	58	30.7	69	29.7

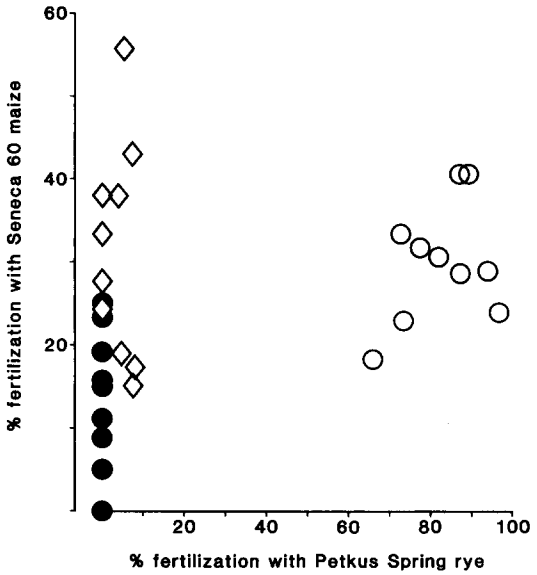

Fig. 1. Overall percentage of fertilization in each of ten plants of 'Highbury' (*Kr1, Kr2* ●), 'Chinese Spring (Hope 5B)' (*Kr1, kr2* ◇) and 'Chinese Spring' (*kr1, kr2* ○). N.B.: Two 'Highbury' points fall at 25% on the vertical axis

Maize pollen tubes, easily recognised by their large size and distinct outline, reached 64.6 and 61.6% of the embryo sacs respectively and successfully fertilized the egg cell, polar nuclei or both in almost half of these cases. The results for 'Chinese Spring (Hope 5B)' showed more between spike variation than those from 'Chinese Spring' (Fig. 1), but neither the mean frequency of embryo formation (27.0 and 28.0%, respectively) nor the mean total frequency of fertilization (30.7 and 29.7%, respectively) was significantly different. The only difference detected was that a higher proportion of polar nuclei were fertilized in 'Chinese Spring (Hope 5B)' compared with 'Chinese Spring' (11.6 versus 6.0% respectively, $P < 0.05$). Thus while maize pollen tubes reached the embryo sacs of 'Chinese Spring (Hope 5B)' and 'Chinese Spring' with equal frequency, and while the egg cells were fertilized with equal frequency, fertilization of the polar nuclei was more successful in 'Chinese Spring (Hope 5B)'.

In 'Highbury' (*Kr1, Kr2*) × 'Seneca 60' crosses pollen tubes reached 24.7% of embryo sacs. The frequency of embryo formation (14.4%) and the total frequency of fertilization (14.4%) were about half the values obtained for 'Chinese Spring (Hope 5B)' and 'Chinese Spring', this difference being significant for both comparisons ($P < 0.01$). The frequency with which the polar nuclei were fertilized appeared to be similar to that observed in 'Chinese Spring (Hope 5B)'. Although the frequency of fertilization in 'Highbury' was lower than in either of the other two genotypes, only one spike was found in which no fertilization had occurred (Fig. 1). This is unlikely to have been an effect of genotype since two spikes from the same plant analysed in subsequent experiments contained embryos, one at a frequency of 11/28 florets (39.3%), the highest frequency recorded for any 'Highbury' ear.

c) The extent of embryo and endosperm development in wheat × maize crosses 48 h after pollination

In all three crosses the cytological events observed 48 h after pollination were similar. All but one embryo had undergone at least two rounds of cell division to produce four cells and most (112/127, 88.2%) had eight or more cells (Table 2). The cell numbers were similar to those of parental selfs of the same age. However, hybrid embryos invariably showed chromosome elimination (Fig. 2a–c) which was due to the failure of maize chromosomes to attach to the spindles during mitoses (Fig. 2d). This suggests that the mechanism of elimination is similar to that observed in *Hordeum* hybrids (Finch and Bennett 1983). Elimination occurred early in embryo development since micronuclei (Fig. 2e) were present in every embryo with 4 or more cells, and mitotic figures from embryos with 8 cells or more invariably showed only 21 wheat sized chromosomes (Fig. 2f).

All three crosses showed a low frequency of endosperm formation (Table 1) and where an endosperm was produced it invariably contained an abnormally low number of nuclei (1 to 124, Table 2) compared to 'Chinese Spring' selfs of the same age (Bennett et al. 1973). Furthermore, wheat × maize endosperms often showed a marked asynchrony of cell cycle stage and frequently displayed cytological abnormalities such as chromatin bridges (Fig. 2g), misshapen cells, elimination of maize chromosomes and the presence of micronuclei. The reason for the low number of nuclei in even the least aberrant wheat × maize endosperms is unknown.

d) The frequency of fertilization in wheat × rye crosses

The results of the wheat × rye crosses were as expected, confirming the presence of alleles for reduced crossability in the 'Highbury' and 'Chinese Spring (Hope 5B)' stocks used in the present experiment (Table 3, Fig. 1). No fertilization was seen in any of the 10 'Highbury' ears examined, while in 'Chinese Spring (Hope 5B)' fertilization occurred in only 4.3% of florets. 'Chinese Spring', lacking either *Kr1* or *Kr2*, had an overall frequency of fertilization of 83.3%. That fertilization was the result of pollination by rye was confirmed by a chromosome count, where possible, and by the presence in the endosperm of aberrant nuclei typical of wheat × rye hybrids (Kaltsikes et al. 1974; Bennett 1977).

Discussion

a) The effect of Kr genes on the frequency of fertilization in wheat × maize

The present results show that the wheat genotypes 'Chinese Spring' (*kr1, kr2*), 'Chinese Spring (Hope 5B)' (*Kr1, kr2*) and 'Highbury' (*Kr1, Kr2*) can be repeatably hybridized with 'Seneca 60' maize.

The data from the 'Chinese Spring (Hope 5B)' × 'Seneca 60' and 'Chinese Spring' × 'Seneca 60' crosses show that the 'Hope' 5B chromosome substitution had little or no effect on either the frequency with which maize pollen tubes reached the embryo sac (64.6 and

Table 2. The number of embryo cells and endosperm nuclei per floret in developing wheat × maize crosses 48 h after pollination

		'Highbury' × 'Seneca 60'	'Chinese Spring (Hope 5B)' × 'Seneca 60'	'Chinese Spring' × 'Seneca 60'
No. of cells per embryo	max	10	16	22
	min	4	2	2
	mean	7.9	11.4	11.6
	No. of embryos scored	21	46	60
No. of nuclei per endosperm	max	43	124	72
	min	1	1	1
	mean	27.0	39.1	22.9
	No. of endosperms scored	8	19	13

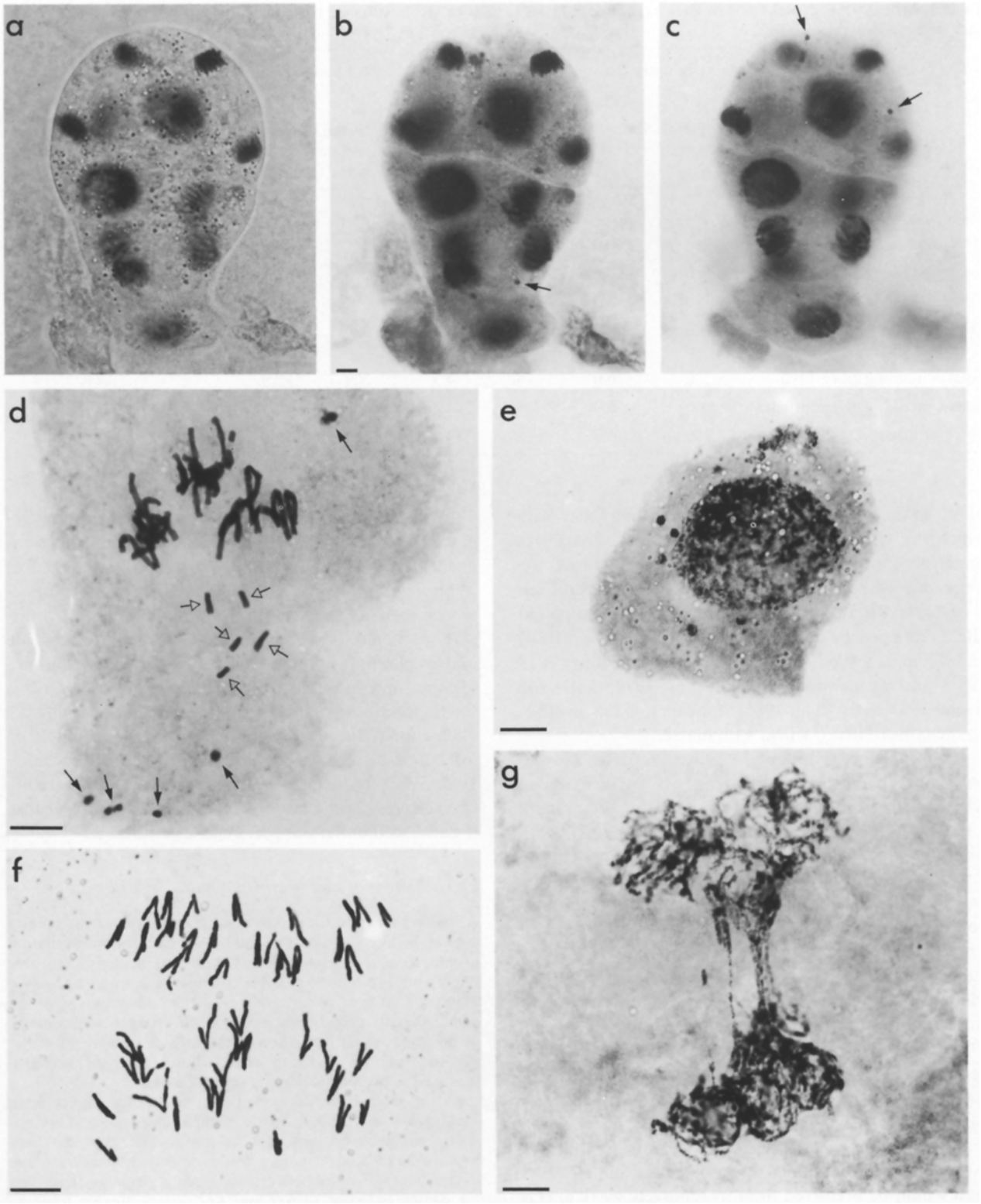

Fig. 2a–g. 'Chinese Spring' × 'Seneca 60' crosses fixed 48 h after pollination. Feulgen stained embryo (**a**) in which micronuclei (*examples arrowed*) can be seen after additional acetic orcein staining (**b, c**). (**d**) Cell from a 6 celled embryo with micronuclei (*solid arrows*) and 5 maize chromosomes (*open arrows*) which have apparently failed to attach to the spindle. (**e**) Micronuclei in a cell from an 8 celled embryo. (**f**) Anaphase cell from an 8 celled embryo with 21 wheat chromosomes moving to each pole and no maize chromosomes. (**g**) Chromatin bridges between two endosperm nuclei. All bars represent 10 μm

Table 3. Wheat × rye. Number of ovaries examined and frequency of fertilization in ten spikes of each wheat genotype

No. of ovaries	'Highbury' × 'Petkus Spring'		'Chinese Spring (Hope 5B)' × 'Petkus Spring'		'Chinese Spring' × 'Petkus Spring'	
	n	%	*n*	%	*n*	%
Total	261		184		252	
Unfertilized	261	100.0	176	95.7	42	16.7
Containing only an embryo	0	0.0	0	0.0	2	0.8
Containing only an endosperm	0	0.0	0	0.0	1	0.4
Containing an embryo and an endosperm	0	0.0	8	4.3	207	82.1
Total containing an embryo	0	0.0	8	4.3	209	82.9
Total containing an endosperm	0	0.0	8	4.3	208	82.5
Total fertilized	0	0.0	8	4.3	210	83.3

61.6% of florets, respectively), or on the frequency with which the egg cell was fertilized (27.0 and 28.0%, respectively), although it did appear to increase the frequency with which the polar nuclei were fertilized (11.6 and 6.0%, respectively). Thus *Kr1*, the most potent allele reducing the crossability of wheat with rye (Riley and Chapman 1967; Falk and Kasha 1983; Sitch et al. 1985) and *H. bulbosum* (Snape et al. 1979; Falk and Kasha 1983; Sitch et al. 1985), appears to have no effect on the crossability of wheat with maize.

In contrast the 'Highbury' × 'Seneca 60' cross showed both a reduction in the frequency with which pollen tubes reached the embryo sac (to 24.7% of florets) and a reduction in the frequency of fertilization (to 14.4%). Although it cannot be proven from the present data this may have been due to the combined action of *Kr1* and *Kr2*. If so, this would imply a threshold for inhibition of the maize pollen tubes which was only reached when *Kr1* and *Kr2* were present. Alternatively 'Highbury' could have a more powerful *Kr1* allele than 'Hope' since there may be allelic variation for reduced crossability at the *Kr* loci (Falk and Kasha 1983; Sitch 1984). There could also be species specific interactions between alien pollen tubes and the *Kr* genes since *Kr2* has been reported to have a greater inhibitory effect on the pollen tubes of rye than on those of *H. bulbosum* (Falk and Kasha 1983). It is therefore possible that *Kr2* exerts a greater inhibitory effect on maize pollen tubes than would be predicted from its relatively weak effects on the pollen tubes of rye and *H. bulbosum*. A third alternative is that the reduced crossability with 'Highbury' was due to genes other than *Kr1* and *Kr2*. Further experiments would be needed to test these possibilities.

What is clear, however, is that as fertilization occurred in 14.3% of 'Highbury' florets despite the presence of *Kr1* and *Kr2* it will probably be possible to hybridize maize with a wide range of wheats irrespective of their *Kr* gene status. The success of such hybridizations could be influenced by the genotype of the maize parent as genetic variation exists within rye (Tanner and Falk 1982) and *H. bulbosum* (Sitch 1984) for the ability to set seed on wheat plants carrying *Kr* alleles for reduced crossability. If the same holds true for maize it may be possible to find genotypes which give higher frequencies of fertilization since 'Seneca 60' was selected for the present experiments simply because it grows well under our greenhouse conditions.

b) The potential uses of wheat × maize hybridization

A major barrier to the recovery of plants from wheat × maize crosses is likely to be the failure of endosperm formation (Zenkteler and Nitzsche 1984; Laurie and Bennett 1986; this paper) but it might be possible to mitigate this and to recover plants via embryo culture. In this context the genotype of the wheat parent could be important since the highest frequency of polar nuclei fertilization and the highest number of nuclei per endosperm were found when 'Chinese Spring (Hope 5B)' was used as the female parent (Tables 1 and 2).

If a method is developed for recovering plants from wheat × maize crosses then the elimination of maize chromosomes could be exploited for the production of wheat haploids. Wheat × maize crosses could offer a major advantage over wheat × *H. bulbosum* crosses since it appears that even the combined action of *Kr1* and *Kr2* cannot prevent fertilization when maize is used as the male parent.

Furthermore, it has been shown that the genotype of the *bulbosum* parent can affect the viability of haploid wheat embryos from wheat × *H. bulbosum* crosses (Sitch 1984). It has been suggested that rapid uniparental chromosome elimination is advantageous in these circumstances and in wheat × *H. vul-*

gare crosses (Finch and Bennett 1982) since the embryo reaches the balanced condition of a haploid wheat genome early in development. Wheat × maize crosses might therefore be expected to produce viable haploid embryos since the elimination of maize chromosomes in the crosses so far investigated has been very rapid, and appears to have been complete in the first three cell cycles.

This rapid elimination of maize chromosomes is, however, disadvantageous to our main aim of transferring maize genes, including active transposable elements, into wheat via sexual hybridization. It may be possible to incorporate segments of maize chromosome into wheat by inducing translocations prior to chromosome elimination but gene transfer would be made considerably easier if karyotypically stable hybrids could be produced. The production of stable hybrids from the stocks used in the present work seems unlikely but the inability of *Kr1* and *Kr2* to prevent fertilization by maize means that a wide range of hexaploid wheats should be available for hybridization experiments and this may enable more stable genome combinations to be found. It would also be of interest to investigate the cytological behaviour of a wider range of parental genotypes in order to determine the effect of factors such as ploidy level on the karyotypic stability of hybrids.

Acknowledgements. This work was funded by the United Kingdom Overseas Development Administration (Project R3797). We thank Dr. J. W. Snape for valuable discussion and for seed of 'Highbury' and 'Chinese Spring (Hope 5B)' and Professor D. B. Walden for seeds of 'Seneca 60'.

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