Euphytica 29 (1980) 571–579

THE SITE OF ACTION OF THE CROSSABILITY GENES (Kr_1, Kr_2) BETWEEN *TRITICUM* AND *SECALE*. I. POLLEN GERMINATION, POLLEN TUBE GROWTH, AND NUMBER OF POLLEN TUBES

B. S. JALANI[1] and J. P. MOSS[1]

Department of Agricultural Botany, University of Reading, Reading, England

Received 13 November 1979

INDEX WORDS

Triticum aestivum, wheat, *Secale cereale*, rye, site of action, crossability, pollen germination, pollen tube growth, number of pollen tubes.

SUMMARY

Seven genotypes of common wheat (*Triticum aestivum* L.) were crossed with rye (*Secale cereale* L.) in order to find the site or sites of action of the crossability genes, Kr_1 and Kr_2, of wheat. The data obtained, by fluorescence microscopy, were compared to the controls (wheat × wheat). The results indicate that the crossability genes have little effect on pollen germination and on the time taken for the pollen tubes to reach the microphyle, irrespective of their crossabilities with rye. The number of pollen tubes reaching the microphyle is, however, affected by the *Kr*-genes, as high crossable genotypes have more pollen tubes than the low crossable ones. There was a high correlation between the mean number of pollen tubes at the micropyle with seed set, which also reflects the crossability. The *Kr*-genes seem to manifest themselves in the retardation and inhibition of pollen tube growth between the style base and the top of the embryo sac, where the effect is most distinct in the low crossable genotypes.

INTRODUCTION

Hybrids between wheat (*Triticum* sp.) and rye (*Secale* sp.) which were first produced in 1875, are still being subjected to investigation as many stages in their production and establishment are not fully understood. One area where comparatively little is known is the production of the first hybrid embryo following intergeneric pollination. In general, crosses between wheat and rye succeed when wheat is the female parent, but are very difficult in the reciprocal direction. Besides, the species and even varieties have different crossabilities, and possible different causes of incompatibility, with rye. TOZU (1966) classified the varieties of *T. aestivum* (2n = 6x = 42) which he used into high (47–66%), medium (17–20%) or low (0–10%) crossabilities. LANGE & WOJCIECHOWSKA (1976) recently showed that more than 85% of the 177 varieties of *T. aestivum* which they partitioned into different crossabilities has less than 20% crossability with rye.

BACKHOUSE (1916) first showed that ready or high crossability is recessive and his

[1] *Present address*: B. S. Jalani, Genetics Unit, Universiti Kebangsaan Malaysia (The National University of Malaysia), Kuala Lumpur 22-12, Malaysia; J. P. Moss, ICRISAT, 1-11-256 Begumpet, Hyderabad-500 016, A.P., India.

result was confirmed by LEIGHTY & SANDO (1928), MEISTER & TJUMJAKOFF (1928) and TAYLOR & QUISENBERRY (1935). Among others, LEIN (1943) showed that in wheat there are two genes Kr_1 and Kr_2, which regulate the seed set when wheat is pollinated with rye. LEIN concluded that Chinese 466, a high crossable variety, is genetically $kr_1\ kr_1\ kr_2\ kr_2$, while very low crossable varieties are $Kr_1\ Kr_1\ Kr_2\ Kr_2$, and other varieties which have an intermediate level of crossability are $Kr_1\ Kr_1\ kr_2\ kr_2$. It has been concluded that the presence of Kr_1 results in a more marked reduction in crossability than that of Kr_2. RILEY & CHAPMAN (1967) used Chinese Spring, Hope and 21 Chinese Spring/Hope substitution lines to check which chromosomes controlled crossability with rye. The mean crossability of lines 5A, 5B and 5D, with a Hope chromosome substituted for the corresponding Chinese Spring chromosome was 26.2, 6.4 and 52.2% respectively, while Chinese Spring was 74.3% and Hope had nil. They concluded that in Hope, chromosome 5B carries Kr_1, and chromosome 5A carries Kr_2 and that the alternative alleles are present in Chinese Spring. They showed that Kr_1 was an inhibitor of crossability, rather than kr_1 being a promoter, and also indicated that Kr_1 and Kr_2 are either complementary or additive. LANGE & RILEY (1973) used telosomic analysis to locate Kr_1 on the long arm of chromosome 5B and also confirmed the strong effect of chromosome 5B.

It has been thought that both stigma and ovule might contribute to the differences in crossability, but TOZU (1965, 1966) claimed, on the basis of a qualitative analysis of amino acids of the wheat used, that there were no amino acid differences connected with crossability. He also concluded that the difference in crossability (high or low) was not caused by differences in pollen tube growth as claimed by BOYES & THOMPSON (1937), and ZEVEN & VAN HEEMERT (1970) found that the wheat varieties used did not differ in rate of germination of pollen grains or in rate of growth of the pollen tubes in the pistil. Previously, the evidence accumulated on the crossability between these two genera is mostly on the basis of post-fertilization developments: endosperm development and seed set (MOSS, 1965, 1970; KROWLOW, 1970). Consequently, most of what is known of the causes of low crossability between *Triticum* and *Secale* is concerned with the failure of fertilization, and endosperm breakdown leading to low seed set, or the production of shrivelled seed, or both. LANGE & WOJCIECHOWSKA (1976) and WOJCIECHOWSKA & LANGE (1977) recently showed that the poor crossability of rye with low crossable wheat varieties or genotypes resulted from absence of fertilization. They also found that the crossability genes manifested themselves through retardation and inhibition of pollen tubes at the style base and in the ovary wall. Many of the studies on pollen tube growth in wheat-rye crosses rarely quantify the differences in the number of pollen tubes in different parts of the pistil, proportion of different parts of the pistil with pollen tubes among *Triticum* and *Secale* species as well as their relationships with the degree of crossability in these crosses.

The objectives of our study were to investigate the manifestation of the *Kr*-genes on pollen germination and pollen tube growth in a wider range of varieties of hexaploid wheats crossed with rye, with the aim of elucidating and identifying the site or sites of action of the crossability genes. The results will be presented in two parts and this paper presents the results on pollen germination and pollen tubes in different parts of the pistil of various genotypes of hexaploid wheat at different intervals after pollination with rye.

MATERIALS AND METHODS

The genotypes of common wheat (*T. aestivum*, 2n = 6x = 42) used were Chinese Spring ($kr_1\ kr_1\ kr_2\ kr_2$), Hope ($Kr_1\ Kr_1\ Kr_2\ Kr_2$), Svenno ($Kr_1\ Kr_1\ Kr_2\ Kr_2$) and four substitution lines of Chinese Spring/Hope, namely CS/Hope 1B ($kr_1\ kr_1\ kr_2\ kr_2$), CS/Hope 5A ($kr_1\ kr_1\ Kr_2\ Kr_2$), CS/Hope 5B ($Kr_1\ Kr_1\ kr_2\ kr_2$) and CS/Hope 5D ($kr_1\ kr_1\ kr_2\ kr_2$). The control consisted of the pooled mean of Chinese Spring, Hope and Svenno which were selfed as well as Chinese Spring × Svenno. The rye species used was *S. cereale* cv. Petkus (2n = 2x = 14). Plants were grown under controlled conditions in the glasshouse, with an average temperature of 20 °C and a 16 h day length. Immature spikes were emasculated prior to anthesis, bagged and hand pollinated. Pistils were collected at a predetermined time after pollination and fixed in Carnoy's solution (6 absolute ethanol: 3 chloroform : acetic acid) for a few hours and stored in 70% alcohol at 1–2 °C until required.

To study pollen germination and pollen tube growth in the style, the fixed pistils were gradually brought down to water, squashed with 0.1% aniline blue (water soluble) in 0.1 N K_3PO_4 and observed with ultraviolet illumination. A Zeiss fluorescence microscope was used, with exciter filter BG3 transmitting light of wavelengt 320–400 nm, and a barrier filter transmitting light of wavelength longer than 470 nm. Under these conditions the callose of pollen tubes fluoresces and appears yellow (MARTIN, 1959). Sodium hydroxide softening as used by Martin was not necessary for the wheat and rye styles.

For the observation of the growth and behaviour of pollen tubes from the style to the micropyle (Fig. 1) the fixed pistils were dehydrated through a series of alcohols and alcohol mixtures into chloroform and embedded, five pistils to a block, for simultaneous sectioning. Sections were cut at about 20 μm, and the wax was removed in xylene and the sections gradually hydrated to water and finally stained with aniline blue. The important criteria for distinguishing pollen tubes and fluorescent sieve tubes of the materials were similar to those of MARTIN (1959), KHO & BAER (1968) and CHOU & HARBERD (1970). Observation were made, under the above fluorescence microscopy, from temporary sections only.

RESULTS

Pollen grain germination. A series of pollination was performed to ascertain the behaviour of pollen germination, at 5, 10 and 15 min after pollination. The pollen grains germinated within 5 min after pollination on the stigmatic hairs where they happen to fall. The speed of germination was similar between wheat genotypes after self-pollination (the controls) and after cross-pollination with rye. We found that there were no significant differences in the mean pollen germination between genotypes when crossed with rye or when compared with the control (wheat × wheat) at these periods (Table 1). In fact the low crossable CS/Hope 5B had the highest mean pollen germination compared to other genotypes, implying that crossability does not affect pollen germination in our material.

Table 1. Pollen germination at various intervals after pollination (*T aestivum* × *S. cereale*).

Genotypes crossed with rye		Level of crossability with rye	Pollen germination (%)			Mean
			time after pollination			
			5 min	10 min	15 min	
Chinese Spring	$kr_1\ kr_1\ kr_2\ kr_2$	hig	61.8	55.8	61.1	59.6
CS/Hope 1B	$kr_1\ kr_1\ kr_2\ kr_2$	high	57.5	66.0	67.6	63.7
CS/Hope 5D	$kr_1\ kr_1\ kr_2\ kr_2$	high	60.1	65.0	61.6	61.4
CS/Hope 5A	$kr_1\ kr_1\ Kr_2\ Kr_2$	medium	60.4	65.0	61.6	62.3
CS/Hope 5B	$Kr_1\ Kr_1\ kr_2\ kr_2$	low	63.3	64.0	68.8	65.4
Hope	$Kr_1\ Kr_1\ Kr_2\ Kr_2$	low	60.3	64.3	66.5	63.7
Svenno	$Kr_1\ Kr_1\ Kr_2\ Kr_2$	low	57.1	58.8	69.4	61.8
Control	(wheat × wheat)	–	56.5	54.4	55.5	55.5

Behaviour of pollen tubes from pollination to fertilization. Pollen grains germinated within 5 min after pollination. Within another 5 min, the pollen tubes have lengthened and can be seen traversing the styles, but the rates of growth differ, and the slow ones never reach the base of the styles. During the course of growth towards the micropyle, some tubes exhibit morphological aberrations either with swollen tips, or not having a uniform outline, or branching out in different directions. These were similar to those reported by LANGE & WOJCIECHOWSKA (1976). By 15–20 min after pollination some pollen tubes have reached the base of the style (Fig. 1).

From the style, the pollen tubes enter the body of the ovary and after traversing the full length of the S-shaped band of conducting tissue along the median line of the ovary, make contact with the cone-shaped projection of the outer integument (top of embryo sac). Here the pollen tubes leave the conducting tissue and proceed down the inner epidermis of the ovary wall and the outer integument of the ovule (Fig. 1). This portion of the path is typical in an anatropous ovule.

At the micropylar cavity, the pollen tubes may grow over the surface of the outer integument or they may follow the inner wall of the ovary for a short distance and then grow freely through the cavity to enter the micropyle. Only one penetrates the minute aperture of the nucellus into the embryo sac (Fig. 2) and discharges its nuclei, a typical condition in porogamy. At the average temperature (20°C) at which the experiments were conducted, the time taken for the first pollen to grow from the stigma to the micropyle is up to 30 min, except for the cross Hope × rye, where pollen tubes do not reach the micropyle until 45 min after pollination.

Number of pollen tubes at different parts of the pistil. The number of pollen tubes at five different points from the stigma to the micropyle was recorded at $\frac{1}{2}$, $\frac{3}{4}$, 1, 2, 6 and 12 h after pollination (Table 2). Transverse-oblique sections as shown in Fig. 3, 4, 5 and 6 were used for this purpose. It was possible, therefore, to study and compare the rate of growth and number of pollen tubes within and between genotypes as well as between times at various parts of the pistil. It can be seen that there was considerable variation in the number of pollen tubes from genotype to genotype and time to time after pollination. We found that there was no significant difference between the pooled mean of the number of pollen tubes at the five intervals after pollination at the style and base of

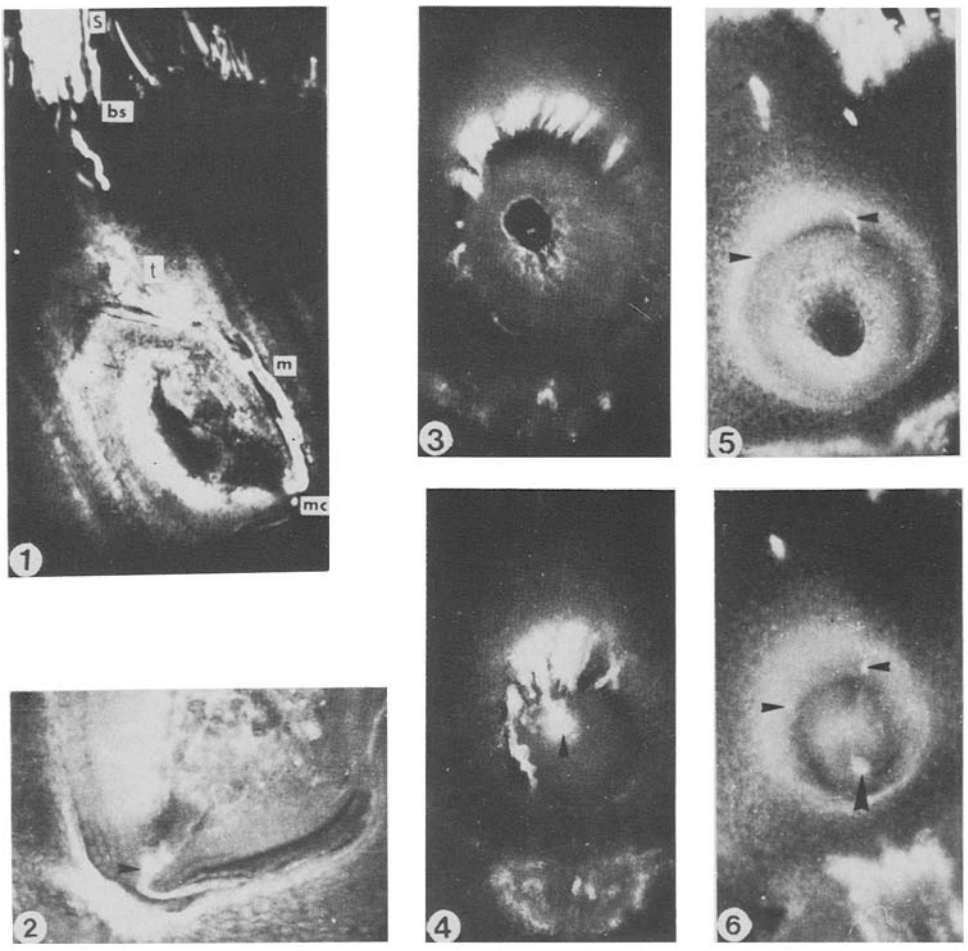

Fig. 1–6. The growth of pollen tubes. Pollen tubes in different regions of the pistil (Fig. 1, s = style, bs = base of style, t = top of embryo sac, m = mid-embryo sac, mc = micropyle).
One pollen tube (arrow) enters the micropylar aperture (Fig. 2).
Pollen tube growth in the ovary of a high crossable genotype at mid-embryo sac (Fig. 3) and at micropyle (Fig. 4), where one has entered the micropylar aperture (arrow).
Polen tube growth in the ovary of a low crossable genotype where two faintly fluorescing pollen tubes (small arrows) at mid-embryo sac (Fig. 5) and at the micropyle (Fig. 6) in which one has entered the micropylar aperture (large arrow).

styles, but was significant at the top and mid-embryo sac and micropyle. It seemed that the number of pollen tubes reaches its maximum at the top and mid-embryo sac and micropyle from 2 to 6 h after pollination, but this varies with genotypes. Since the number of pollen tubes at the micropyle was of the prime interest, more detailed analyses were undertaken at this part of the pistil.

Table 2. Mean number of pollen tubes at various parts of pistil at different intervals after pollination (*T. aestivum* × *S. cereale*).

Genotypes	Level of crossability with rye	h after pollination	Number of pistils	Parts of the pistil				
				style	base of style	embryo sac		micropyle
						top	mid	
1. Chinese Spring	High	½	20	14.9	5.5	2.2	1.0	0.8
		¾	40	17.1	5.9	1.9	1.6	1.3
		1	50	19.4	10.1	5.5	4.4	4.2
		2	60	18.2	11.6	7.6	6.3	5.0
		6	60	19.6	13.7	10.8	8.9	7.5
		12	40	19.6	12.8	9.2	8.2	7.0
2. CS/Hope 1B	High	½	20	16.8	4.5	1.4	0.5	0.5
		¾	30	19.4	11.8	6.3	5.1	5.1
		1	60	17.7	10.4	5.6	5.0	4.8
		2	60	24.8	10.1	9.9	8.9	8.1
		6	60	21.6	14.7	10.2	8.4	7.7
		12	40	20.6	14.6	10.7	8.2	6.6
3. CS/Hope 5D	High	½	20	15.8	6.4	1.0	0.6	0.6
		¾	60	15.0	5.6	1.3	0.8	0.7
		1	60	17.1	9.4	3.8	2.7	2.6
		2	60	24.2	13.5	6.7	5.1	4.8
		6	60	23.6	13.1	6.6	5.3	5.0
		12	40	19.8	11.7	7.6	6.7	5.2
4. CS/Hope 5A	Medium	½	20	15.1	6.6	0.9	0.8	0.8
		¾	60	21.7	10.4	1.3	1.0	0.9
		1	60	23.3	13.8	3.8	2.6	2.3
		2	60	24.6	10.6	2.9	2.5	2.2
		6	60	27.5	16.7	7.9	6.6	5.8
		12	40	22.8	11.5	5.1	4.1	3.8

Number of pollen tubes at the micropyle. It took 1 h for the number of pollen tubes to reach a maximum in the control (wheat × wheat) and 2–6 h for the cross-pollinated pistils irrespective of the level of crossability (Table 2). It can be seen that high crossable genotypes had more pollen tubes than the lower crossable ones. We found that there were significant differences among genotypes at a particular interval after pollination. It is worthwhile to note therefore, that there were more pollen tubes at the micropyle in the high crossable genotypes, in fact the number of the pollen tubes at this region corresponds to the level of crossability with rye.

DISCUSSION

The behaviour of pollen tubes within the pistil can be related to the crossability between wheat and rye, and to the action of the crossability genes, Kr_1 and Kr_2, in a number of ways. Firstly, the *Kr*- genes mentioned do not affect the germination of rye pollen on

Table 2. Continued.

Genotypes	Level of crossability with rye	h after pollination	Number of pistils observed	Parts of the pistil				
				style	base of style	embryo sac top	embryo sac mid	micropyle
5. CS/Hope 5B	Low	½	20	13.4	3.8	0.2	0.2	0.2
		¾	50	15.6	5.2	0.4	0.3	0.2
		1	60	19.3	6.7	1.6	0.7	0.6
		2	60	20.3	8.8	4.3	2.5	2.3
		6	60	21.3	9.1	3.9	2.4	1.9
		12	40	17.9	6.4	2.0	0.9	0.8
6. Hope	Low	½	30	13.7	2.6	0	0	0
		¾	60	17.4	5.1	0.4	0.3	0.3
		1	60	19.9	6.5	0.8	0.5	0.4
		2	60	21.5	8.0	2.1	0.9	0.8
		6	60	18.6	6.6	1.9	1.4	1.4
		12	40	16.1	4.8	0.8	0.6	0.6
7. Svenno	Low	½	30	12.9	2.4	0.4	0.3	0.3
		¾	60	14.1	3.5	0.5	0.4	0.4
		1	60	16.5	4.7	0.6	0.4	0.4
		2	60	14.9	4.6	0.8	0.7	0.7
		6	60	16.0	4.3	0.9	0.6	0.6
		12	40	17.5	4.8	0.6	0.5	0.5
8. Control (wheat × wheat)		½	20	8.8	3.8	1.7	0.8	0.8
		¾	50	8.3	4.3	2.6	2.5	2.4
		1	40	9.7	5.6	4.3	4.2	4.2
		2	50	9.4	4.9	3.4	3.3	3.3
		6	60	10.1	5.3	3.8	3.7	3.7
		12	40	12.1	6.5	4.6	4.2	3.6

wheat stigmas (Table 1). Irrespective of whether the pollen was rye or wheat, germination took place within 5 min after pollination. These results are in agreement with those of POPE (1937) on barley, TOZU (1966), ZEVEN & VAN HEEMERT (1970), MEYER (1971) and LANGE & WOJCIECHOWSKA (1976) on *Triticum* × *Secale*.

TOZU (1966) who studied the rate of pollen tube growth of rye and wheat, found that there was no evidence of difference in crossability due to the speed of pollen tube growth, for in some cases rye pollen tubes grow faster than those of wheat. In the present study, irrespective of whether the wheat genotypes are of low or high crossability with rye, the pollen tubes reached the micropyle in about 30 min, except in Hope where it took about 45 min. These results seem to be in general agreement with those of ZEVEN & VAN HEEMERT (1970), MEYER (1971), BENNETT et al. (1973) and LANGE & WOJCIECHOWSKA (1976). The time taken for the pollen tubes to reach the micropyle, however, is also affected by many factors, besides the degree of crossability, such as humidity, light, and temperature (DORSEY, 1919; BUCHLOZ & BLAKESLEE, 1927; POPE,

1943; MEYER, 1971). It would seem that *Kr*-genes have little effect on time to reach the micropyle. These results seem, therefore, to support the conclusion by LANGE & WOJCIECHOWSKA (1976) that the recessive alleles of the genes have no or little influence on the rapidity of growth of rye pollen tubes in wheat pistils.

The number of pollen tubes reaching the micropyle is affected by the *Kr*-genes, as high crossable genotypes have more pollen tubes than the low crossable ones (Table 2). According to ZEVEN & VAN HEEMERT (1970) only one pollen tube grows to the micropyle from the style though they have not seen tubes entering the micropyles. Besides, they also showed that there was no difference in pollen tube growth between cultivars of *T. aestivum*, which do not produce a viable seed when pollinated with *S. segetale*, and cv. Chinese Spring, which produces viable seeds. As a result, they conclude that the barrier is not in the stigma, style or overy wall.

Our results also show that the barrier is not in the stigma and style, but do not agree with them regarding the ovary wall. JALANI (1973) has shown that more than one pollen tube, up to 26, reach the micropyle, though only one enters the micropyle, leaving the rest outside (Fig. 2), as reported by COOPER (1938), POPE (1946), and LANGE & WOJCIECHOWSKA (1976). The diameter of the micropyle is the same as the diameter of the pollen tube, so only one tube can enter it. Our results also indicate that the most prominent place of reduction or inhibition of pollen tube growth is between the style base and the top of the embryo sac, where the effect is most obvious in the low crossable genotypes, e.g., CS/Hope 5A and 5B, Hope, and Svenno (Table 2). There was also a marked inhibition of pollen tube growth from the top-to mid-embryo sac and to the micropyle. The reduction in the number of pollen tubes in these regions results in a large proportion of pistils of low crossable genotypes in which pollen tubes do not reach the micropyles.

These results indicate that there is a marked reduction in number of pollen tubes in the region of the ovary wall, resulting in the failure of any pollen tube to reach the micropyle in most of the ovaries of the low crossable genotypes.

REFERENCES

BACKHOUSE, O. W., 1916. Note on inheritance of crossability. J. Genet. 6: 91–94.

BENNETT, M. D., M. K. RAO, J. B. SMITH & M. W. BAYLISS, 1973. Cell development in the anther, the ovule, and the young seed of *Triticum aestivum* L. var. Chinese Spring. Phil. Trans. R. Soc. London, B. Biol. Sci. 266: 39–81.

BOYES, J. W. & W. P. THOMPSON, 1937. The development of the endosperm and embryo in reciprocal interspecific crosses in cereals. J. Genet. 34: 203–227.

BUCHLOZ, J. T. & A. F. BLAKESLEE, 1927. Pollen tube growth at various temperatures. Amer. J. Bot. 32: 103–106.

CHOU, M. C. & D. J. HARBERD, 1970. Note on visual distinction of fluorescent callose of pollen tubes and of sieve tubes in styler tissue of *Brassica* and its allies. Euphytica 19: 379–381.

DORSEY, M. J., 1919. A study of sterility in the plum. Genetica 4: 417–488.

JALANI, B. S., 1973. Crossability, cytogenetics and fertility in Gramineae. Ph.D. Thesis, University of Reading, England.

KHO, Y. O. & J. BAER, 1970. A microscopical research on the incompatibility in the cross *Rhododendron impeditum* × *R. williamsianum*. Euphytica 19: 303–309.

KROWLOW, K.-D., 1970. Untersuchungen über die Kreuzbarkeit zwischen Weizen und Roggen. Z. Pflanzenzüchtg 64: 44–72.

LANGE, W. & R. RILEY, 1973. The position on chromosome 5B of wheat of the locus determining crossability

with rye. Genet. Res. 22: 143–153.
LANGE, W. & B. WOJCIECHOWSKA, 1976. The crossing of common wheat (*Triticum aestivum* L.) with cultivated rye (*Secale cereale* L.). I. Crossability, pollen grain germination and pollen tube growth. Euphytica 25: 609–620.
LEIGHTY, C. E. & SANDO, 1928. Natural and artificial hybrids of Chinese wheat and rye. J. Hered. 19: 28–61.
LEIN, A., 1943. Die genetische Grundlage der Kreuzbarkeit zwischen Weizen und Roggen. Z. indukt. Abstamm. -u. Vereblehre 81: 28–61.
MARTIN, F. W., 1959. Staining and observing pollen tubes in the style by means of fluorescence. Stain Technol. 34: 125–128.
MEISTER, N. & TJUMJAKOFF, 1928. Rye-wheat bybrids from reciprocal crosses. J. Genet. 20: 233–244.
MEYER, H., 1971. Blütenbiologische Untersuchungen bei Getreidekreuzungen. I. Mitt. Das Wachstum von Roggen- und Weizenpollenschläuchen in der Weizennarbe und die Entwicklung des Fruchtkrotens bis 48 Stunden nach der Bestäubung. Arch. Züchtungsforsch. 1: 171–183.
MOSS, J. P., 1965. Chromosome behaviour in plant breeding. D. Phil. Thesis, Oxford University, England.
MOSS, J. P., 1970. Endosperm failure and cross incompatibility in crosses between *Triticum* and *Secale*. Chromosomes Today 3: 124–132.
POPE, M. N., 1937. The time factor on pollen tube growth and fertilization in barley. J. Agr. Res. 54: 525–529.
POPE, M. N., 1943. The temperature factor in fertilization and growth of the barley ovule. J. Agr. Res. 66: 389–402.
POPE, M. N., 1946. The course of the pollen tube growth in cultivated barley. J. Amer. Soc. Agron. 38: 432–440.
RILEY, R. & V. CHAPMAN, 1967. The inheritance in wheat of crossability with rye. Genet. Res. 9: 259–267.
TAYLOR, J. W. & K. S. QUISENBERRY, 1935. Inheritance of rye crossability in wheat hybrids. J. Amer. Soc. Agron. 27: 149–153.
TOZU, T., 1965. On the crossability between wheat and rye, especially reference to the pollen tube growth, fertilization and aminò acids, of the stigma and ovule. Jap. J. Breed. 15: 69.
TOZU, T., 1966. Crossability between wheat and rye. Seiken Zihô 18: 33–38.
WOJCIECHOWSKA, B. & W. LANGE, 1977. The crossing of common wheat (*Triticum aestivum* L.) II. Fertilization and post-fertilization developments. Euphytica 26: 287–297.
ZEVEN, A. C. & C. VAN HEEMERT, 1970. Germination of pollen of weed rye (*Secale segetale* L.) on wheat (*Triticum aestivum* L.) stigma and the growth of the pollen tubes. Euphytica 19: 175–179.