RELATION BETWEEN WHEAT-RYE CROSSABILITY AND SEED SET OF COMMON WHEAT AFTER POLLINATION WITH OTHER SPECIES IN THE HORDEAE

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SUMMARY

Cultivars of common wheat (Triticum aestivum L. em. Thell.) of high wheat-rye (Secale cereale L.) crossability set more seed with pollen of other related species than did wheats of low wheat-rye crossability. This was found to be true for pollen parents from the genera Triticum, Aegilops, Secale, Agropyron and Elymus.

INTRODUCTION

Chromosomes 5A and 5B from the hexaploid wheat variety Hope, when substituted for their homologue in the variety Chinese Spring, inhibit the ability of rye pollen to set seed on wheat (RILEY & CHAPMAN, 1967). The same two substitutions of 'Hope' chromosomes into 'Chinese Spring' also inhibit the ability of pollen from *Hordeum bulbosum* to set seed on wheat (SNAPE et al., 1979). Since only these two 'Hope' chromosomes appear to reduce wheat-rye crossability and wheat-bulbosum crossability, the genes for low crossability, present in 'Hope' and absent in 'Chinese Spring', appear to be identical in each case. More generally SNAPE et al. (1979) found a strong positive correlation between wheat-rye and wheat-bulbosum crossabilities among a diverse set of wheat varieties. This report examines the relation between wheat-rye crossability and seed set in a number of interspecific and intergeneric crosses where hexaploid wheat is used as the female parent.

MATERIALS AND METHODS

A number of wheats which varied in wheat-rye crossability were selected as female parents (Table 1). Spikes were emasculated as described by Thomas & Anderson (1978). Crosses between wheat and cultivated rye were pollinated by the 'go-go' method (Thomas & Anderson, 1978) after the stigmas reached full size and the glumes began to separate.

A number of species more or less closely related to common wheat were selected as

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Table 1. Wheat-rye crossabilities (%) of fourteen common wheats.

Wheat	Field El Batan 1976	Glass-house El Batan 76/77	Field Obregon 1977	Glass-house Winnipeg 77/78	Glass-house Beaverlodge 1978	Glass-house Average Beaverlodge 78/79	Average
Siesta II (= ChSpr/4g. elong./[Tobari) Chinese Spring Siesta I (= ChSpr/4g. elong./[Tobari) Nyu Bai Rfn*2/4/fr/[KAD/Gb/3/Sam	- - 83.8 (2) 89.1 (2)	73.7 (1) - 60.4 (4)	100.0 (1)* 91.2 (1) 59.9 (2) - 25.3 (2)	77.3 (3) 71.2 (2) 74.4 (3) 28.2 (3) 38.4 (2)	68.6 (3)	70.4 (20) 65.8 (5) 66.0 (30) 47.2 (5) 60.8 (5)	82.6 75.5 66.8 57.6 53.4
Tob//KI.Pet/Raf/3/Tzpp/Son'64//Npo'63 Nai'60/8156//Inia 'S' MN69146S/3/AT//11.60.105/RR646'68 S331/Nor'67	61.3 (2) 53.2 (2) 18.3 (2) 3.2 (2)	1 1 1 1	13.1 (5) 15.6 (2) -	4.0 (3) 18.9 (1)	1 1 1 t	25.5 (5) 15.8 (5)	34.6 28.2 18.3 11.1
Glenlea Cno/7C//CC/Tob/3/7C/4/Cno/Chris//Flr/No'66 Super X MN69146S/MN69101S MN6930/3/Meng/8136//At'66	0.0 (2) 0.0 (2) 0.0 (2) 0.0 (2)	3.1 (3)	1111	4.3 (2) 6.5 (2) 0.0 (5) 2.1 (2) 0.0 (15)	1 1 1 1 1	0.0 (5) 0.0 (5) 0.0 (5)	4.3 3.3 0.7 0.0

* Figures in parentheses are the numbers of spikes tested.

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Table 2. Seed set obtained in several interspecific and intergeneric crosses in relation to wheat-rye crossability.

Female	Pollen parent	rent									
Valent	Secale cereale	Secale montanum	4		Aegilops ovata	Aegilops variabilis	Triticum timopheevi	·	Triticum turgidum		Triticum monococcum
	WRC bulk ^a	2D23b	2D35	2D59		4C72	ΚΤ°	4B286	4B55	4B56	MEd
Siesta II Chinese Spring	82.6	- 19/60	- 18/56	1 1	1 1	10/14°	l f	24/58	1 1	-	9/22
Siesta I	66.0	- 10/41	11/20	0/20	1	11/18	- 15/40	101	19/24		(
Rfn*2/4/fr//KAD	53.4	02/9	8/46	1	5/24	14/20	42/46	12/18	ı k	18/22	1 1
Tob//KI.Pet/Raf Nai'60/8156//Inia 'S' MN69146S/3/AT// S331/Nor '67	34.6 28.2 18.3 11.1	1/45 7/14 _ 2./46	0/45 2/18 _ 1/98	1 1 1	1 1 1 1	1 1 1 1	19/53 _ _ 20/43	_ 15/53 _ _	1 1 1 1	23/36	t 1 <u>f</u> 1
Cno/7C//CC/Tob Glenlea Super X MN69146S/MN69101S MN6930/3/Meng/8156	6.5 4.3 0.8 0.7	3/23 - 0/16	1/70 0/42 0/32 0/35	I I I I I	1 1 1 1 1	- - 8/20 9/22 -	0/43 0/36 1/49 0/31 0/36	f ₁ 1 1 1	1 1 1 1	5/28 - 7/21 9/18	_ 0/22 2/24

^a WRC bulk is a bulk of 30 varieties of spring rye from the world rye collection.

^b University of Manitoba accession numbers.

[°] KT is Kimbers timopheevi, described in Kimber & Salle (1976).

^d ME is Metzger's einkorn, a monococcum obtained from R. J. Metzger with some fertility in the secondary floret.

^{*} Number of seeds set over number of florets pollinated.

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Table 3. Seed set obtained in several intergeneric crosses in relation to wheat-rye crossability.

Female	Pollen pa	arent					
parent	Secale cereale	Agropyron junceum	Agropyro elongatur		Elymus giganteus	Elymus arenarius	
	WRC bulk ^a	•	10E22b	2E92		+GA ₃ °	−GA ₃
Chinese Spring	75.5	-	17/52 ^d	0/25	83/922	10/102	_
Nyu Bai	57.6	-	5/40	_		_	1/135
Rfn*2/4/fr//KAD	53.4	13/64	6/22	0/18	-	5/198	1/60
Tob//Kl.Pet/Raf	34.6		3/22	0/33		_	0/98
Nai'60/8156//Inia 'S'	28.2	_	5/40	****	_	-	-
MN69146S/3/AT//	18.3	2/24	_	_		0/30	0/28
S331/Nor'67	11.1	_	0/18	-	-	-	-
Cno/7C//CC/Tob	6.5	_	0/14	_	_	_	-
Super X	0.8	_	_	_	_	0/142	0/102
MN69146S/MN69101S	0.7	1/60	2/21	0/28	_	_	_

^a WRC bulk is a bulk of 30 varieties of spring rye from the world rye collection.

male parents (Table 2; Table 3). Cross pollinations were made with these by dusting pollen from a freshly dehiscing anther held with a pair of forceps directly onto the stigma. Pollinations were made shortly after the time at which the female spike would have begun to shed pollen had it been left unemasculated. In some crosses (Agropyron junceum and all Elymus pollinations), this was judged based on stigma size and glume separation. In other crosses (all other species except S. cereale), the lowermost pair of full size florets were left unemasculated and the day on which they first shed pollen in the primary floret was recorded. To prevent contamination of the emasculated spikelets by this pollen, the spikelet in question was excluded from the glassine bag during maturation and was removed before the bag was reopened for pollination.

The number of florets pollinated and the number of seeds obtained were than recorded (Table 2; Table 3). To analyse the data, wheats were grouped into three categories based on their crossability with cultivated rye (Table 1; Table 4). Limits of these groups were set arbitrarily at 0 to 10% (low crossability), 10 to 50% (intermediate crossability) and 50 to 100% (high crossability). All pollinations by a single species within each group were pooled (Table 4). For this purpose the diploid and decaploid accessions of Agropyron elongatum and the pollinations with Elymus arenarius, with and without GA₃, were considered separately (Table 3; Table 4). Contingency tables were established for each species of male parent with the number of florets forming seed and the number of empty florets as categories on one side and with the high, intermediate and low crossability categories of wheat on the other side of the table (Table 4). Chi square tests for independence between the rows and the columns were then calculated for each contingency table separately (Table 4).

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^b University of Manitoba accession numbers.

^c Florets filled with 75 ppm GA₃ 24H after pollination.

^d Number of seeds obtained over number of florets pollinated.

Table 4. The number of pollinated florets setting and not setting seed in several interspecific and intergeneric crosses.

Wheat-rye	Pollen parent							!	
group of	Secale	Aegilops	Triticum	Triticum	Triticum	Agropyron	Agropyron	Elymus arenarius	,ns
icinale palent	montanam	variabilis	umopneevi	ıurgıanın	шопососсии		eiongaiam	+GA ₃	-GA ₃
	seed: no seed seed: no seed	seed: no seed	seed: no seed seed: no seed	seed: no seed					
50-100%	83:265	35:17	103:86	43:18	9:13	13:49	28:86	15:285	2:193
10-50%	13:253	J	54:95	44:14	1	2:22	8:72	0:30	0:126
0-10%	4:214	17:25	1:194	21:46	2:44	1:59	2:33	0:142	0:102
χ^2 for independence 80	80.2	8.9	138.4		14.7	11.8	10.8	6.8	2.4
Degrees of freedom	2		2	2		2	2	2	2
Probability	* *	*	* *	* * *	**	*	*	*	us

^a This is the decaploid (10 ×) accession 10E22.

 $+GA_3$ = Florets filled with 75ppm GA_3 24h after pollination. *** P < 0.001, ** P < 0.01, ** P < 0.05, ns Non significant.

RESULTS AND DISCUSSION

No seed at all was obtained with the diploid accession of *Agropyron elongatum*. Despite the high fertility of this accession and the presence of dehiscent anthers, spontaneous dehiscence was not observed directly during working hours. Although some pollen was obtained by forcible rupture of yellow anthers, it may have been damaged or immature. Therefore pollinations with this accession are not considered further. All other species could be induced to shed pollen on demand by mechanical stimulation or by warming.

In all but one case, when all the florets pollinated by a particular species were cross classified for seed set and for wheat-rye crossability of the female parent, significant heterogeneity was detected in the resulting contingency table (Table 4). The exceptional case (common wheat × Elymus arenarius without GA₃) does not seem to have been a true exception. Instead the sample size, large though it was, was simply not big enough to reach significance given the low average crossability (Table 4). In all cases more seed was obtained when wheats that cross easily with cultivated rye were used as female parents than when poorly crossable wheats were used (Table 2; Table 3; Table 4). Seed set obtained with the intermediate crossability class was about equal to seed set obtained in the highly crossable class where Triticum turgidum var. dicoccum was used as male (Table 2; Table 4). On the other hand no seed was set in either the intermediate or the poorly crossable class where Elymus arenarius was used as male (Table 3; Table 4). In all other cases, seed set in the intermediate class was also intermediate (Table 4).

Two general conclusions may be drawn from these findings. Firstly the genes in wheat which are best known for their role in reducing seed set in crosses with cultivated rye also act to prevent the pollen of a variety of other related species from setting seed on common wheat. Secondly this correlation between interspecific crossabilities is general in common wheat and is not restricted to Chinese Spring, Hope and their joint derivatives (see also SNAPE et al., 1979).

In general average seed set was lower when more distantly related taxa were used as pollen parents. Thus low wheat-rye crossability in common wheat was not a serious barrier to hybridization with emmer (*T. turgidum* var. *dicoccum*) but even high wheat-rye crossability did not guarantee high rates of seed set in crosses with *Elymus* species (Table 4). Even so the use of highly crossable wheats allowed crosses to be made with *Elymus arenarius* which would otherwise seem to have been difficult or impossible (Table 4).

In conclusion genes for low interspecific crossability in wheat act against a wide spectrum of related potential pollinators. The mechanism for low crossability seems to involve the inhibition of alien pollen tubes somewhere between the base of the stigma and the micropyle (Lange & Wojciechowska, 1976; Wojciechowska & Lange, 1977; Tozu, 1966; Zeven & van Heemert, 1970). It is suggested that the ovule non-specifically excludes all pollen except those which are recognised as 'self' and that the role of genes for low crossability is to narrow the basis for such recognition. From the practical point of view, the use of common wheats of high wheat-rye crossability in interspecific hybridization will increase the recovery of hybrids in many wide crosses.

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