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Genetic Control of Embryo Lethality in Crosses between Common Wheat and Rye

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Abstract—The phenotypic manifestation and genetic control of embryo lethality observed in crosses between common wheat and rye were studied. It was found that crosses between common wheat and inbred self-fertile rye lines L2 and 535 gave rise to ungerminating grains, in which the development and differentiation of the hybrid embryo are arrested. Study of the degree of embryo development in the hybrid grains obtained by crossing common wheat varieties with inbred rye lines L2 and 535 showed that genotypes of the parents affected the ratio between undifferentiated embryos of various sizes. Analysis of this trait was performed by test crosses according to a novel pedigree program with the use of interlineal hybrids and a set of fourth-generation hybrid recombinant inbred lines. Rye line L2 was shown to bear the *Eml* (Embryo lethality) gene, which terminates the development of the hybrid embryo in amphihaploids. The suggestion of complementary interaction between wheat and rye genes during formation of a “new” character in wheat–rye F_1 hybrids is discussed. A method of detecting an allele not complementary to the rye *Eml* allele in wheat is proposed. The proposed test program allows appropriate study of the system of wheat and rye genes involved in complementary interaction in the genotype of a distant hybrid.

INTRODUCTION

Distant hybridization of plants is often accompanied by noncrossability, embryo and seedling lethality, death at later developmental stages, and morphological abnormalities. These manifestations of genome interaction, as well as sterility of amphidiploids, were described by Karpechenko as incompatibility (incongruence) between genomes of different species [1]. He suggested that in some cases such interactions could be defined by particular genes with specific effects. At present, it is known that the wide range of such genes can involve those controlling intercellular interactions, morphogenesis, and programmed cell death. Our study is based on an original pedigree program [2, 3], which allows detection and study of parental genes responsible for intergenomic interactions in allopolyploids. The first stage of this analysis involves development of hybrids (amphihaploids) and/or primary triticales from a single wheat genotype and as many inbred rye lines as possible. The purpose of this stage is to detect differences between amphihaploids and/or primary triticales in the expression of genes formerly found in rye or differences in characters of allopolyploids that can be explained by specific interaction between polymorphic rye genes and wheat genes in the hybrid genome. The second stage involves analysis of segregation to determine the number, effects, and interaction pattern of the genes whose polymorphism was revealed at the first stage by comparison of amphihaploids and/or primary triticales, and to map them. With the use of this approach, rye genes specifically expressed in the

genome of a wheat–rye hybrid were detected for the first time. These genes are responsible for intergenomic interactions at various developmental stages of the hybrid plant. They manifest themselves in termination of the development of the hybrid embryo, hybrid dwarfness, hybrid weakness, hybrid chlorosis and necrosis, distortions of leaf morphology (onion-like leaves) combined with various degrees of ear reduction, and sterility of amphidiploid plants with normal development [2].

This work is dedicated to comprehensive study of embryo lethality in crosses of various common wheat varieties to four self-fertile inbred rye lines from the Peterhof genetic collection. These lines differ in the gene(s) involved in intergenomic interactions, which controls the development of hybrid embryos obtained by crossing wheat and rye.

MATERIALS AND METHODS

Experiments were performed with eight common wheat accessions. Common wheat cultivar Chinese Spring (CS) and Priekul'skaya 421 variety derived from it possess two recessive alleles of the *kr1* and *kr2* genes for easy crossability to rye. We received them from the Peterhof collection. Varieties Sibirka Yartsevskaya (k-38587), Shin Chuunaga (k-43241), and a Mongolian accession (k-08034) were kindly provided by the wheat department of the All-Russia Institute for Plant Production (VIR) (parenthesized are accession numbers according to the VIR catalog. Varieties Kras-

naya Zvezda, Suvon 85, and C.J. L2633 were kindly provided by A. Berner, Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany. Four inbred self-fertile rye lines (L2, L6, L7, and 535) [4] from the unique Peterhof collection were used as a paternal form. Hybrids of line L2 to lines L6 and L7 were obtained to use them as paternal in test crosses according to our original program [2, 3]. In addition, we crossed CS wheat to a set of rye recombinant inbred lines (RILs) of the fourth generation obtained by cross L7 × L2. The state of the embryo in nongerminating hybrid grains was studied by the tetrazole method [5], allowing differentiation between viable and inviable tissues in the hybrid embryo. Hybrid grains were germinated on filter paper in petri dishes at 24°C for 36 h. The germinating grains were classified as grains with differentiated embryos. Nongerminating grains were cut lengthwise, stained with tetrazole, and examined for the presence or absence of a differentiated embryo. All germinating grains were planted in soil, and 7-day seedlings were tested for their hybrid status by electrophoretic isoenzyme analysis.

Statistical evaluation of the results was performed using χ^2 and parametric tests [6].

RESULTS

In our former crosses of CS to 101 self-fertile inbred rye lines, ungerminating grains were found in four hybrid combinations. Numerous crosses of these four rye lines to CS performed in various years did not yielded a single germinating grain. In contrast, the germination in the progeny of the remaining 97 self-fertile lines was 60–100%, pointing to the presence of normal embryos in most hybrid grains. Three of the four rye lines (L2, L3, and 564) were closely related, being derived from accession Ku-2/63, and one line (535) had an independent parent, accession KsBbL (4/77). Lines L2 and 535 were used as paternal for further investigation of this character.

During its long-term studies, line L2 was crossed to eight common wheat genotypes, and line 535, to two. We analyzed 681 grains obtained by pollination of common wheat with L2 pollen and 336 grains obtained with line 535 pollen (Table 1). All these grains were ungerminating. Crosses of self-fertile rye lines L6 and L7 and variety Volkhova to the same common wheat genotypes yielded high percentages (74.9–92.1%) of hybrid grains, which germinated and gave rise to normal hybrid plants. These results suggest that rye line L2, the related lines L3 and 564, and line 535 bear a rye factor, or factors, which specifically expresses itself in the wheat–rye hybrid genotype and participates in the genetic control of embryo development.

Morphological study of embryos of ungerminating swelling hybrid grains revealed absence of normal differentiated embryos from these amphihaploids. All ungerminating amphihaploid grains analyzed were

divided into four groups according to the state of the hybrid embryo:

- (1) embryo completely absent (seeds without embryos);
- (2) reduced undifferentiated embryo about one-tenth the normal size;
- (3) reduced undifferentiated embryo about half the normal size;
- (4) large embryo of normal size without visible signs of tissue differentiation.

The degrees of embryo development in hybrid grains obtained by crossing common wheat varieties to rye inbred lines L2 and 535 showed that the rates of occurrence of undifferentiated embryos of various sizes are affected by parental genotypes (Table 2). The most pronounced effect of the mother on the level of embryo development was observed in cross 38 587 × L2. In all hybrid grains of this cross, undifferentiated embryos were of normal size. In contrast, 36.4% of grains obtained by the cross C.J.L 2633 × L2 had no embryos, and 50.0% of the grains had small embryos (one-tenth the normal size). The effect of the father component on the level of hybrid embryo development was evaluated by the χ^2 test. Experiments with pollination of CS and 43241 with L2 pollen performed in different years revealed no significant differences in the ratios of hybrid embryos of different sizes (CS × L2: $\chi^2 = 2.2$, d.f. = 3, $P > 0.25$; 43 241 × L2: $\chi^2 = 1.61$, d.f. = 3, $P > 0.25$), whereas the cross Priekul'skaya 421 × L2 showed significant differences ($\chi^2 = 39.23$, d.f. = 3, $P < 0.01$). However, we attribute these differences to random factors, and hereafter use the data obtained for this cross in 2000 in further analysis. Comparison of the effect of the paternal component on the level of hybrid embryo development showed that 42.1–63.6% of grains obtained by pollination of common wheats CS, Priekul'skaya 421, 43 241, and Krasnaya Zvezda with pollen of L2 rye had undifferentiated embryos of the normal size. No significant differences were found in these crosses: $\chi^2 = 15.32$, d.f. = 9, $P > 0.05$. In contrast, the development of hybrid embryos obtained by pollination of CS and Priekul'skaya 421 with pollen of rye line 535 halts at earlier stages. Normal-size undifferentiated embryos were found only in 12.6% of grains from cross CS × 535 and in 30.9% of Priekul'skaya 421 × 535, the differences being significant for comparison of the paternal component: for CS $\chi^2 = 76.16$, d.f. = 3, $P < 0.01$, and for Priekul'skaya 421, $\chi^2 = 15.3$, d.f. = 3, $P < 0.01$ (Table 2).

Test crosses of line L2, producing ungerminating seeds when crossed to wheat, were performed with two unrelated lines (L6 and L7), yielding highly germinating (75.0–81.8%) wheat–rye hybrid seeds (Table 1).

All hybrid combinations between CS and interlinear rye hybrids F₁ L6 × L2, L2 × L6, L2 × L7, and L7 × L2 and crosses between Priekul'skaya 421 and interlinear rye hybrids L7 × L2 and L2 × L6 (Table 3) showed the 1 : 1 segregation for the presence of differentiated or

Table 1. Development of embryos in hybrid grains obtained by crossing various common wheat accessions to inbred rye lines of cv. Volkhova

Parental accession		Year of seed collection	Number of seeds	Embryo		Percentage of seeds with differentiated embryos
rye ♂	wheat ♀			differentiated	undifferentiated	
L2	CS	1997	54	0	54	0.0
		1999	88	0	88	0.0
		2000	165	0	165	0.0
		Total	307	0	307	0.0
	Priekul'skaya	1997	47	0	47	0.0
		1999	36	0	36	0.0
		2000	123	0	123	0.0
		Total	206	0	206	0.0
	43241	2001	8	0	8	0.0
		2002	23	0	23	0.0
		Total	31	0	31	0.0
	38587	2001	22	0	22	0.0
		2002	24	0	24	0.0
		Total	46	0	46	0.0
08034	2001	23	0	23	0.0	
	2000	33	0	33	0.0	
Krasnaya Zvezda	2000	13	0	13	0.0	
	2000	22	0	22	0.0	
Suvon 85	2000	13	0	13	0.0	
	2000	22	0	22	0.0	
C.J.L2633	2000	22	0	22	0.0	
	Total	681	0	681	0.0	
535	CS	2000	52	0	53	0.0
		2002	203	0	203	0.0
		Total	255	0	255	0.0
	Priekul'skaya	2000	81	0	81	0.0
Total	336	0	336	0.0		
Volkhova	CS	1999 (3p.)*	99	73	26	73.7
	Priekul'skaya	2001 (1p.)*	43	39	4	90.7
		(3p.)*	73	49	24	67.1
	Total	215	161	54	74.9	
L6	Suvon 85	2000	16	12	4	75.0
	C.J.L2633	2000	6	6	0	100.0
		Total	22	18	4	81.8
L7	CS	1999	44	44	0	100.0
		2000	41	36	5	87.8
		Total	85	80	5	94.1
	38587	2001	11	9	2	81.8
		Priekul'skaya	2000	5	4	1
	Total	101	93	8	92.1	

Note: Numbers of plants of cv. Volkhova tested for self-incompatibility

Table 2. Development of embryos in hybrid grains obtained by crossing various common wheat accessions to rye inbred lines L2 and 535

Parental accession		Year of seed collection	Number of seeds	Percentage of seeds without embryos or having undifferentiated embryos of various sizes			
rye ♂	wheat ♀			no embryo	10% of normal size	50% of normal size	100% (Normal size)
L2	CS	1999	88	8.0	6.8	43.2	42.0
		2000	165	5.5	10.9	37.6	46.0
		Total	253	6.3	9.5	39.5	44.7
	Priekul'skaya	1999	36	2.8	36.1	61.1	0.0
		2000	123	6.5	8.1	30.9	54.5
		Total	159	5.7	14.5	37.7	42.1
	43241	2001	8	0.0	12.5	25.0	62.5
		2002	23	17.4	8.7	17.4	56.5
		Total	31	12.9	9.7	19.4	58.0
	38587	2001	22	0.0	0.0	0.0	100.0
		2002	24	0.0	0.0	0.0	100.0
		Total	46	0.0	0.0	0.0	100.0
	08034	2001	23	4.35	4.35	8.7	82.6
		Krasnaya Zvezda	2000	33	12.1	9.1	15.2
	Suvon 85	2000	13	0.0	0.0	46.2	53.8
C.J.L2633	2000	22	36.4	50.0	13.6	0.0	
535	CS	2000	52	0.0	19.25	61.5	19.25
		2002	203	5.9	30.5	52.7	10.9
		Total	255	4.7	28.2	54.5	12.6
	Priekul'skaya	2000	81	3.7	21.0	44.4	30.9

undifferentiated embryos in hybrid grains. The segregation data are uniform ($\chi^2 = 1.98$, d.f. = 6, $P > 0.75$), which ensures the same 1 : 1 ratio in total ($\chi^2 = 2.58$, d.f. = 1, $P > 0.10$). The results suggest that the genotypes of L2 and related lines contain a genetic factor blocking the development of the hybrid embryo in triticale amphihaploids. This gene (factor) was named *Eml* (Embryo lethality) [3]. Note that the class of grains with undifferentiated embryos in the hybrid analysis is usually more numerous, because it includes both embryos with the mutant *Eml* allele and part of embryos with the wild-type *eml* allele, whose development had stopped because of random causes.

To confirm the monogenic control of the development of the hybrid embryo by the rye parent, we crossed CS to several plants of rye RILs of the fourth generation obtained by the cross L7 × L2. A total of

76 lines were crossed (one plant of each line). Examination of hybrid grains from each cross revealed 32 plants homozygous for the mutant *Eml* allele, which yielded only ungerminating hybrid seeds when crossed to CS. Twenty-eight plants were homozygous for the wild-type *eml* allele. The hybrid progeny of these plants contained more than 50% grains with normally developing hybrid embryos. Sixteen plants were determined as heterozygotes for this gene (Table 4). All recombinant lines whose progeny either showed the statistically significant 1 : 1 ratio between grains with differentiated and undifferentiated embryos or contained, in addition to predominant grains with undifferentiated embryos, grains giving rise to normal seedlings electrophoretically identified as hybrids, were assigned to the heterozygote class. The ratio between homozygous and heterozygous lines in the fourth generation of interlin-

Table 3. Segregation for the degree of embryo development in hybrid grains obtained by crossing two common wheat varieties to interlinear rye hybrids

Parental accession		Year of seed collection	Number of seeds	Embryo		χ^2 1 : 1
wheat ♀	rye hybrid ♂			differentiated	undifferentiated	
CS	L2 × L6	1997	137	63	74	0.73
		2000	138	67	71	0.116
	L6 × L2	1999	148	66	82	1.73
	L2 × L7	1997	181	91	90	0.00
	L7 × L2	1999	142	66	76	0.70
Priekul'skaya 421	L2 × L6	2000	64	30	34	0.250
	L7 × L2	1999	276	132	144	0.52
		2000	191	84	87	0.512
Total	F ₁	1997–2000	1257	599	658	2.58

ear rye hybrids is expected to be as follows (1) 43.75% *Eml/Eml* lines (yielding nongerminating hybrid seeds), (2) 43.75% *eml/eml* (yielding highly germinating hybrid grains), and (3) 12.5% heterozygous *Eml/eml* lines (yielding progeny segregating in the 1 : 1 ratio). The ratio obtained by crossing 76 lines to CS (32 *Eml/Eml* lines, 28 *eml/eml* lines, and 16 heterozygous *Eml/eml* lines) does not differ significantly from our null hypothesis of the monogenic control of this character by the rye *Eml* gene ($\chi^2 = 5.32$, d.f. = 2, $P > 0.05$; Table 4). Thus, test crosses with the use of interlinear hybrids and a series of RILs indicate that line L2 differs from L6 and L7 in the single *Eml* gene, which participates in intergenomic interactions and controls hybrid embryo development in wheat–rye crosses.

DISCUSSION

One of the fundamentals of genetics is that any character or process is controlled by corresponding genes. Expression of these genes can vary in the course of mutations. Genes responsible for inviability of distant hybrids or sterility of allopolyploids can be assigned to the class of genes controlling incompatibility between genomes of different species [1]. Such genes were discovered in experiments on intraspecific and intergeneric crosses of polyploid wheats. They include commonly known complementary genes for hybrid necrosis, hybrid chlorosis, and hybrid dwarfness [7, 8]. These genes have multiple alleles, and combinations of certain alleles in F₁ hybrids cause lethality. Two genes for hybrid necrosis were found in inbred rye lines. They were complementary to each other and to corresponding genes for hybrid necrosis in wheat [9]. As early as in 1937, Dobzhansky suggested existence of comple-

mentary genes, determining lethality or sterility in distant hybrids [10]. This notion is in perfect agreement with recent data of other researchers (see [11] for review) and can be important for understanding mechanisms of genomic interaction in allopolyploids. This interaction can be based on existence of two or more complementary homologous genes in both parents. Each gene has at least two alleles: “normal” (noncomplementary) and “abnormal” (complementary). The abnormal phenotype appears only in an intraspecific (intergeneric) hybrid with “abnormal” alleles of the complementary genes of both parents. According to this model, any abnormal (or new) manifestation of the character in a distant F₁ hybrid can result from interaction of at least two complementary genes.

Embryo lethality is a familiar postzygotic mechanism of reproductive isolation in some wheat–rye hybrids. For example, crosses of tetraploid wheats to rye, particularly, with the use of *T. durum* Desf. as the maternal form, result in abortion of hybrid embryos, and mature grains contain dead embryos [12, 13]. In this case, hybrid lethality, caused by incompatibility of genomes of parental species, can be overcome by isolation of immature embryos followed by their cultivation on artificial media [14–16]. On the other hand, most seeds obtained by crosses between hexaploid wheat *T. aestivum* L. and rye have normally developed endosperm, and few of them are unable to germinate [17–19]. Plants and methods used by now do not allow recognition of particular genes of parental species controlling certain developmental stages of the hybrid embryo. The new approach to hybrid analysis proposed by us in [2, 3, 20] and based on using interlinear hybrids of rye and a set of RILs allowed identification of a rye

Table 4. Analysis of embryo development in hybrids obtained by crosses CS × RIL (4th generation)

Homozygotes for the allele terminating embryo development (no embryo)				Homozygotes for the allele allowing embryo development				Heterozygotes for the allele terminating embryo development (segregating)			
RIL no.	number of grains			RIL no.	number of grains			RIL no.	number of grains		
	total	with embryo	without embryo		total	with embryo	without embryo		total	with embryo	without embryo
91 p.1	8	0	8	97 p.3	16	12	4	92 p.2	86	51	35
94 p.1	58	0	58	98 p.1	34	29	5	96 p.2	11	4	7
95 p.3	61	0	61	102 p.3	11	11	0	99 p.1	43	19	24
101 p.1	9	0	9	105 p.3	38	35	3	100 p.1	14	7	7
103 p.2	21	0	21	108 p.1	64	54	10	104 p.2	6	3	3
106 p.2	4	0	4	114 p.2	73	54	19	113 p.1	52	33	19
107 p.1	11	0	11	120 p.3	46	41	5	128 p.1	67	39	28
110 p.3	14	0	14	121 p.1	38	30	8	133 p.2	61	26	35
111 p.2	46	0	46	122 p.3	7	5	2	139 p.1	6	4	2
112 p.2	8	0	8	127 p.3	52	45	7	142 p.2	13	7	6
115 p.3	21	0	21	131 p.1	13	11	2	143 p.2	21	5	16
116 p.1	25	0	25	132 p.1	18	13	5	148 p.2	9	5	4
117 p.2	30	0	30	137 p.1	4	4	0	150 p.3	8	2	6
118 p.2	50	0	50	138 p.1	4	4	0	151 p.1	21	5	16
119 p.1	56	0	56	140 p.1	5	5	0	158 p.3	14	8	6
123 p.2	7	0	7	145 p.3	115	106	9	165 p.2	22	15	7
125 p.2	15	0	15	147 p.2	50	35	15				
126 p.2	13	0	13	149 p.1	14	12	2				
129 p.1	15	0	15	153 p.2	33	29	4				
135 p.2	13	0	13	155 p.3	53	51	2				
136 p.2	4	0	4	156 p.3	107	95	12				
144 p.2	15	0	15	160 p.1	17	15	2				
154 p.1	27	0	27	163 p.2	12	9	3				
157 p.1	59	0	59	167 p.1	40	34	6				
159 p.1	25	0	25	170 p.2	23	19	4				
162 p.3	10	0	10	172 p.2	20	18	2				
168 p.1	24	0	24	175 p.1	7	6	1				
169 p.1	36	0	36	177 p.2	1	1	0				
171 p.1	10	0	10								
174 p.1	48	0	48								
176/4p1	19	0	19								
178 p.2	13	0	13								

gene involved in forming interspecific incompatibility barriers between wheat and rye at the postgametogenesis stage of fertilization, which participated in the genetic control of the development of the hybrid embryo. The corresponding rye gene was named *Eml* (Embryo lethality). This gene is represented by at least two alleles differing in function. One allele is present in L2 and, probably, in the two related lines; the other allele is present in L6, L7, and most other lines tested. At present, we cannot determine these alleles as dominant and recessive, because their expression was tested in the haploid state. According to the rate of occurrence in rye lines and expression in wheat-rye F₁ hybrids, the *eml* allele (L6 and L7) may be defined as normal, and *Eml* as abnormal. The appearance of the "new" character in wheat-rye F₁ hybrids suggests complementary interaction between wheat and rye genes. According to this suggestion, the *Eml* allele (L2) is complementary to the corresponding gene (allele) of CS wheat, unlike the *eml* allele (L6 and L7). Interaction between these complementary genes (alleles) causes embryo lethality. If this suggestion is correct, the noncomplementary wheat allele can be detected by crossing a large set of wheat varieties (tetra- and hexaploids) to rye line L2. If any cross yields viable hybrid seeds with normally differentiated embryos, this will point to the presence of an allele noncomplementary to the rye *Eml* allele. This approach allows investigation of the set of wheat and rye genes involved in complementary interaction in the genotype of a distant hybrid. It is likely that such genes (alleles) with complementary effect can also be detected in intraspecific crosses; however, the rate of occurrence of abnormal alleles with complementary effect must be low, because their combinations are lethal. Nevertheless, different complementary alleles can be independently recognized in inbred rye lines or wheat varieties.

A special test for allelism between the mutations characteristic of L2 and unrelated line 535 will add to understanding the interaction between the genomes of the parental species and the genetic control of embryo development in distant wheat-rye hybrids. To solve the question of the allelism of mutations in L2 and 535, we plan a cross between CS and the interlinear L2 × 535 F₁ hybrid. If these genes are allelic, all hybrid grains obtained in this cross will contain undifferentiated and inviable embryos. If the genes are nonallelic and linked, the hybrid grains will segregate into two classes: grains with abnormal (undifferentiated) embryos and grains with normal viable ones in the 3 : 1 ratio. Further cytological, genetic, and molecular study of the abnormal development of hybrid embryos will provide new insight into interaction between wheat and rye genomes at the earliest stages of stabilization and evolution of the newly emerging combined genome. These results may be applicable to triticale breeding.

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