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Hybrid necrosis in triticale and the expression of necrosis genes in allopolyploids

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Summary. The occurrence in triticale of four different genes causing hybrid necrosis is described: *Ne1* and *Ne2* in the B genome of wheat and *Ner1* and *Ner2* in the rye genome. Hybrid necrosis develops due to dominant complementary interaction of two genes. This interaction in triticale, however, may take place not only between genes belonging to the same genome but also between genes of different genomes. In triticale, these genes can cause hybrid necrosis in four different combinations. The inheritance of the phenomenon in triticale is, therefore, more complicated than it is in wheat or rye. To avoid hybrid necrosis in triticale, attention should be paid that no necrosis genes are introduced into the primary triticale stocks from the wheat and rye parents. The expression of necrosis genes is influenced by the level of ploidy. Any additional genome – A, B, D, or R – may exert a suppressing effect on the expression of necrosis genes. Therefore, when identifying genotypes of triticale with regard to their necrosis genes, the level of ploidy has to be accounted for. Moreover, the present results illustrate that gene expression in polyploids is not only determined by interactions with other single genes but that it may also be modified by the total genotype of the respective individual.

Key words: Triticale – Hybrid necrosis – Gene complementation – Polyploidy

Introduction

Triticale is a synthetic amphidiploid derived from hybridization between the genera *Triticum* and *Secale*. During the last four decades, triticale has developed from a mere research subject to a commercial crop plant. According to the latest estimates, about 100 triticale varieties are presently grown on more than a million ha area all over the world (Varughese et al. 1987), indicating intensive breeding efforts. This increasing interest in triticale justifies research on basic as well as applied aspects of this synthetic crop plant. Based on his studies of primary triticale genotypes produced from well-defined pure lines of parental wheat and rye, Lelley (1984) has drawn attention to the importance of genetic interactions between the two parents which are obviously most influential in shaping the phenotype of triticale. Further research on these interactions between the genes in different genomes should provide valuable insights into the genetic functioning of a polyploid species; it should also help to develop breeding methods which are better adapted to the specific requirements of triticale.

Genes causing hybrid necrosis by a dominant complementary interaction are particularly suited to studying gene interactions in polyploids. This phenomenon has been investigated in great detail in wheat (Zeven 1981). Several alleles of two necrosis genes, *Ne1* and *Ne2,* were found acting in different combinations to cause various degrees of the necrosis symptoms in wheat hybrids (Hermsen 1963). Both necrosis genes were localized in the B genome, the *Ne1* locus on 5BL and the *Ne2* locus on 2BS (Tsunewaki 1960; Zeven 1972; McIntosh 1973). While in hexaploid wheat both genes occur regularly, in tetraploid wheat only *Ne1* has been observed so far (Nishikawa 1967; Zeven 1981). Thus, octoploid triticale originating from crosses between hexaploid wheat and diploid rye can obtain both necrosis genes, whereas primary hexaploids only carry the *Ne1* gene from their tetraploid wheat parent. However, secondary hexaploids arising whenever hexaploid triticale is crossed either with

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octoploids or with bread wheat may obtain both necrosis genes and, for this reason, hybrid necrosis can occur in hexaploid triticale, too. Hybrid necrosis in hexaploid triticale has been described by Gregory (1973) and by Behl and Manerchandani (1983).

By studying primary hexaploid triticale produced with the same parental tetraploid wheat but different rye genotypes, Jung and Lelley (1985) detected an inbred rye genotype which caused necrosis in the respective primary triticale. A crossing experiment revealed that one gene of the inbred rye genotype was responsible for the phenomenon in dominant interaction with the *Ne1* gene (Jung and Lelley 1985). Simultaneously, Scoles (1985) reported another gene in a different inbred rye which led to necrosis in hybrids between bread wheat and rye. In further studies, Ren and Lelley (1988) verified the existence of two genes in diploid rye which cause hybrid necrosis in rye by dominant complementary interaction. Moreover, these two rye genes can cause hybrid necrosis in triticale by interacting with necrosis genes of the B genome, *Ne1* or *Ne2*. The two genes in rye, according to their correspondence to the two genes in the B genome, were named *Ner1* and *Ner2* (Ren and Lelley 1988). These results suggested that hybrid necrosis could be a more important limiting factor in triticale breeding than in the breeding of hexaploid wheat. While only two necrosis genes exist in wheat, a combination of four necrosis genes, two in the B and two in the R genome, may lead to hybrid necrosis in triticale. Apart from these limitations for a breeding program, necrosis genes represent an excellent subject for basic studies on gene interaction between different genomes in an allopolyploid species.

This paper describes in detail how hybrid necrosis is caused in triticale by interaction of the necrosis genes in the B and R genome, and it reports on effects of the ploidy level on the expression of necrosis genes.

Materials and methods

Five primary hexaploid and five primary octoploid triticale lines derived from pure lines of wheat and inbred lines of rye, and their respective parents, were used in this study (Table 1). All of these primaries were developed in our laboratory. Some of the lines show weak necrosis symptoms (Jung and Lelley 1985). The tetraploid wheats D400 and D800 carry a moderate or medium (m) allele of the gene *Ne1*, the inbred rye lines L155 and L256 carry a weak allele (w) of the gene *Ner2*, and the inbred rye IR136-3, a strong allele (s) of the gene *Ner1* (Ren and Lelley 1988). The hexaploid wheat line 'Siesta I' (a carrier of *Ne2m*) and the inbred rye line IR136-3 were obtained from Dr. G. J. Scoles (University of Saskatchewan, Saskatoon, Canada). The genotype of *Triticum turgidum* (Turgidum 34) was provided by Mrs. Dr. G. Oettler (University of Hohenheim, Germany). For identification of the genotype with respect to genes for hybrid necrosis, all wheat parents except 'Chinese Spring' (Wa4) were crossed with two known carriers of necrosis genes, NP839 (*Ne1s*) and 'Touzelle' (*Ne2s*); these were received from Dr. A. C. Zeven (Agricultural University, Wageningen). In this study, the term 'genotype' refers to the necrosis genes and their alleles only. The variety 'Chinese Spring' is known from the literature as a carrier of *Ne1w* (Hermsen 1963).

Crosses were made in all possible combinations between the five octoploid and five hexaploid triticale lines. To study gene expression, additional crosses were made between wheat and rye and between wheat and triticale. The plant material was grown in the greenhouse. Hybrid necrosis was classified according to Hermsen (1963). A detailed description of their phenotypes and the use of gene symbols is given by Ren and Lelley (1988).

Table 1. The primary triticales, their parentage and the degree of hybrid necrosis exhibited by the amphiploids

Primary triticales	Parents		Degree of hybrid necrosis
	Wheat	Rye	
Hexaploids			
400-155	D400	L155	2-3
400-256	D400	L256	2-3
800-155	D800	L155	2-3
800-256	D800	L256	2-3
T-136	Turgidum 34	IR136-3	0
Oktoploids			
Jub-155	Jubilar	L155	0
Jub-256	Jubilar	L256	0
Kom-155	Kormoran	L155	0
Wa4-155	Chinese Spring	L155	0-2
Wa4-256	Chinese Spring	L256	0-2

Table 2. Degree of hybrid necrosis of F_1 plants from crosses of wheat lines used in the present study with the two testers NP839 and 'Touzelle', known to carry *Ne1s* and *Ne2s*, respectively

Combination		Degree of hybrid necrosis
Jubilar	× NP839	0
Jubilar	× Touzelle	0
Siesta I	× NP839	6-7
Siesta I	× Touzelle	0
Kormoran	× NP839	7-8
Kormoran	× Touzelle	0
NP839	× D400	0
Touzelle	× D400	6-7
NP839	× D800	0
Touzelle	× D800	6-7
NP839	× Turgidum 34	0
Touzelle	× Turgidum 34	0

Results

Identification of the wheat genotypes

To identify the genotypes of the wheat lines involved in the parentage of the primary triticales, these lines were crossed with the testers NP839 and 'Touzelle', carriers of the necrosis genes *Ne1s* and *Ne2s*, respectively. The F_1 plants from crosses of 'Jubilar' and 'Turgidum 34' with the two testers did not exhibit hybrid necrosis (Table 2);

Table 3. The genotype and degree of hybrid necrosis in triticale × triticale and triticale × wheat hybrids

Combination		Genotype	Degree of hybrid necrosis
Korm-155	×400-155	***Ne1m*** *ne1*/***Ne2ms*** *ne2/ner1 ner1/Ner2w Ner2w*	4–5
Korm-155	×400-256		4–5
Korm-155	×800-155		4–5
Krom-155	×800-256		4–5
Korm-155	×T-135	*ne1 ne1*/***Ne2m*** *ne2*/***Ner1s*** *ner1/Ner2w ner2*	5–6
Jub-155	×400-155	***Ne1m*** *ne1/ne2 ne2/ner1 ner1*/***Ner2m*** *Ner2w*	4–5
Jub-155	×400-256		4–5
Jub-155	×800-155		4–5
Jub-155	×800-256		4–5
Wa4-256	×400-155	***Ne1m*** *Ne1w/ne2 ne2/ner1 ner1*/***Ner2m*** *Ner2w*	4–5
Wa4-256	×400-256		4–5
Wa4-256	×800-155		4–5
Wa4-256	×800-256		4–5
Jub-256	×400-155	***Ne1m*** *ne1/ne2 ne2/ner1 ner1*/***Ner2w Ner2w***	2–3
Jub-256	×400-256		2–3
Jub-256	×800-155		2–3
Jub-256	×800-256		2–3
Wa4-155	×400-155	***Ne1m*** *Ne1w/ne2 ne2/ner1 ner1*/***Ner2w Ner2w***	2–3
Wa4-155	×400-256		2–3
Wa4-155	×800-155		2–3
Wa4-155	×800-256		2–3
Jub-155	×T-136	*ne1 ne1/ne2 ne2*/***Ner1s*** *ner1*/***Ner2m*** *ner2*	5–6
Wa4-256	×T136	*Ne1w ne1/ne2 ne2*/***Ner1s*** *ner1*/***Ner2m*** *ner2*	5–6
Jub-155	×NP839		5–6
Jub-155	×Touzelle		0
Wa4-256	×NP839		5–6
Wa4-256	×Touzelle		0

this indicates that the hexaploid wheat cultivar 'Jubilar' and the tetraploid wheat 'Turgidum 34' do not carry a dominant allele of a necrosis gene. The wheat cultivar 'Jubilar' has been developed from three wheat lines, 'Derenburger Silber 41', 'Taca 42', and 'Schernauer' (Zeller 1985), all of them being classified by Hermsen (1963) as non-carriers of necrosis genes. The F_1 plants of the cross 'Kormoran' × NP839 exhibited severe hybrid necrosis with a degree of 7–8 on an arbitrary scale of 0–9. The wheat cultivar 'Kormoran' originates from the cross 'Cappelle 46' × 'Merlin' (Zeller 1985). According to Hermsen (1963), 'Cappelle 46' is an *Ne2ms* (between medium and strong) carrier. Most probably 'Kormoran' inherited the *Ne2ms* allele from this parent. The results of all test crosses are summarized in Table 2. Based on these data the genotype of the wheat lines can be described as follows:

Hexaploid wheat	Genotype
'Siesta I'	*ne1 ne1/Ne2m Ne2m*
'Kormoran'	*ne1 ne1/Ne2ms Ne2ms*
'Jubilar'	*ne1 ne1/ne2 ne2*

Tetraploid wheat	
D400	*Ne1m Ne1m/ne2 ne2*
D800	*Ne1m Ne1m/ne2 ne2*
'Turgidum 34'	*ne1 ne1/ne2 ne2*

Hybrid necrosis in triticale

Hybrid necrosis in triticale can occur due to different combinations of necrosis genes in the B and R genomes (Table 3). The F_1 plants from crosses between the octoploid triticale line, Korm-155, and four hexaploid triticale lines, 400-155, 400-256, 800-155, and 800-256, showed uniform hybrid necrosis with a degree of 4–5. Necrosis started at tillering stage and the plants died at the time of heading. The genotype of the F_1 plants from these crosses is

Ne1m *ne1*/***Ne2ms*** *ne2/ner1 ner1/Ner2w Ner2w*.

Necrosis alleles which are printed bold determine the phenotype. The allele *Ne1m* originated from the durum wheat D400 and D800, and the allele *Ne2ms* from the wheat cultivar 'Kormoran'. Since the four hexaploid tri-

Table 4. Expression of the necrosis genes at different ploidy level

Combination		Genome and genotype	Degree of hybrid necrosis
Kormoran	× D400	AABBD ***Ne1m** ne1/**Ne2ms** ne2*	5–6
Korm-155	× 400-155	AABBDRR ***Ne1m** ne1/**Ne2ms** ne2/ner1 ner1/Ner2w Ner2w*	4–5
Siesta I	× IR136-3	ABDR *ne1 **Ne2m**/**Ner1s** ner2*	7–8
T-136	× Siesta I	AABBDR *ne1 ne1/**Ne2m** ne2/**Ner1s** ner2*	5–6
Kormoran	× IR136-3	ABDR *ne1 **Ne2ms**/**Ner1s** ner2*	7–8
Korm-155	× T-136	AABBDRR *ne1 ne1/**Ne2ms** ne2/**Ner1s** ner1/Ner2w ner2*	5–6

ticale lines containing the wheats D400 and D800 showed weak hybrid necrosis (Table 1), the moderate hybrid necrosis of the above genotypes was apparently caused by the interaction between the two necrosis genes in the B genome of wheat. The two *Ner2w* alleles in the rye genome did not have an additional effect on the necrosis.

The F_1 plants of the cross Korm-155 × T-136 showed a hybrid necrosis with a degree of 5–6 (Table 3). The primary hexaploid triticale line T-136 is derived from the tetraploid wheat line 'Turgidum 34', which carries no dominant allele of necrosis genes (Table 2). However, its diploid rye component IR136-3 is known to possess the *Ner1s* gene (Ren and Lelley 1988). Thus, the genotype of the F_1 plants from this cross has to be:

*ne1 ne1/**Ne2ms** ne2/**Ner1s** ner1/Ner2w ner2.*

The gene *Ne2ms* originates from the wheat cultivar 'Kormoran' and the gene *Ner1s* from the inbred rye IR136-3. Therefore, in this case, hybrid necrosis was caused by the interaction between the gene *Ne2ms* in the B genome of wheat and the gene *Ner1s* in the R genome of rye.

The F_1 plants of crosses between the primary octoploid triticale lines, Jub-155 and Wa4-256, and the primary hexaploid triticale lines, 400-155, 400-256, 800-155, and 800-256, appeared to be moderately necrotic, with a degree of 4–5, whereas in the crosses of the lines Jub-256 and Wa4-155, with the same hexaploid triticale lines, the symptoms reached only a lower expression of 2–3 (Table 3). This difference in the appearance of the symptom in these two cross series can only be explained by assuming that the two rye inbred lines, L155 and L256, were genetically heterogeneous for the necrosis gene *Ner2* (Ren and Lelley 1988). A hexaploid triticale with the wheat D400 and D800 will not survive with a rye genome containing an *Ner2m* allele. When producing these triticale types, selection occurred against such a rye genotype. Since the wheat 'Jubilar' has none and 'Wa4' has only an *Ne1w* allele, no selection against a rye genotype with a moderate *Ner2* allele will occur, and both types of octoploid triticale can be established. According to the above data, the octoploid triticales, Jub-155 and Wa4-256, contain a moderate allele of the gene *Ner2,* whereas in the triticale lines, Jub-256 and Wa4-155, a weak allele is present. Thus, the F_1 plants from the crosses of Jub-155 and Wa4-256 with the hexaploid triticale lines, 400-155, 400-256, 800-155, and 800-256, possess the following genotype

***Ne1m** ne1/ne2 ne2/ner1 ner1/**Ner2m** Ner2w.*

In these crosses, hybrid necrosis was again caused by the interaction between the gene *Ne1m* in the B genome and the gene *Ner2m* in the R genome. The F_1 plants from the crosses of Jub-256 and Wa4-155 with the same hexaploid triticale lines had the genotype

***Ne1m** ne1/ne2 ne2/ner1 ner1/**Ner2w** Ner2w.*

The weak hybrid necrosis of these hybrids was due to the interaction between the alleles *Ne1m* and *Ner2w.*

The F_1 plants of the crosses Jub-155 × T-136 and Wa4-256 × T-136 exhibited hybrid necrosis with a degree of 5–6 (Table 3). These F_1 plants represent the following genotypes:

*ne1 ne1/ne2 ne2/**Ner1s** ner1/**Ner2m** ner2* and
*Ne1w ne1/ne2 ne2/**Ner1s** ner1/**Ner2m** ner2,*

respectively. Hybrid necrosis in both crosses is being caused by the interaction of the two necrosis genes in the R genome.

Expression of the necrosis genes in allopolyploids

In the present study the expression of the necrosis genes could be investigated at different levels of polyploidy (Table 4). The bread wheat cultivar 'Kormoran' carries the necrosis gene *Ne2ms.* The durum wheat line D400 contains the gene *Ne1m.* The F_1 plants from the cross

Kormoran × D400, which has the genomic formula of

AABBD

and thus the genotype of

Ne1m ne1/Ne2ms ne2,

exhibited hybrid necrosis with a degree of 5–6. The plants began to show symptoms of necrosis on the first leaf in the three-leaf stage; they did not tiller, and died a few weeks later with a total of five to six leaves. The triticale lines Korm-155 and 400-155 were derived from the two above-mentioned wheats and the inbred rye L155. The F_1 plants from the cross of these two triticale lines, Korm-155 × 400-155, with the genomic formula of

AABBDRR

and with the genotype of

Ne1m ne1/Ne2ms ne2/ner1 ner1/Ner2w Ner2w,

showed weaker symptoms of hybrid necrosis than the F_1 from the cross of the two wheat parents (Table 4). The progeny from the triticale cross started to exhibit hybrid necrosis only at the stage of tillering. After producing some tillers, these F_1 plants died at about spike emergence.

The hybrids from the cross between the hexaploid wheat line 'Siesta I' and the inbred rye IR136-3, with the genomic formula of

ABDR

and the genotype of

ne1 Ne2m/Ner1s ner2,

exhibited a very severe necrosis with a degree of 7–8. Necrosis of the first leaf started in the two- to three-leaf stage. These plants died in a very early stage of development. The primary hexaploid triticale line, T-136, originated from the tetraploid wheat line 'Turgidum 34', which carries no dominant necrosis allele, and the rye inbred line IR136-3 with a strong necrosis allele. The F_1 plants of the cross T-136 × 'Siesta I', which has the genomic formula of

AABBDR

and the genotype of

ne1 ne1/Ne2m ne2/Ner1s ner2,

showed clearly weaker symptoms of hybrid necrosis than the hybrid from 'Siesta I' × IR136-3 with the degree of 5–6, although the genotype of these F_1 plants corresponds with that of the wheat/rye cross. The same phenomenon was observed in the case of the crosses Korm-155 × T-136 and 'Kormoran' × IR136-3. It is apparent that the symptoms of hybrid necrosis exhibited in the triticale combinations was clearly weaker than in the crosses of the corresponding wheat and rye parents.

Discussion

Hybrid necrosis caused in wheat by the dominant complementary interaction of two genes in the B genome, *Ne1* and *Ne2*, was also found in hexaploid triticale. It was assumed that the same two necrosis genes in the B genome are responsible for the phenomenon (Gregory 1973; Behl and Manerchandani 1983). However, later works have supposed that the hybrid necrosis in triticale could be caused by interaction between necrosis genes in B and R genomes, too (Jung and Lalley 1985; Scoles 1985). Ren and Lelley (1988) described two genes in rye, which were named *Ner1* and *Ner2,* causing hybrid necrosis in the same complementary fashion as the genes *Ne1* and *Ne2* do in wheat. The results of the present study (Table 3) have proven that the necrosis genes in wheat and in rye can complement in triticale not only within the genome, which carry them, but also between genomes, even though the two genomes wheat and rye belong to two different genera. The phenomenon of hybrid necrosis in triticale is more complicated than in wheat or in rye. While in wheat and in rye, only two different dominant alleles of the necrosis genes may exist at the same time and, therefore, only one kind of complementation can occur, in triticale containing both the B and the R genomes, four different necrosis genes can be involved allowing the production of four different combinations:

1. *Ne1* and *Ne2* in the B genome
2. *Ner1* and *Ner2* in the R genome
3. *Ne1* in the B and *Ner2* in the R genome
4. *Ne2* in the B and *Ner1* in the R genome

The different cross-combinations in the present study (Table 3) illustrate the way hybrid necrosis can occur in triticale by the above-mentioned interactions. Knowledge about the distribution of necrosis genes in wheat and rye could help to avoid their introduction into newly synthesized primary triticale or into secondary ones through crosses with wheat or rye.

Existing rye varieties may be heterogeneous for different alleles of the necrosis genes as has been indicated by Ren and Lelley (1988). The octoploid triticale lines, Jub-155 and Wa4-155, which have been derived from the same rye inbred line L155, obviously carry different alleles of the gene *Ner2*. The same is true for the octoploid triticale lines Jub-256 and Wa4-256. The wheat parent of the octoploid triticale Jub-155, the variety 'Jubilar', containes a dominant necrosis allele (Table 2); the variety 'Chinese Spring' (Wa4), according to Hermsen (1963), is a *Ne1w* carrier. In all triticale hybrids (Table 3) involving these two hexaploid wheat genotypes, the *Ne1m* gene responsible for hybrid necrosis from the wheat side was contributed from either of the two tetraploid wheats D400 or D800. The higher degree of necrosis found in the hybrids Jub-155 × 400-155 and Wa4-256 × 400-155 in comparison to the hybrids Jub-256 × 400-155 and Wa4-155 × 400-155 can, thus, only be explained if one assumes that the original inbred lines L-155 and L-256 contained both a weak (*Ner2w*) and a moderate (*Ner2m*) dominant necrosis allele. When the wheat variety 'Jubilar' was fertilized with the inbred line L-155 to create the octoploid triticale Jub-155, this obtained an *Ner2m* allele, whereas 'Wa4' was fertilized with a gamete containing *Ner2w*. The reverse situation must have occurred in the case of L-256, which provided 'Jubilar' with an *Ner2w* and 'Wa4' with an *Ner2m* allele. An *Ner2m* allele could not be included into a hexaploid triticale because tetraploid wheat contains a moderate necrosis allele (*Nerm*) and plants which combine two moderate complementing alleles do not survive. The results of the crosses of Jub-155 and Wa4-256 with NP839, a carrier of *Ne1s*, provide further evidence for the occurrence of *Ner2m* in the rye genotypes L-155 and L-256 (Table 3).

The genotype of primary triticale lines and of secondary ones with known parentage with respect to their genes of hybrid necrosis can be identified by parental analysis. The genotypes of the triticale lines used in the present study can be described as follows:

Oktoploid triticale

Korm-155	*ne1 ne1/Ne2m Ne2m/ner1 ner2/Ner2w Ner2w*
Jub-155	*ne1 ne1/ne2 ne2/ner1 ner1/Ner2m Ner2m*
Jub-256	*ne1 ne1/ne2 ne2/ner1 ner1/Ner2w Ner2w*
Wa4-155	*Ne1w Ne1w/ne2 ne2/ner1 ner1/Ner2w Ner2w*
Wa4-256	*Ne1w Ne1w/ne2 ne2/ner1 ner1/Ner2m Ner2m*

Hexaploid triticale

400-155, 400-256, 800-155 and 800-256	*Ne1m Ne1m/ne2 ne2/ner1 ner1/Ner2w Ner2w*
T-136	*ne1 ne1/ne2 ne2/Ner1s Ner1s/ner2 ner2*

To detect necrosis genes in triticale with unknown parentage genotypes like T-136, a carrier of *Ner1s* or Korm-155 containing *Ne2m* can be used as a tester. However, the location of complementary gene, whether in the B or in the R genome, cannot be determined. Only if the tester possessed *Ne1* or *Ner1* and the wheat parent of the triticale being tested were a durum wheat, can a complementary necrosis gene be located in the rye genome. Since so far *Ne2* was never found in a tetraploid wheat, it has to be *Ner2*.

Expression of necrosis genes in allopolyploids

Sarkisian et al. (1971) have suggested that the *Ne1* allele carried by *T. durum* is stronger than the *Ne1s* allele of *T. aestivum*. However, Zeven (1973) attributed this difference to the suppression of the necrosis symptoms in hexaploid wheat by the D genome. Scoles (1985) has reported that the necrosis gene carried by rye inbred line IR136-3 produces a more severe symptom with the wheat line 'Siesta I' (ABDR) than the gene *Ne1s* in the hexaploid wheat (AABBDD). The present study provides further support to the observation of a different degree of expression of the necrotic phenotype if the number of genomes differs (Table 4). Necrosis in the hybrids between the primary triticale lines, Korm-155 and 400-155 (AABBDRR), appeared distinctly weaker than in the hybrids between the two parental wheats (AABBD), although an enhancement of the phenotypic expression of necrosis due to a cumulative effect of the additional two weak necrosis alleles in the R genome, *Ner2w Ner2w*, would be more logical. The only genotypic difference between these two crosses is the addition of two R genomes in the triticale hybrid.

The same phenomenon can be observed comparing the combination 'Siesta I' × IR136-3 (ABDR) and T-136 × 'Siesta I' (AABBDR). In this case the genotype of the two crosses differs by an additional A and B genome in the T-136 × 'Siesta I' hybrid (Table 4). This hybrid showed a distinctly weaker hybrid necrosis than the wheat/rye cross. Similar observation was made in a third pair of hybrid combinations (Table 4). It is apparent that any additional genome, A, B, D, or R, has a suppressing effect on the expression of hybrid necrosis. According to these results, the symptom of hybrid necrosis is not only defined by different combinations of necrosis genes and alleles, but also by the number of genomes contained in the hybrid. Thus, for identifying the genotype for necrosis genes, the ploidy level of the hybrid has to be considered.

In recent plant breeding, introduction of alien genetic material into cultivated plant species by chromosome manipulation or gene technology has become increasingly attractive. The results of the present study, however, indicate that the expression of alien genes in polyploids may not only be influenced by interactions with other specific genes of the recipient genotype, but it may also be modified by the entire genotype according to its level of polyploidy.

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