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GENETICAL ANALYSIS OF RYE (*SECALE CEREALE* L.) IV. LOCALIZATION OF GENES FOR HAIRY LEAF SHEATH AND HAIRY PEDUNCLES[1]

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Summary. By trisomic analyses four "hairy" genes of rye were localized. The major gene *Ha*1 controlling hairy leaf sheath and hairy peduncle was localized on chromosome 5R. Modifying genes controlling hairy peduncle were found on chromosomes 1R (*Ha*4), 4R (*Ha*2) and 6R (*Ha*3). Different mono-, di- and trigenic inheritance types of hairy peduncle were observed. Because of the close relationship of localization of genes controlling hairy leaf sheath and hairy peduncle the symbols *Hs* and *Hp* were replaced by the symbols *Ha*1 and *Ha*2, respectively.

Peduncle pubescence (hairy neck, hairy peduncle) has long been known to be associated with a rye chromosome (Kattermann 1937) and is a very useful genetic marker in wheat-rye hybrids. O'Mara (1951) observed the monogenic-dominant inheritance of hairy peduncle (*Hp*) and located controlling it gene on the chromosome arm 5RL. Using the monotelodisomic wheat-rye addition line 5RL (Chang 1975) estimated the linkage between the centromere and gene *Hp* (44.1 to 49.5 crossover units). The marker hairy peduncle was used to identify chromosome 5R in a number of wheat-rye substitutions and translocations (Zeller, Hsam 1983, Miller 1984).

A further "hairy" gene was described by Surikov and Romanova (1978). They observed the monogenic-dominant inheritance of the marker hairy leaf sheath (*Hs*). Simultaneously a linkage between *Hs* and the gene for spring type *Sp* (*Ae*) of 32.3% was found.

Already Balkandschiewa (1971) and Sturm (1978) reported about the increased peduncle pubescence of trisomic B, which is identically with chromosome 5R (Melz, Schlegel unpubl.), but it was found previously that a further "hairy" gene is located on chromosome E of the trisomic set (Melz et al. 1984) which was identified meanwhile to be chromosome 4R (Melz, Schlegel unpubl.).

Furthermore it was observed in earlier investigations that there are changing relationships between *Hp* and *Hs* and segregations of *Hp* do not fit the expected

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3 : 1 — segregation. For these reasons more intensive investigations of "hairy" genetics using trisomics and self-fertile lines were started. The results are presented in this paper.

MATERIAL AND METHODS

First of all a number of "hairy" lines was crossed with "hairless" lines selected in the Gülzow marker material to get first information about inheritance types and relationships between the markers for hairy leaf sheath and hairy peduncle. Then the trisomics of cv. Esto (Sturm 1978) were crossed with the self — fertile lines "vd" and "Z13." Line "vd" is a Polish mutant having violet seeds, line Z13 originated from a twin selected in Gülzow. Both lines showed no peduncle pubescence whereas the trisomics were selected for this marker.

Trisomic 7R was absent in the set because of its poor vitality and fertility. The F_1-trisomics having hairy leaf sheath and peduncle were selfed. The resulting disomic parts of the F_2-generations were analysed and the segregations were compared with the expected segregations using the *Chi*-square test (Weber 1978).

RESULTS

DISOMIC ANALYSES

The results of disomic analyses of the marker *Hs* show clearly, that there are two different segregation types, the expected 3 : 1-segregation and the 8 : 1 or 15 : 1-segregation controlled by two or more genes (Table 1). Because in trisomic analyses of the gene *Hs* only monogenic segregations were found the di- or trigenic inheritance types will be investigated in further tests. Segregation of the marker *Hp* is very complicated. It was observed, that in nearly all the cases the segregations can be interpreted by relationships between the gene *Hs* and one or more *Hp*-genes. The combinations 606 to 609 and 637 to 639 demonstrate, that the gene *Hs* is a necessary supposition for the expression of "hairy peduncle". But, besides the expected 3 : 1-segregation different segregations occurred in the combinations 78 and 89. These segregations cannot be interpreted by monogenic inheritance. Therefore some di- and trigenic models (Table 2) were tested to fit the observed segregations. It was found that the 45 : 19-segregation (model III, Table 3) fits the observed segregation very well. Model III is based on the assumption that "hairy peduncle" is controlled by the gene *Hs* and two additional genes modifying the gene *Hs*. This model was confirmed by a backcross analysis (combination 64) fitting the expected 3 : 5-segregation. Totally nine different inheritance types out of an unknown number were constructed (Table 2), seven of them were found in the described di- and trisomic analyses. The results of disomic test crosses permit to expect, that at least three different *Hp*-genes control the expression of "hairy peduncle".

Table 1. F_2-segregations of 'hairy leaf sheath' (*Hs*) and 'hairy peduncle' (*Hp*) from crosses 'hairy' × 'hairless' — disomics

Combination	Number of plants observed								χ^2-values				
	Hs	*hs*	*Hp*	*hp*	*HsHp*	*Hshp*	*hsHp*	*hshp*	3:1	8:1	45:19	1:1	8:5
714	60	14							1.5				
716	53	16							0.1				
741	68	7							9.8*	0.1			
742	51	17							2.0				
754	88	5							19.1*	2.8			
755	283	87							0.4				
35			144	26					8.7*	2.9			
36			131	52					1.0				
37			144	35					3.0				
38			86	38					2.1				
78			437	192					10.4*		0.2		
81			391	129					0.1				
89			674	247					4.5		0.8		
93			223	77					0.1				
BC 64			116	160								7.0*	2.4
									3:0:0:1	27:21:0:16		3:1:0:0	
606					35	34	0	21		1.1			
607					79	0	0	24	0.2				
608					100	0	0	35	0.1				
609					64	0	0	23	0.1				
637					94	31	0	0				0.0	
638					39	21	0	0				3.2	
639					149	38	0	0				2.3	

* Significant at $\alpha = 0.05$

Table 2. Inheritance types of 'hairy peduncle' — some possible models

Model	Genotype of F_1-generation	Frequency of phenotypes in F_2-generations				Example combination
		HsHp	*Hshp*	*hsHp*	*hshp*	
I	*Ha1ha1 Ha2Ha2 Ha3Ha3 ha4ha4*	3	0	0	1	607 - 609
II	*Ha1ha1 Ha2ha2 Ha3Ha3 ha4ha4*	9	3	0	4	—
III	*Ha1ha1 Ha2ha2 Ha3ha3 ha4ha4*	45	3	0	16	78, 89
IV	*Ha1ha1 Ha2ha2 Ha3ha3 ha4ha4*	—	—	—	—	35
V	*Ha1ha1 Ha2ha2 ha3ha3 Ha4ha4*	27	21	0	16	606
VI	*Ha1Ha1 Ha2ha2 Ha3Ha3 ha4ha4*	3	1	0	0	637 - 639
VII	*Ha1Ha1 Ha2ha2 Ha3ha3 ha4ha4*	15	1	0	0	3R × Z 18/2
VIII	*Ha1Ha1 Ha2ha2 ha3ha3 Ha4ha4*	9	7	0	0	1R × Z 13
IX	*Ha1Ha1 Ha2ha2 Ha3ha3 Ha4ha4*	—	—	—	—	—

TRISOMIC ANALYSIS OF MARKER: HAIRY LEAF SHEATH

Monogenic segregations of gene *Hs* were observed in the F_2-progenies of combinations trisomics × "vd" (Table 4). Since in the combination trisomic 3R × "vd" the dominant trisomic 5 : 4-segregation appeared, the gene *Hs* is located on chromosome 5R. Since the gene *Sp* (Spring type) is located on chromosome 5R too

Table 3. Expected trigenic disomic F_2-segregations of 'hairy peduncle' from crosses primary trisomics × 'vd' (Model III)

Genotype	Frequency of genotypes				Phenotype
	disomic	trisomic gene *Ha*1	trisomic gene *Ha*2	trisomic gene *Ha*3	
*Ha*1.*Ha*2.*Ha*3	27	45 (72)	45 (72)	45 (72)	hairy
*ha*1*ha*1*ha*2.*Ha*3	9	36 (9)	15 (24)	15 (24)	hairless
*Ha*1.*ha*2*ha*2*Ha*3	9	15 (24)	36 (9)	15 (24)	hairy
*Ha*1.*Ha*2.*ha*3*ha*3	9	15 (24)	15 (24)	36 (9)	hairy
*ha*1*ha*1*ha*2*ha*2*Ha*3	3	12 (3)	12 (3)	5 (8)	hairless
*ha*1*ha*1*Ha*2.*ha*3*ha*3	3	12 (3)	5 (8)	12 (3)	hairless
*Ha*1.*ha*2*ha*2*ha*3*ha*3	3	5 (8)	12 (3)	12 (3)	hairless
*ha*1*ha*1*ha*2*ha*2*ha*3*ha*3	1	4 (1)	4 (1)	4 (1)	hairless

segregation
model III
– dominant 45 : 19 75 : 69 96 : 48 96 : 48
– recessive 45 : 19 120 : 24 105 : 39 105 : 39

(Schlegel et al. 1986), the linkage between the genes *Hs* and *Sp* (Surikov, Romanova 1978) was confirmed. According to the initial cross the recessive trisomic 8 : 1-segregation was expected instead of the observed dominant segregation. However, trisomic 5R was not analysed for homozygocity and, therefore, it is possible that the F_1-generation had the genetic configuration *Hshshs* resulting in the obser-

Table 4. Disomic F_2-segregations of 'hairy leaf sheath' (*Hs*) and 'hairy peduncle' (*Hp*) from crosses primary trisomics × Z13 and vd, respectively

Combination	Number of plants observed		χ^2-values		Number of plants observed		χ^2-values		
	Hs	*hs*	3 : 1	5 : 4	*Hp*	*hs*			
							3 : 1	15 : 21	24 : 12
1R × Z 13	32	0			13	19	20.2*	0.0	
2R × Z 13	92	0			0	92	–		
3R × Z 13	146	0			108	38	0.1		
4R × Z 13	109	0			68	41	9.6*		1.8
5R × Z 13/1	58	0			43	15	0.1		
5R × Z 13/2	129	0			114	15	12.0*		
6R × Z 13	60	0			44	16	0.1		
							45 : 19	75 : 69	96 : 48
1R × vd/1	86	38	2.1		84	35	0.0		
1R × vd/2					113	35	2.6		
2R × vd	145	57	1.1		240	95	0.2		
3R × vd	129	58	3.6		110	35	2.1		
4R × vd	143	63	3.4		209	119	7.1*		1.4
5R × vd	108	102	62.2*	1.8	187	165	48.8*	0.2	
6R × vd	114	48	1.8		63	39	3.6		1.1

* Significant at $\alpha = 0.05$

ved dominant segregation. No segregation of the gene *Hs* was found in the combinations trisomics × Z13. That means, that the gene *Hs* was homozygous in the F_2-generation.

TRISOMIC ANALYSES OF MARKER: HAIRY PEDUNCLE

Combinations trisomics × Z13 have the advantage that the observed segregations were controlled by *Hp*-genes only because the gene *Hs* is homozygous. The segregations (Table 4) demonstrate that one gene is located on chromosome 4R and another on chromosome 1R. Recessive digenic complementary or dominant monogenic segregations were found in the combinations trisomic 4R × Z13, whereas dominant digenic complementary inheritance was observed in the combination trisomic 1R × Z13. The segregation in the combination trisomic 5R × Z13/2 did not fit the expected 3 : 1-segregation, however, the interpretation of the observed 8 : 1-segregation is difficult. On the one hand, it can be a monogenic trisomic segregation of an additional gene on chromosome 5R. On the other hand, three different *Hp*-genes may be the cause. Further tests will have to answer this problem.

Because of segregation of the gene *Hs*, mono-, di- and trigenic inheritance types were expected in the F_2-progenies of combinations trisomics × "vd". There were some difficulties in discrimination of single segregation types because of a limited number of plants in some combinations. It was impossible to separate exactly 5 : 4- and 9 : 7-segregations from each other. Therefore, these segregations were not tested. However, on the basis of trigenic model III (Table 2 and 3) the F_2-progenies of combinations trisomics 4R × "vd" and 6R × "vd" were identified as trisomic segregations (Table 4). This means, that the gene *Hs* (5R) was modified by two *Hp*-genes located on chromosomes 4R and 6R. However, it was impossible to distinguish exactly the segregation in the combination trisomic 6R × "vd", but a close linkage between a "hairy" gene and a gene inducing grass dwarfness was observed in another trisomic analysis. Both genes are located on chromosome 6R and it is very likely that this "hairy" gene and the gene found in the combination trisomic 6R × vd are the same.

Because of close relationships between the located genes controlling hairy leaf sheath and hairy peduncle the gene symbols *Hs* and *Hp* should be replaced by *Ha*1 (5R) and *Ha*2 (4R), respectively. The genes located on chromosomes 1R and 6R were designated *Ha*4 and *Ha*3, respectively.

DISCUSSION

The results of trisomic analyses show clearly that there are still many open questions and that the hitherto existing model of "hairy" genetics is incomplete. The existence of more than one gene controlling hairy peduncle and different interactions between these genes have some negative effects on the use of hairy peduncle as a marker gene in breeding. Because of the extreme allogamy of rye populations genetic results have to be limited to given populations and the marker is suitable only for this special case. This restriction is demonstrated by the different inheritance types found in the relatively small material analysed. It was tried to estimate linkage between genes *Ha*1 and *b*, both located on chromosome 5R (De Vries, Sybenga

1984), but the back-cross resulted in the unexpected 3 : 5-segregation of hairy peduncle (combination 64, Table 1). This is one example of the difficulties in using the marker: hairy peduncle. Similar observations were made in trisomic analyses of the marker: coleoptile colour. There are at least four genes controlling coleoptile colour depending on the used rye material. It seems that some of the hitherto analysed markers are only special configurations of more complicated genetic systems and that inheritance depends on mutated loci.

The presented results are partly in conflict with findings obtained from analyses of wheat-rye-additions. Miller (1984) reported about the location of *Hp* and *Hs* only on the chromosome arm 5RL. Therefore, the results of wheat-rye-addition analyses should be considered as special cases too, because only an extremely limited number of rye gametes participated in the construction of lines, and it is impossible to interpret the complicated genetic system of rye using a limited genetic information of added rye chromosomes of one to three addition sets. Another problem is the expression of rye genes in the wheat backgrounds. It seems very probable that only such genes are expressed which are completed by corresponding wheat genes.

Therefore, a single method cannot be successful, and all possible methods like translocation, trisomic, addition and complementary linkage analyses should be complementary to each other in a sensible way.

Some confusion was caused by different locations of "hairy" genes (Miller 1984, Schlegel et al. 1986). However, different genes were not the reason of conflicting results but of difficulties in the identification of trisomics. Trisomics were crossed with translocations (Sybenga et al. 1985). By analysing M I multivalent configurations it was possible to identify trisomics. On the basis of these results the nomenclature of the trisomics B, D and E should be changed according to the identification of Schlegel et al. (1986).

Now the nomenclature of trisomics is: A=7R, B=5R, C=2R, D=3R, E=4R, F=4R and G=1R (Melz, Schlegel in press).

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ANALIZA GENETYCZNA ŻYTA (*SECALE CEREALE* L.) IV. LOKALIZACJA GENÓW OWŁOSIENIA POCHWY LIŚCIOWEJ I OWŁOSIENIA KŁOSA

Streszczenie

Zastosowano analizę trisomiczną dla zlokalizowania w chromosomach genów owłosienia. Główny gen owłosienia pochwy liściowej i owłosienia osadki kłosa zlokalizowano w chromosomie 5R. Geny modyfikatory kontrolujące owłosienie osadki kłosa zlokalizowano w chromosomach 1R (*Ha*4), 4R (*Ha*2) i 6R (*Ha*3). Obserwowano mono-, di- i trigeniczne typy dziedziczenia owłosienia osadki kłosa. Bliskie sąsiedztwo w chromosomach genów kontrolujących owłosienie pochwy liściowej i owłosienie osadki kłosa uzasadnia zastąpienie dotychczas stosowanych symboli *Hs* i *Hp* symbolami *Ha*1 i *Ha*2.

ГЕНЕТИЧЕСКИЙ АНАЛИЗ РЖИ *SECALE CEREALE* L. IV. ЛОКАЛИЗАЦИЯ ГЕНОВ ВОЛОСИСТОСТИ

Резюме

С помощью трисомных анализов были локализированы 4 гена волосистости. Главный ген *Ha*1, контролирующий ,,волосистое листовое влагалище" и ,,волосистый черешок", был локализирован на хромосоме 5R. Модифицирующие гены, контролирующие ,,волосистый черешок", были обнаружены на хромосомах 1R (*Ha*4), 4R (*Ha*2) и 6R (*Ha*3). Наблюдались различные моно-, ди- и три- генетические типы наследования ,,волосистого черешка". Ввиду близкой связи между ,,волосистым листовым влагалищем" и ,,волосистым черешком" символы *Hs* и *Hp* были заменены соответственно символами *Ha*1 и *Ha*2.