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AN ATTEMPT TO DETERMINE LINKAGES BETWEEN GENES CONTROLLING SOME QUANTITATIVE TRAITS OF INBRED LINES OF RYE (*SECALE CEREALE* L.).
II. LINKAGES OF GENES CONTROLLING PUBESCENCE UNDER THE SPIKE AND THE SHAPE OF LIGULE WITH GENES CONTROLLING OTHER QUALITATIVE TRAITS[1]

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Summary. In the previous studies it was found that such traits, as coloration of ligule and auricles, pubescence under the spike, ligule shape, flagleaf shape and waxy coating, are inherited by 2 - 5 pairs of genes. There is, therefore, a possibility of linkage, particularly of genes controlling anthocyanin coloration with the remaining genes.

Observations on segregations of the studied traits in the F_2 generation showed a possibility of linkage between individual genes controlling all the mentioned traits.

Since 1 pair of genes controlling pubescence under the spike are located on the chromosome 5*R* (6), it should be recognized that genes, determining these traits, are located on the same chromosome.

In the previous part of the work (Ruebenbauer et al. 1986) devoted to linkages of genes controlling coloration of auricles, ligule and nodes of rye the authors confined themselves to meditations on possibilities of the existence of common genes. Results of the studies permit to infer that genetic systems controlling coloration of auricles and ligule are very similar and differ from the genetic system controlling coloration of nodes.

It was decided to separate that group of linkages as different from the others. In the considerations on the genetic system controlling anthocyanin coloration the main point was to check what is the total number of gene pairs participating in the realization of that trait and whether there exist such genes, which simultaneously participate in coloration of different organs.

In the present paper constituting part II of the work, attention was paid to a possibility of detection of adequate linkages mainly between the pubescence under the spike, the ligule shape and the remaining qualitative traits.

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MATERIAL AND METHODS

The material for determination of gene pair linkages were results of phenotype segregations in the second generation of 20 interline rye hybrids observed in 1975.

In the first part of the work (Ruebenbauer et al. 1986) the authors described in detail the method of determination of linkages, which consisted in calculation of theoretical segregations and in finding whether the number of recombinants calculated theoretically is significantly smaller than the number of the observed recombinants using the *chi*-square test. When calculating the theoretical number of recombinants, it was assumed that the inheritance of individual traits is independent. Since theoretical segregations of single traits have been known, the theoretical segregations of two pairs of traits, under the assumption of the lack of linkages, was calculated as a product of probabilities of both segregations. If the distribution of the observed in F_2 generation parental phenotypes and recombinants significantly deviated from the theoretical distribution in favour of an increase in the number of the parental phenotypes, it pointed out to the existence of linkage.

Generally speaking, the size of linkage depends on the distance of two pairs of genes on the chromosome. However, a precise determination of that distance depends also on the:

1) inheritance mode of genes;

2) number of gene pairs controlling linkaged traits polymerically; the larger is the number of gene pairs participating in realization of given pairs of traits, the larger is the number of recombinants;

3) mode of gene linkage; at linkage of the „trans" type the number of recombinants is larger than at linkage of the „cis" type.

It is beyond any doubts that classification of quantitative traits controlled by genes of a polymeric action and frequently displaying continuous variation cannot be precise. Besides that inaccuracy of observations can be also explained by facultative classification of individual traits and by variation of these under the effect of the environment. To that type of unsteadily determined traits there should be added a waxy coating defined as strong, weak and absent, as well as pubescence under the spike determined in two categories — as lacking and occurring. For these reasons, therefore, it was impossible to determine distances between the genes on the chromosomes; we could only try to find whether the gene linkage does or does not exist.

RESULTS AND DISCUSSION

Like in the previous part of the work (Ruebenbauer et al. 1986), beside determination of linkages on the basis of the number of recombinants, the authors took into consideration the analogy or differences in the genetic formulas of pairs of the parents and hybrids of the first generation. A new concept of the so-called linkage detectability has been also introduced. Linkage detectability depends on the number of chromosome and gene pairs, which may be linkaged. In this case a correspon-

ding probability may be considered taking k as the number of the studied gene pairs and n as the number of single chromosomes. The smaller is the number of single chromosomes and the larger is the number of studied genes, the larger are possibilities of linkage detectability. A single or more linkages will occur in the case, when $k \geq n+1$, i.e. when the number of gene pairs is larger than the number of single chromosomes. In the case of rye $n=7$, i.e. for the number of gene pairs equal to 8, at least one or more linkages should be detected.

Table 1. The values of probabilities of linkages for 2 - 8 pairs of the studied genes

No. of studied gene pairs	Probability of linkages		Detectability of linkages (in %)
	in fraction	in %	
2	1/7	14	3.5
3	2/7	29	7.2
4	3/7	43	11.0
5	4/7	57	14.0
6	5/7	71	18.0
7	6/7	86	21.0
8	7/7	100	25.0

Table 1 gives values of probabilities of linkages of two-eight pairs of the studied genes. Taking into consideration that in heterozygous populations there exist 25% of double heterozygotes (*AaBb*), making possible detection of linkages, Table 1 gives the percentage of linkage detectability, which is higher, the larger is the number of gene pairs. These numbers concern the detectability of two gene pairs linkage among the studied k genes, assuming that no linkage occurs between the genes controlling individual traits. On the basis of that assumption certain genetic formulas are ascribed to individual inbred lines, though the assumption should not be always correct. If more than two gene pairs participate in linkage of two traits, the number of recombinants is larger than the expected one, bearing in mind only a single pair. Such cases presumably take place in linkages between the coloration of auricles and ligule and the remaining traits. In that case, assuming linkage, the number of recombinants is more similar to the number occurring at independent inheritance, which has influence on a decrease of the detectability per cent. If, in addition to that, linkage is small, the percentage of the observed linkage

Table 2. Linkages between genes controlling pubescence under the spike and genes controlling the color of ligule, auricles and node, the shape of ligule and flagleaf, and the occurrence of waxy coating

Traits	Number of common gene pairs	Detectability %		Deviations from theoretical values
		observed	theoretical	
Ligule color	7	5	21	−16
Auricle color	7	5	21	−16
Ligule shape	4	5	11	− 6
Flagleaf shape	5	10	14	− 4
Waxy coating	5	15	14	+ 1
Node color	7	10	21	−11

detectability may be significantly lower than the theoretical percentage. Cases of that kind are observed for linkages between the genes controlling pubescence under the spike, on the one hand, and genes controlling the color of the ligule and auricles, on the other (Table 2).

Such deviations in the detectability of linkages between the genes controlling the ligule shape and genes controlling the color of the ligule and auricles occurred to a smaller degree or did not occur at all, which may be caused by a larger in that case linkage of these pairs of genes. Having to do with 20 populations of hybrids of the second generation, which the calculation of linkages was based on, we could calculate (one of 20 populations) with a 50% approximation the occurrence of significantly observed linkages between the genes controlling the ligule shape and genes controlling the remaining traits, which is given in Table 3. Comparing data of linkage detectability in Table 3 with the theoretical data it may be noticed that there

Table 3. Linkages between genes controlling the ligule shape and genes controlling the color of ligule, auricles and nodes, the flagleaf shape and the occurrence of waxy coating and pubescence under the spike

Traits	Number of common gene pairs	Detectability %		Deviations from theoretical detectability
		observed	theoretical	
Ligule color	7	25	21	+ 4
Auricle color	7	15	21	− 6
Flagleaf shape	5	20	14	+ 6
Node color	7	5	21	−16
Waxy coating	5	5	14	− 9
Pubescence under spike	4	5	11	− 6

is significant agreement between them, except detectability of linkages between the ligule shape and node color. In the previous studies (Ruebenbauer et al. 1986) a significant distinctness of the genetic control of the node color as compared to that of the auricle and ligule coloration was found. Presumably, most of genes controlling the node coloration are localized on the other chromosome contrary to genes controlling the coloration of auricles and ligule, which are localized on the same chromosome as genes controlling the ligule shape and pubescence under the spike, the shape of the flagleaf and waxy coating.

OCCURRENCE OF LINKAGES

PUBESCENCE UNDER THE SPIKE AND THE LIGULE COLOR

Significant linkage occurs only in hybrid No. 8. The first generation of that hybrid is a complex heterozygote, making possible the occurrence of 8 different linkages ($Ha_1\ ha_1\ Ha_2\ ha_2\ Su_1\ su_1\ Su_2\ su_2\ Su_3\ su_3\ An_1\ An_1\ An_2\ an_2$). A similarly

complex heterozygote is hybrid No. 4 (*Ha*$_1$ *ha*$_1$ *Ha*$_2$ *ha*$_2$ *Su*$_1$ *su*$_1$ *Su*$_2$ *Su*$_2$ *su*$_3$ *su*$_3$ *An*$_1$ *an*$_1$ *An*$_2$ *an*$_2$) and hybrid No. 3 (*Ha*$_1$ *ha*$_1$ *Ha*$_2$ *ha*$_2$ *Su*$_1$ *su*$_1$ *Su*$_2$ *Su*$_2$ *Su*$_3$ *su*$_3$ *An*$_1$ *an*$_1$ *an*$_2$ *an*$_2$), however, in these hybrids linkages did not take place. Comparing the formulas of these hybrids of the first generation, it may be assumed that one of the genes controlling pubescence under the spike is linkaged with a single gene *Susu*. It is also possible that a single pair of genes controlling pubescence under the spike is linked with a single pair of *Anan* genes. The remaining hybrids of the first generation display a significantly smaller heterozygocity and this may explain the lack of linkages in their progeny. Beside polymeric gene action, a small detectability of linkages may be also caused by a large distance of genes on the chromosome.

PUBESCENCE UNDER THE SPIKE AND THE COLOR OF AURICLES

The degree of heterozygocity of genes controlling the color of auricles of the first generation hybrids is highly analogous to that of genes controlling the color of ligule. Therefore, in hybrid No. 8 also 8 possible linkages have been detected (*Ha*$_1$ *ha*$_1$ *Ha*$_2$ *ha*$_2$ *Su*$_1$ *Su*$_1$ *Su*$_2$ *su*$_2$ *Su*$_3$ *su*$_3$ *An*$_1$ *an*$_1$ *An*$_2$ *an*$_2$). A similar heterozygocity was displayed by hybrid No. 3 (*Ha*$_1$ *ha*$_1$ *Ha*$_2$ *ha*$_2$ *Su*$_1$ *su*$_1$ *Su*$_2$ *su*$_2$ *Su*$_3$ *su*$_3$ *an*$_1$ *an*$_1$ *An*$_2$ *an*$_2$). The remaining hybrids of the first generation show a smaller heterozygocity. In the case of hybrid No. 3 more probable seems to be the linkage of a single pair of genes controlling pubescence under the spike with the anthocyanin synthesis gene (*Anan*), though also possible is the linkage with the gene *Susu*. Like in the previous case, a low detectability of linkages may be caused by a polymeric action of genes or by a large distance of genes on the chromosome.

PUBESCENCE UNDER THE SPIKE AND THE LIGULE SHAPE

Significant linkages have been detected only in a single case, in the second generation of hybrid No. 19, in which a high degree of heterozygocity permitted to observe 4 possible linkages (*Ee*$_1$ *ee*$_1$ *Ee*$_2$ *ee*$_2$/*Ha*$_1$ *ha*$_1$ *Ha*$_2$ *ha*$_2$). A fairly significant value of the *chi*-square (0.8) for hybrid No. 3 may be indicative of the existence of a small linkage, whereas a low number of the expected recombinants in hybrid No. 8 (two individuals) did not permit to detect linkage. One can, therefore, accept the hypothesis that there is a small linkage between one of the genes controlling pubescence under the spike and one of the genes controlling the ligule shape.

PUBESCENCE UNDER THE SPIKE AND THE SHAPE OF THE FLAGLEAF

Like in the previous cases of linkages (1,2,3), significant linkages in this case accompany the largest heterozygocity permitting to detect 6 possible linkages. These are hybrids No. 8 (*Ha*$_1$ *ha*$_1$ *Ha*$_2$ *ha*$_2$/*AaBbIi*) and No. 19 (*Ha*$_1$ *ha*$_1$ *Ha*$_2$ *ha*$_2$/*AaBbIi*). A similarly high degree of heterozygocity occurred only in hybrid No. 11 of the F_1

generation (*Ha*$_1$ *ha*$_1$ *Ha*$_2$ *ha*$_2$/*AaBbIi*). It should, however, be noticed that the mother plant (cv. Węgierskie 1) with regard to the genes controlling the shape of the flagleaf by heterozygote (*AaBbIi*) was capable, beside heterozygotes, of transmitting to its progeny also homozygotes with the gene composition AABB or single homozygotes, which did not permit to detect a larger number of recombinants.

PUBESCENCE UNDER THE SPIKE AND A WAXY COATING

In this case, the highest heterozygocity of individuals in F_1 generation is not always accompanied by significant linkage. A high degree of heterozygocity of individuals in F_1 generation is not always accompanied by significant linkage. A high degree of heterozygocity in hybrid No. 7 occurs as a result of a large heterozygocity of the mother (cv. Horton C_5) with regard to the genes controlling a waxy coating (*Wa*$_1$ *Wa*$_1$ *wa*$_2$ *wa*$_2$ *Wa*$_3$ *wa*$_3$ and *Wa*$_1$ *Wa*$_1$ *Wa*$_2$ *wa*$_2$ *Wa*$_3$ *wa*$_3$). It does not occur in hybrid No. 13, where the parents differ not only with regard to a single gene controlling waxy coating, as a result of which there exists a possibility of linkage of one of the genes controlling pubescence under the spike with the gene *Wa* controlling partially a waxy coating. Quite significant linkages occurring also in hybrids No. 1 and 19 permit to assume that the genes controlling pubescence under the spike and a waxy coating are located fairly close to each other on the chromosome.

THE SHAPE AND COLOR OF LIGULE

Among 20 studied populations five significant linkages display a large conformity of the obtained detectability to the expected percentage of their detectability (Table 3). However, detectability here is not related to the degree of heterozygocity of the F_1 hybrids, which may indicate that linkages concern not only a single pair of genes controlling the color of ligule. This suggestion is supported by the comparison of genetic formulas of hybrids No. 5 (*Su*$_1$ *Su*$_1$ *Su*$_2$ *Su*$_2$ *Su*$_3$ *su*$_3$ *An*$_1$ *an*$_1$ *an*$_2$ *an*$_2$) and No. 19 (*Su*$_1$ *Su*$_1$ *Su*$_2$ *Su*$_2$ *Su*$_3$ *Su*$_3$ *An*$_1$ *an*$_1$ *An*$_2$ *an*$_2$), on the one hand, and by the comparison of genetic formulas of hybrids No. 19, 11 and 15, on the other. In the first case, the gene controlling the shape of ligule should be linked with one of the genes of anthocyanin synthesis (*Anan*). In the second case differences of genetic formulas for the color of ligule are as follows: hybrid No. 19 (*Su*$_1$ *su*$_1$ *Su*$_2$ *Su*$_2$ *Su*$_3$ *Su*$_3$ *An*$_1$ *An*$_1$ *an*$_2$ *an*$_2$), hybrid No. 11 (*Su*$_1$ *su*$_1$ *Su*$_2$ *su*$_2$ *Su*$_3$ *Su*$_3$ *An*$_1$ *An*$_1$ *an*$_2$ *an*$_2$) and No. 15 (*Su*$_1$ *su*$_1$ *Su*$_2$ *Su*$_2$ *Su*$_3$ *Su*$_3$ *An*$_1$ *an*$_1$ *an*$_2$ *an*$_2$). It may, therefore, be assumed that in these hybrids we have to do with the linkage of one pair of gene suppressors (*Susu*) with a single pair of genes controlling the shape of ligule. It is also possible that in hybrid 15 there occurs linkage between the genes *Anan* with a single pair of genes controlling the ligule shape. This assumption is supported by the results concerning the linkage of the color of auricles for the same hybrids as well as less certain, but also becoming evident linkages between pubescence under the spike and the color of ligule.

Table 4 (a - i). Segregations of traits concerning linkages in F_2 generation

Table 4a

Hybrid No.	Hybrid origin	Genetic formula of pubescence under spike of		Genetic formula of ligule color		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
3	Kazim. D × Zeel. E	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	$su_1Su_2su_2an_1an_2$	$Su_1Su_2Su_2An_1an_2$	32	36.3	22	17.7	1.554
4	Kazim. D × Dańk. sel. 231	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	$su_1Su_2su_2an_1an_2$	$Su_1Su_2su_2An_1An_2$	12	13.2	3	1.8	0.909
8	Horton C_5 × Dańk. sel. 231	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	$su_1su_2Su_2An_1an_2$	$Su_1Su_2su_2An_1An_2$	22	13.7	9	17.3	9.011

Table 4b

Hybrid No.	Hybrid origin	Genetic formula of pubescence under spike of		Genetic formula of auricle color of		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
3	Kazim. D × Zeel. E	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	$Su_1su_2su_2an_1an_2$	$su_1Su_2Su_2an_1An_2$	37	30.6	17	23.4	3.088
8	Horton C_5 × Dańk. sel. 231	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	$Su_1su_2Su_2an_1an_2$	$Su_1Su_2su_2An_1An_2$	20	13.1	11	17.9	6.294

Table 4c

Hybrid No.	Hybrid origin	Genetic formula of pubescence under spike of		Genetic formula of ligule shape of		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
3	Kazim. D × Zeel. E	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	ee_1Ee_2	Ee_1ee_2	31	27.7	23	26.3	0.807
8	Horton C_5 × Dańk. sel. 231	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	Ee_1ee_2	ee_1Ee_2	29	29.0	2	2.0	0.000
19	Zeel. G × Zeel. E	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	ee_1Ee_2	Ee_1ee_2	25	14.0	8	19.0	15.011

Table 4d

Hybrid No.	Hybrid origin	Genetic formula of pubescence under spike of		Genetic formula of flagleaf shape of		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
8	Horton C_5 × Dańk. sel 231	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	*aaBBII*	*Aabbii*	12	0.4	19	30.6	340.797
19	Zeel. G × Zeel. E	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	*AaBbii*	*aaBBII*	19	0.0	14	33.0	10.939
11	Węgierskie 1 × Zeel. E	$ha_1ha_1Ha_2Ha_2$	$Ha_1Ha_1Ha_2ha_2$	*AaBbii*	*aaBBII*	50	44.2	14	19.8	2.460

Table 4e

Hybrid No.	Hybrid origin	Genetic formula of pubescence under spike of		Genetic formula of waxy coating of		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
1	Kazim. H. × Zeel. E	$ha_1ha_1Ha_2Ha_2$	$Ha_1Ha_1Ha_2Ha_2$	$Wa_1Wa_1wa_2wa_2wa_3wa_3$	$wa_1wa_1wa_2wa_2Wa_3Wa_3$	10	4.3	13	18.7	9.293
7	Horton C_5 × Zeel. E			$Wa_1Wa_1Wa_2wa_2Wa_3wa_3$						
		$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2ha_2$	$Wa_1Wa_1wa_2wa_2Wa_3wa_3$	$wa_1wa_1wa_2wa_2Wa_3Wa_3$	21	6.6	20	34.4	37.411
13	Rogal. Pa × Zeel. E	$ha_1ha_1Ha_2ha_2$	$Ha_1Ha_1Ha_2ha_2$	$wa_1wa_1wa_2wa_2Wa_3wa_3$	$wa_1wa_1wa_2wa_2Wa_3Wa_3$	11	6.5	18	22.5	4.015
19	Zeel.G × Zeel.E	$ha_1ha_1ha_2ha_2$	$Ha_1Ha_1Ha_2Ha_2$	$Wa_1Wa_1Wa_2Wa_2wa_3wa_3$	$wa_1wa_1wa_2wa_2Wa_3Wa_3$	24	3.9	9	29.1	117.476

Table 4f

Hybrid No.	Hybrid origin	Genetic formula of ligule shape of		Genetic formula of ligule color of		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
5	Kazim. C × Zeel. E	ee_1EE_2	EE_1ee_2	$Su_1Su_2su_3an_1an_2$	$Su_1Su_2Su_3An_1an_2$	54	47	8	15	4.309
9	Uniwers. 145 × Zeel. E	EE_1EE_2	EE_1ee_2	$su_1Su_2Su_3An_1an_2$	$Su_1Su_2Su_3An_1an_2$	31	23	4	12	8.116
11	Węgier. 1 × Zeel. E	Ee_1ee_2								
		EE_1ee_2	Ee_1ee_2	$su_1su_2Su_3An_1an_2$	$Su_1Su_2Su_3An_1an_2$	40	21	24	43	25.586
15	Wlerzb. C × Zeel. E									
		ee_1Ee_2	Ee_1ee_2	$su_1Su_2Su_3an_1an_2$	$Su_1Su_2Su_3An_1an_2$	15	3	2	14	58.286
19	Zeel. G × Zeel. E	ee_1Ee_2	Ee_1ee_2	$Su_1Su_2Su_3an_1An_2$	$Su_1Su_2Su_3An_1an_2$	25	15	8	18	12.222

Table 4g

Hybrid No.	Hybrid origin	Genetic formula of ligule shape of		Genetic formula of auricle color of		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
9	Uniwers. 145 × Zeel. E	EE_1EE_2	EE_1ee_2	$Su_1su_2Su_3an_1an_2$	$su_1Su_2Su_3an_1An_2$	35	21	0	14	23.333
16	Wlerzb. B_1 × Dańk. sel 231	EE_1Ee_2	ee_1EE_2	$su_1Su_2Su_3an_1an_2$	$Su_1Su_2su_3An_1An_2$	15	36	41	20	34.300
20	Włoszan. C × Zeel. E	ee_1Ee_2	EE_1ee_2	$Su_1Su_2Su_3an_1An_2$	$su_1Su_2Su_3an_1An_2$	26	18	46	54	4.741

Table 4h

Hybrid No.	Hybrid origin	Genetic formula of ligule shape of		Genetic formula of flagleaf shape of		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
8	Horton C_3 × Dańk. sel 231	EE_1ee_2	ee_1EE_2	*aaBBII*	*Aabbii*	11	6	20	25	5.167
12	Węgier. 1 × Dańk. sel 231	EE_1ee_2	ee_1EE_2	*AaBbii*	*Aabbii*	7	0	26	33	50.485

Table 4i

Hybrid No.	Hybrid origin	Genetic formula of ligule shape of		Genetic formula of waxy coating of		No. of indiv. in type of				χ^2
						parents		recombin.		
		mother	father	mother	father	obser.	theor.	obser.	theor.	
5	Kazim. C × Zeel. E	ee_1Ee_2	Ee_1ee_2	$Wa_1Wa_1Wa_2wa_2Wa_3wa_3$	$wa_1wa_1wa_2wa_2Wa_3Wa_3$	58	57	4	5	0.218
19	Zeel. G × Zeel. E	ee_1Ee_2	Ee_1ee_2	$Wa_1Wa_1Wa_2Wa_2Wa_3Wa_3$	$wa_1wa_1wa_2wa_2Wa_3Wa_3$	25	15	8	18	12.222
20	Włoszan. C × Zeel. E	ee_1Ee_2	Ee_1ee_2	$Wa_1Wa_1Wa_2Wa_2wa_3wa_3$	$wa_1wa_1wa_2wa_2Wa_3Wa_3$	14	21	58	51	3.294

LIGULE SHAPE AND OTHER TRAITS

If in the linkages between the pubescence under the spike and the genes controlling the remaining traits there became evident regularities consisting in the relation between the heterozygocity degree the existence of linkages, a possibility of this kind of explanations in the group of linkages between the genes controlling the ligule shape and other traits is more limited. Differences in the detectability of linkages of these two groups lie in a more facultative classification of the ligule shape in two categories: bordering and conical. Hence, genetic formulas ascribed to individual lines should not be always accurate.

THE SHAPE OF LIGULE AND THE COLOR OF AURICLES

Also in this case the detectability of significant linkages is not related to the heterozygocity degree of F_1 hybrids. In view of the fact that significant similarity was previously revealed between the control systems of the colour of ligule and auricles, it may be expected that analogous genes of the auricle coloration remain in linkage with the genes controlling the ligule shape. A large analogy of the formula of F_1 hybrid No. 9 for the colour of auricles ($Su_1\ su_1\ Su_2\ su_2\ Su_3\ Su_3\ an_1\ an_1\ An_2\ an_2$) to that of the ligule colour indicate that also in this case there exists the linkage of a single pair of gene suppressors with a single pair of genes controlling the ligule shape. A similar linkage exists also in hybrid No. 20, the formula of which is as follows: $Su_1\ su_1\ Su_2\ Su_2\ Su_3\ Su_3\ an_1\ an_1\ An_2\ An_2$. Hybrid No. 16 with the formula $Su_1\ su_1\ Su_2\ Su_2\ Su_3\ su_3\ An_1\ an_1\ An_2\ an_2$ according to the previous assumption rather displays linkage between a single pair of the genes *Anan* and a single pair of genes controlling the ligule shape.

THE SHAPE OF LIGULE AND FLAGLEAF

The expected detectability of linkages (14%) for 5 pairs of genes controlling the both traits does not differ much from the obtained one (10%) (2 cases among 20 populations). In the both cases, a significant heterozygocity of F_1 hybrids (e.g. hybrid No. 8 with the formula $Ee_1\ Ee_1\ Ee_2\ Ee_2\ AaBbIi$ and hybrid No. 12 with the formula $Ee_1\ Ee_1\ Ee_2\ Ee_2\ AABbii$) does not permit to find which gene pairs are presumably linked.

PUBESCENCE UNDER THE SPIKE AND COLORATION OF NODES

Though the occurrence of linkage was found in hybrid No. 19 using the *chi*-square test, however the fact that this kind of linkage did not repeat in at least three cases, according to the expectations of Table 2 for seven pairs of the studied genes, indicates that the linkage was accidental. It should be mentioned that no case of linkage

between the genes controlling the color of nodes and genes controlling pubescence under the spike has been detected. Since pubescence under the spike is undoubtedly linked with the colour of auricles and ligule, but genes controlling coloration of nodes show distinctness as compared to the genes controlling coloration of auricles and ligule, it may be believed that not any pair of genes controlling coloration of nodes linked with other genes has been detected.

THE LIGULE SHAPE AND A WAXY COATING

A low degree of the found detectability of linkages (5%) as compared to the expected one (14%) permits to infer that the linkage occurring in hybrid No. 19 is not significant. This is indicated also by the fact that in hybrids No. 5 and 20 there occurs full heterozygocity ($Ee_1\ Ee_1\ Ee_2\ Ee_2\ Wa_1\ wa_1\ Wa_2\ wa_2\ Wa_3\ wa_3$) according to the existence of linkages.

CONCLUSIONS

Comparing theoretical detectability of linkages with the obtained one and comparing genetic formulas for significantly detected linkages, one can draw the following conclusions:

1. Presumably two pairs of genes controlling coloration of both auricles and ligule (*Susu* and *Anan*) are linked with a single pair genes controlling pubescence under the spike. Because of a lower than expected detectability of that kind of linkages, it may be assumed that the corresponding pairs of genes are quite distant on the chromosome. On the other hand, the size of true linkages may be larger, since at the action of two pair of linked genes the number of recombinants will be larger than the number found at the action of a single pair.

2. Also presumably small linkage occurs between one of the genes controlling pubescence under the spike and one of the genes controlling the ligule shape.

3. Presumably a somewhat larger linkage than that mentioned in conclusion 2 occurs between a single pair of genes controlling pubescence under the spike and a single pair of genes controlling the shape of the flagleaf.

4. A single pair of genes controlling pubescence under the spike is presumably quite close linked with the gene $Wa_3\ wa_3$ controlling a waxy coating together with the gene Wa_1 and Wa_2.

5. The same, presumably two pairs of genes (*Susu* and *Anan*) controlling the coloration of auricles and ligule, linked with the genes controlling pubescence under the spike are also linked with a single pair of genes controlling the ligule shape. This linkage is presumably considerably larger than linkages of the genes *Susu* and *Anan* with genes controlling pubescence under the spike. On the basis of these linkages it should have been believed that between the genes controlling pubescence under the spike and genes controlling the ligule shape there also exists linkage. The experimental data permit to suggest that this linkage is not large.

6. A single pair of genes controlling the ligule shape is presumably linked with a single pair of genes controlling the flagleaf shape.

7. All the genes controlling the colorations of nodes do not belong to the discussed group of linkages.

8. Since a single pair of genes controlling pubescence under the spike is located on chromosome 6 (acc. to Heneen), i.e. on chromosome 5*R* (acc. to Riley), it should be considered that the mentioned genes controlling partially the ligule shape, the coloration of ligule and auricles as well as the waxy coating and the shape of the flagleaf, are located on the same chromosome.

The presented results concerning linkages and ascribed to chromosome 6 (5*R*) do not permit to determine the location of genes on it because of a small number of individual populations. Moreover, the lack of information concerning linkages between the color of ligule and auricles and the shape of the flagleaf as well as between the shape of the flagleaf, color of auricles and ligule and the waxy coating does not allow for a linear arrangement of genes.

However, detection of linkable groups will facilitate further studies on the localization of genes on that chromosome, which will be possible, when mainly translocated lines will be applied and when crossings of corresponding lines will be repeated.

REFERENCES

1. Ruebenbauer T., Kubara-Szpunar Ł., Kaleta S. (1980). Genes governing qualitative characters of inbred lines of rye (*Secale cereale* L.). Genetica Polonica, 21: 377 - 393.
2. Ruebenbauer T., Kubara-Szpunar Ł., Łoś T. (1981). Genes controlling quantitative traits in rye (*Secale cereale* L.). Genetica Polonica, 22: 397 - 410.
3. Ruebenbauer T., Kubara-Szpunar Ł., Kaleta S., Pająk K. (1986). An attempt to determine linkages between genes controlling some qualitative traits of inbred lines of rye (*Secale cereale* L.). I. Linkage of genes controlling anthocyanin coloration of nodes, auricles and ligule. Genetica Polonica, 27: 25 - 43.

PRÓBA OKREŚLENIA SPRZĘŻEŃ MIĘDZY GENAMI KONTROLUJĄCYMI NIEKTÓRE CECHY JAKOŚCIOWE LINII WSOBNYCH ŻYTA (*SECALE CEREALE* L.) II. SPRZĘŻENIA GENÓW KONTROLUJĄCYCH OMSZENIE POD KŁOSEM I KSZTAŁT JĘZYCZKA A GENAMI KONTROLUJĄCYMI POZOSTAŁE CECHY JAKOŚCIOWE

Streszczenie

W poprzednich badaniach stwierdzono, że takie cechy jak zabarwienie języczka i uszek, omszenie pod kłosem, kształt języczka, kształt liścia flagowego i nalot woskowy są uwarunkowane 2 do 5 parami genów.

Obserwacje rozszczepień badanych cech w pokoleniu F_2 potwierdziły wysunięte wcześniej przypuszczenie o istnieniu sprzężeń między poszczególnymi genami kontrolującymi wszystkie wymienione cechy. Ponieważ 1 para genów kontrolujących omszenie pod kłosem znajduje się na chromosomie 5*R*, przeto można uznać, że geny warunkujące wspomniane cechy są zlokalizowane na tym samym chromosomie.

ПОПЫТКА ОПРЕДЕЛЕНИЯ СЦЕПЛЕНИЙ МЕЖДУ ГЕНАМИ, КОНТРОЛИРУЮЩИМИ НЕКОТОРЫЕ КАЧЕСТВЕННЫЕ ПРИЗНАКИ ИНБРЕДНЫХ ЛИНИЙ РЖИ (*SECALE CEREALE* L.) II. СЦЕПЛЕНИЯ ГЕНОВ, КОНТРОЛИРУЮЩИХ ОВЛОСЕНИЕ ПОД КОЛОСОМ И ФОРМУ ЯЗЫЧКА, И ГЕНОВ, КОНТРОЛИРУЮЩИХ ОСТАЛЬНЫЕ КАЧЕСТВЕННЫЕ ПРИЗНАКИ

Резюме

В предыдущих исследованиях было установлено, что такие признаки, как окраска язычка и ушек, овлосение под колосом, форма язычка, форма флагового листа и восковой налёт, обусловлены 2 до 5 парами генов.

Наблюдения сегрегаций исследуемых признаков в поколении F_2 подтвердили сделанные ранее предположения о существовании сцеплений между отдельными генами, контролирующими все упомянутые выше признаки. Поскольку 1 пара генов, контролирующих овлосение под колосом, находится на хромосоме $5R$, можно считать, что гены, обуславливающие упомянутые признаки, находятся на этом же хромосоме.