The inheritance of plant height in crosses involving short-stem rye genotypes

Roman IZDEBSKI

Department of Genetics, Institute of Plant Breeding and Acclimatization, Radzików

Abstract. The paper presents results of studies on the inheritance of plant height in four short-stem genotypes of rye selected from genotypically different collection materials. Short-stem genotypes P-2, P-9, P-30 and P-52 were crossed to a tall-stem inbred line Uniwersalne 145 (S_{17}). The genotype P-2 was additionally crossed to a related, but tall-stem line P-2 W. In each cross combinations six generations – P_1, P_2, F_1, F_2, B_1 ($F_1 \times P_1$) and B_2 ($F_1 \times P_2$) – were examined. Distribution of plant height in hybrid generations had a continuous character, which indicated a polygenic determination of short stem in all "P" genotypes under study. Results of the genetic analysis (degrees of dominance, Burton method, Mather and Cavalli scaling tests, a six-parameter model of inheritance) showed a significant role of additive, dominant and epistatic gene action in genetic determination of short stem in the "P" genotypes. Only in the cross Uniwersalne 145 × P-52 one of the applied methods (a six-parameter model) has not confirmed a significant role of epistasis and dominance. In the cross combinations Uniwersalne 145 × P-2, Uniwersalne 145 × P-9 and Uniwersalne 145 × P-30 a reduction of the plant height was influenced by homozygote × homozygote and homozygote × heterozygote interactions as well as by dominance effects, whereas the plant height increase was influenced by heterozygote × heterozygote interaction as well as by effects of additive gene action. The combination P-2W × P-2 was found to have reverse relationships. The revealed epistasis had a duplicate character. The heritability of plant height was relatively high and varied from 70.4% to 84.9% depending on the cross combination.

Key words: gene action, heritability, inheritance, plant height, *Secale cereale* L., short-stem genotypes.

Despite a continuous progress in rye breeding, expressed in the introduction of intensive cultivars into culture, the yielding potential of this plant has not been fully utilized yet. A significant role in increasing rye productivity is

ascribed to short-straw cultivars (KOBYLJAŃSKI 1971, 1975, 1982a, 1982b, KONDRATENKO, GONCHARENKO 1974, GROCHOWSKI 1975, 1982, WĘGRZYN, GROCHOWSKI 1978, BAUER 1979, CHUDOERKO 1979, VELIKOVSKY 1979, WINKEL 1979, WOLSKI et al. 1980). Breeding of these cultivars is based on the use of short-stem carriers. At present, two basic types of short-stem donors are distinguished in rye:

1) monogenic, including that with a recessive or dominant determination of plant height (ANTROPOV, ANTROPOVA 1936, SYBENGA, PRAKKEN 1962, KUNAKBAEV 1969, FEDOROV et al. 1970, KOBYLJAŃSKI 1971, 1982b, KONDRATENKO, GONCHARENKO 1973, NALEPA, GRZESIK 1975, RYBA 1975, MADEJ, WARZECHA 1977, RUEBENBAUER et al. 1983, De VRIES, SYBENGA 1984, MELZ et al. 1984, SCHLEGEL et al. 1986).

2) polygenic (TSCHERMAK 1906 cited after TARKOWSKI 1984, KOBYLJAŃSKI 1975, 1982b, RUEBENBAUER 1978, ŁAPIŃSKI, PARZYSZEK 1982).

The first type of donors has been utilized especially intensively in the former Soviet Union, where on the basis of dominant sources of short-stemness many cultivars with the yield about 10 dt/ha higher than that from traditional cultivars have been bred in the last few years (KOBYLJAŃSKI 1982a, KOBYLJAŃSKI 1988 – personal information). Attempts to use dominant genes of short-stemness made in other countries including Poland, have not been successful so far. A barrier in cultivar breeding, among others, appeared to be difficulties in obtaining non-segregating hybrid populations selected on the basis of these sources. The use of recessive genes of short-stemness, however, was partially a success in the former GDR (cvs. Pollux, Donar and Muro) and in Poland (cv. Madar). The effectiveness of using short-stem rye genotypes in rye and triticale breeding against other cereals is low. In this connection, new donors of short-stemness, which would be widely applicable in breeding, are being searched for. These donors, like sources of other traits, should distinguish by a diverse origin and a desirable level of agronomic traits.

The aim of the present paper was to examine genetic determination of plant height in four short-stem rye genotypes selected by the author from genetically different collection materials distinguishing by a desirable level of some agronomic traits (IZDEBSKI 1987, 1988a, b). Besides, the influence of the direction of crossing on the inheritance of this trait as well as its heritability were evaluated.

Material and methods

Four short-stem "P" genotypes (P-2, P-9, P-30, P-52) selected from collection materials (IZDEBSKI 1987, 1988) and two tall-stem inbred lines (P-2W,

Uniwersalne 145) were studied. Description of the studied material is as follows:

P-2 – a progeny of an individual selected in 1978 from the old Polish cv. Zeelandzkie. Plants have stiff, coarse stems, erectoid leaves, long and awned spikes with light and shapely grains (1000-kernel weight up to 50 g).

P-9 – a progeny of two plants, encountered in 1979 among the hybrids of wild, annual rye species, obtained from the "VIR" Institute in Leningrad as *Secale cereale* ssp. *vavilovii*. Long spikes have small grains, with a very high protein content (up to 20%).

P-30 – a progeny of an individual selected in 1977 in the population designated MI-2.1(12). Plants are characterized by higher tillering and longer spikes. This is the only genotype among short-stem genotypes under study, which shows no reaction to GA_3 and represents the so-called "ga-ins" type (IZDEBSKI 1988b).

P-52 – a progeny of two plants isolated in 1979 from the breeding line MF-14 related to the Canadian cv. Kodiak. Plants are characterized by a potentially high productivity, long and awned spikes as well as by light and shapely grains.

P-2W – a progeny of three tall-stem plants related to the short-stem genotype P-2.

Uniwersalne 145 – an inbred line (reproduced in inbreeding for 17 years) of a normal height obtained from prof. Ruebenbauer, Agriculture University in Cracow.

Short-stem genotypes and tall-stem inbred lines were crossed in the following five combinations:

P-2W × P-2
Uniwersalne 145 × P-2
Uniwersalne 145 × P-9
Uniwersalne 145 × P-30
Uniwersalne 145 × P-52.

Progenies of short-stem plants separated from different initial populations were reproduced on special plots. After several years of selection, some non-segregating short-stem genotypes were obtained. These genotypes were reciprocally crossed with tall-stem breeding lines. In the autumn of 1985, seeds of the parental P_1 and P_2 forms, F_1, F_2, B_1 and B_2 hybrids were sown in rows on plots 2-m long with 20-cm spacing between the rows and 5-cm spacing between plants in the row. The experimental random block design with three replications was applied. P_1 and P_2 seeds were sown in 2 rows, F_1, B_1 and B_2 seeds – in one row and F_2 seeds – in 4 rows.

The significance of differences between the means of F_1 hybrids and respective reciprocal F_1 hybrids was tested by nonparametric Kruskall-Wallis test (SUM RANG program in SPETO laboratory in Radzików). The adequacy of the additive-dominant model was tested by Mather scaling tests (MATHER, JINKS 1977, 1982). Genetic parameters were estimated according to the formula given by Jinks and Jones (MATHER, JINKS 1982). The significance of particular parameters was tested using t statistics. Heritability coefficients in a broad sense were estimated by the formula given by MAHMUD and KRAMER (1951). The theoretical means of F_1 and F_2 hybrids were calculated according to the method proposed by Burton (HOFF et al. 1973).

The significance of differences between empirical means and expected means of F_1 and F_2 hybrids were tested by the t-Student's test (ELANDT 1964). The degrees of dominance h_1 and h_2 were calculated by the method given by PETR and FREY (1966).

Results and discussion

Parental forms, despite overlapping of their variation ranges, clearly differed from one another in the average plant height (Table 1), thereby fulfilling the basic requirement of the use of quantitative genetics methods concerning difference between crossed parents (PLARRE, FISHER 1975, VELIKOVSKY, MACHÁN 1982, MATHER, JINKS 1982). These differences ranged from 20 cm (Uniwersalne 145 × P-52) to 55 cm (P-2W × P-2) depending on the cross combination. Variation of the plant height in the majority of the hybrid generations F_1, F_2, B_1 and B_2 (in 22 out of studied 25) had a continuous character (Table 1), which suggested a polygenic determination of that trait and simultaneously indicated genetic distinctiveness of "P" genotypes from the carriers of a shortened stem with a monogenically determined plant height, which are known and described in the literature. In cases of monogenic determination of a shortened stem in F_2 hybrids a segregation into short-stem and tall plants in the ratio 3:1 or 1:3 was observed (SYBENGA, PRAKKEN 1962, KUNAKBAEV 1969, FEDOROV et al. 1970, KOBYLJAŃSKI 1971, 1982a, NALEPA, GRZESIK 1975, MADEJ, WARZECHA 1977, WĘGRZYN, FABIJANOWSKI 1980, RUEBEN-BAUER et al. 1981, De VRIES, SYBENGA 1984, KUBICKA 1987). Though distributions of plant height in the F_1, B_1 and B_2 generations in the cross combination P-2W × P-2 indicated that the short-stem of the form P-2 was determined by a single dominant gene (Table 1), the distribution of plant height in the F_2 generation significantly differentiated from that suggested by the

segregation into short-stem and high plants in the 3:1 ratio. However, the occurrence of a separate group of plants 30-50 cm high in that generation indicated segregation in the ratio 1:15, which proved that plant height of that class was determined by a duplicate action of two recessive genes.

Means of plant height in the F_1 generations (except the combination P-2W × P-2) were intermediate in relation to those of the parental forms. The F_2 generation was found to have plants exceeding the value of this trait in the parental forms. One of the combinations (Uniwersalne 145 × P-9) was even found to have individuals exceeding the value of this trait in the both parental forms. The contribution of plants exceeding plant height of one of the parental forms in the F_2 generations was 7.5% as a maximum (Uniwersalne 145 × P-2). The occurrence of the above plants may indicate transgression, but its unbiased detection requires studies in the successive generations. Means of plant height in B_1 generations were lower than those of tall parents, and depending on the combination they were higher or lower than the means of F_1 generations (Table 1). Means of plant height in B_2 generations were lower than those of B_1 generations (for a given hybrid combination). Simultaneously these means were higher than those of their relevant short-stem parents. Relations between the means of backcross generations and those calculated from F_1 generation and from one of the parents showed inadequacy of the additive-dominant model in the inheritance of plant height, since these means were noticeably different.

The influence of direction of crossings on plant height

An important role in inheritance may be played by direction of crossing, which is connected with the action of extranuclear factors. Out of the four studied "P" genotypes, a significant influence of the direction of crossings on plant height was found only in the line P-9 selected from the hybrid of wild annual species (IZDEBSKI 1987). Plants of F_1 generation derived from the line Uniwersalne 145 crossed to that form were as many as 20 cm higher in comparison to plants obtained from a reciprocal crossing (Table 2). This fact should be taken into consideration when the line P-9 is used in breeding short-straw cultivars.

Literature reports on the influence of cross direction upon plant height in rye, particularly in short-stem forms are few. KOBYLJAŃSKI (1971, 1973, 1982b) found no such influence in his studies on the short-stem mutant EM-1. He reports, however, on a significant influence of the direction of crossings on that trait in the group of dwarf forms with polygenic and recessive determination of plant height. An insignificant influence of the direction of crossings on the plant height was found in the hybrid Dańkowskie Złote/Kustro (WĘGRZYN, GROCHOWSKI 1978).

Table 1. Distribution of rye plant height for parents and hybrid generations

Parental form and cross combination	Plant height (cm)														n[a]	$\bar{x}$	SD[b]
	35	45	55	65	75	85	95	105	115	125	135	145	155	165			
Parental forms																	
P-2W										10	19	15	7	2	53	139.5	10.7
Uniwersalne 145							4	3	27	23	3				60	117.8	8.6
P-2				3	17	25	20	3							68	84.7	9.1
P-9			7	8	17	25	15								72	79.5	12.4
P-30			7	5	21	24	10								67	79.0	11.6
P-52				2	13	23	14	14	6						58	86.2	9.9
Generations F₁																	
P-2W × P-2				5	10	9	12	6	4						46	89.2	14.2
Uniwersalne145 × P-2				4	6	11	11	4	6	4	10	3			59	112.8	23.9
Uniwersalne145 × P-9					2	6	7	18	4	2	2	9	10		60	116.8	25.2
Uniwersalne145 × P-30					12	8	4		2	3	15	10	3		57	114.3	28.8
Uniwersalne145 × P-52						12	8	20	6	2	2				50	101.9	12.0
Generations F₂																	
P-2W × P-2	3	15	...	39	57	69	52	34	17	29	6	9	3		333	90.8	18.7
Uniwersalne145 × P-2				18	20	57	49	41	37	28	33	19	4		306	104.8	22.6
Uniwersalne145 × P-9		6	3	12	24	59	67	36	23	47	16	7			300	99.7	21.2
Uniwersalne145 × P-30			15	17	27	60	44	52	47	14	40	19	1		336	102.0	24.0
Uniwersalne145 × P-52				14	44	103	84	41	26	31	8	3			354	95.0	17.0

Table 1, cont.

	35	45	55	65	75	85	95	105	115	125	135	145	155	165	n[a]	x̄	SDb
Generations B₁																	
P-2W×P-2						4	24	4	12		28	20	3	1	96	122.6	21.9
Uniwersalne145×P-2				10	10	29	22	10	22	11	4	2			120	98.6	19.2
Uniwersalne145×P-9				4	24	14	10	14	9	5	3	3			86	95.0	20.3
Uniwersalne145×P-30			2	2	10	28	22	6	10	14	12	6			112	102.3	22.7
Uniwersalne145×P-52					8	20	30	6	10	38	10				122	106.6	18.7
Generations B₂																	
P-2W×P-2					18	36	36	21							111	91.2	9.7
Uniwersalne145×P-2					5	9	32	44	40	4	2				136	103.6	10.9
Uniwersalne145×P-9	2		2	22	14	22	16	6	2	4	2	4			96	85.8	22.2
Uniwersalne145×P-30			2	6	30	30	10	2	8	10	6	2			106	92.1	21.5
Uniwersalne145×P-52			6	9	6	24	3	3	18						96	87.6	13.8

a – number of analysed plants, b – standard deviation

Heritability

The basic problem of genetic studies on quantitative traits is estimation of genetic variation in phenotypic variation by calculating heritability coefficients in a broad and narrow sense (WĘGRZYN 1972). This paper presents heritability coefficients only in a broad sense, since coefficients in a narrow sense are distorted in the case of nonallelic interactions, which was supported by calculations of the same coefficients performed on the material presented in this paper (the obtained values were negative, approximated zero or exceeded coefficients in a broad sense).

Table 2. Means of plant height, heritability coefficients and degrees of dominance in five reciprocal crosses of rye

Cross combination	Means		Difference	H^2** (%)	Degrees of dominance	
	F_1	F_1^+			h_1	h_2
P-2 W × P-2	105.0	106.7	−1.7	82.4	−0.84*	−1.85*
Uniwersalne 145 × P-2	136.6	133.1	3.5	84.9	0.70*	0.42*
Uniwersalne 145 × P-9	149.7	129.5	20.2[a]	76.2	0.95*	0.11
Uniwersalne 145 × P-30	131.6	135.4	−3.8	82.6	0.82*	0.19*
Uniwersalne 145 × P-52	111.8	117.2	−5.4	70.4	−0.006	−0.89*

a – difference significant according to Kruskall-Wallis test at $\alpha = 0.05$
** H_s^2 – heritability coefficient according to MAHMUD and KRAMER (1951)
* h_1 and h_2 – significantly different from zero
+ reciprocal cross.

In all hybrid combinations under study it was found that plant height was determined by genetic factors to a large degree. That was indicated by high heritability coefficients, which ranged from 70.4% (Uniwersalne 145 × P-52) to 84.9% (Uniwersalne 145 × P-2) (Table 2). Data on heritability coefficients of plant height in short-stem forms of rye are missing in the literature. But there is numerous information concerning genetic variation of the discussed trait in populations with a normal plant height. In most studies on this trait a high value of heritability coefficients in a broad sense was registered (ŁA-PIŃSKI 1976, PATYNA, GROCHOWSKI 1978, WĘGRZYN, GROCHOWSKI 1978, KOMENDA et al. 1982, KEDROV-ZICHMAN et al. 1985). In some studies the value of the discussed coefficients varied depending on the hybrid combination. In studies on interlinear hybrids (RUEBENBAUER et al. 1981), statistically

insignificant heritability coefficients were found for most cross combinations. A low heritability for plant height was obtained in the studies conducted with the cv. Dańkowskie Złote (KACZMAREK 1985).

Degree of dominance

In the cross combination P-2W × P-2 the degrees of dominance h_2 and h_2 had significantly negative values, which indicated dominance of a short stem over a tall one (Table 2). In the combination Uniwersalne 145 × P-52 the dominance degree h_1 was close to zero, whereas the dominance degree h_2 had a significantly negative value. That could arise from the fact that the plant height in the F_1 generation of the combination Uniwersalne 145 × P-52 was determined by the action of additive genes; however, in the F_2 generation of that combination, dominance of a short stem over a tall one was observed. In other cross combinations the degrees of dominance h_1 and h_2 had significantly positive values (except the degree of dominance h_2 in the combination Uniwersalne 145 × P-9), which in turn indicated dominance of a tall stem over a short one.

Gene action

Burton method

Interrelations of empirical and expected means in the F_1 and F_2 generations were studied. In the combination P-2W × P-2 the expected mean of the F_1 generation was significantly higher than the observed one, indicating partial dominance of a low value of this trait over a high one (Table 3).

Table 3. Differences between empirical and expected mean values for plant height of rye in cross combinations involving short-stem and tall-stem genotypes

Cross combination	Difference between empirical and expected mean values		
	F_1	F_2	
	emp.–arith.	emp.–arith.	emp.–geom.
P-2W × P-2	–22.9*	–9.9*	–6.9*
Uniwersalne 145 × P-2	11.5*	–2.2	–1.4
Uniwersalne 145 × P-9	18.1*	–8.0*	–6.5*
Uniwersalne 145 × P-30	15.9*	–4.4*	–3.0*
Uniwersalne 145 × P-52	–0.1	–7.0*	–6.4*

* differences significant at the α = 0.05.

In the combination Uniwersalne 145 × P-52 these means did not differ significantly, which indicated an indirect inheritance of plant height in that combination. In the remaining cases, the expected means were significantly lower than the observed ones, which suggested that the trait of short-stem in the discussed combinations had a recessive character (Table 3). In the F_2 generations, statistically significant differences were also noticed between the observed and arithmetic means as well as between geometrical means (in 4 out of 5 cross combinations).

Mather scaling tests and joint Cavalli test

The complexity of the inheritance of short-stem in "P" genotypes was confirmed by results of A, B, C Mather tests and joint Cavalli test (Table 4). Therefore, the additive-dominant model appeared to be inadequate to explain the inheritance of plant hight in the studied hybrids. That model appeared to be improper also after logarithmic transformation of the original data (Table 5). A significant role of nonallelic interaction in the inheritance of plant height in rye was also observed by ŁAPIŃSKI and PARZYSZEK (1982), as well as by JEDYŃSKI and KACZMAREK (1986), whereas a significant role of non-additive gene action in the inheritance of that trait without separating epistasis and dominance was proved by WĘGRZYN and GROCHOWSKI (1978) as well as by RUEBENBAUER et al. (1981). Results indicating that plant height in rye was

Table 4. Results of Mather and Cavalli tests and estimates of genetic parameters for plant height in rye

Test, parameter	Cross combination				
	P-2W × P-2	Uniwersalne × P-2	Uniwersalne × P-9	Uniwersalne × P-30	Uniwersalne × P-52
A	16.5*	−34.4*	−44.6*	−27.5*	−6.5
B	8.5*	9.7*	−24.7*	−9.1	−12.9*
C	−39.4*	−8.9	−32.1*	−17.4	−27.8*
$\hat{m}$	111.9*	101.1*	97.6*	98.0*	100.3*
$[\hat{d}]$	26.3*	13.7*	18.7*	18.8*	16.5*
$[\hat{h}]$	−22.3*	10.0*	2.9	6.5*	−4.8*
$\chi^2_{(3)}$	91.1	102.8	67.5	22.9	30.8
$\hat{m}$	47.7*	117.1*	135.9*	117.6*	93.6*
$[\hat{d}]$	27.4*	16.6*	19.2*	19.4*	15.8*
$[\hat{h}]$	130.9*	−44.8*	−125.6*	−59.1*	−2.7
$[\hat{i}]$	64.4*	−15.8*	−37.2*	−19.2*	8.4
$[\hat{j}]$	8.0	−44.1*	−19.9*	−18.4*	6.4
$[\hat{l}]$	−89.4*	40.5*	106.6*	55.8*	11.0

* test or parameter values significantly different from zero.

Table 5. Results of Mather tests (A, B, C) for plant height of rye – data after log transformation

Cross combination	A	B	C
P-2W × P-2	0.074*	0.044*	–0.186*
Uniwersalne 145 × P-2	–0.151*	0.058*	–0.041
Uniwersalne 145 × P-9	–0.191*	–0.116*	–0.129*
Uniwersalne 145 × P-30	–0.115*	–0.029	–0.064
Uniwersalne 145 × P-52	–0.033	–0.064*	–0.129*

* value significantly different from zero

determined only by the additive gene action were also obtained (PATYNA, GROCHOWSKI 1978, RUEBENBAUER et al. 1981).

Estimation of genetic parameters

The most precise results were obtained after the use of a six-parameter model of inheritance (Table 4). The parameters [d] deteremining additive gene action were significant in all combinations. Differences in the inheritance of plant height in different cross combinations concerned first of all parameters connected with dominance and nonallelic interaction.

In the combination P-2W × P-2, genetic variation of plant height was determined by all types of gene action. Out of three parameters determining effects of nonallelic interaction, the parameters [i] and [l] appeared to be significant, which could be indicative of a significant role of interactions between homozygous loci as well as between heterozygous loci. In that combination the parameter [h] had a positive and highly significant value. The direction of gene action in that combination was different in relation to other combinations, which was indicated by positive values of the parameters [h] and [i] and by a negative value of the parameter [l] (in the remaining combinations a reverse situation was observed). A comparison between the mode of gene action in that combination and the mode and direction of gene action in the combination Uniwersalne 145 × P-2 (Table 4) deserves special attention.One of the parents in the both combinations was the same short-stem form, which made it possible to compare the influence of genetically varying maternal forms on the inheritance of plant height. The obtained results showed that variation of plant height in the both combinations was significantly determined by all types of gene action, while genetic differences between maternal forms

influenced the direction of gene action. Opposite directions of the gene action effects in these combinations had their own implications in determining the dominance of a short or tall stem in the F_1 and F_2 generations. In the combination P-2W $\times$ P-2, short-stem plants dominated over tall ones in both F_1 and F_2 generations, which was proved by negative values of the degrees of dominance h_1 and h_2 (Table 2) as well as by significantly lower observed and expected means in the F_1 and F_2 generations (Table 3).

In the combination Universalne 145 $\times$ P-2, the significance of all genetic parameters, including a significant role of all types of epistasis, was observed. Estimates of the parameters [h], [i] and [j] had negative signs, whereas the estimate of the parameter [l] had a positive sign. Likewise was the contribution of individual genetic parameters in cross combinations of the line Uniwersalne 145 with the forms P-9 and P-30. Not in all combinations the role of epistasis was clearly proved. In the combination Uniwersalne 145 $\times$ P-52, the parameters connected with epistatic gene action and the parameter connected with dominance were nonsignificant suggesting that the plant height in that combination was determined only by the additive gene action. That was, however, in contradiction with results of scaling tests, which clearly showed a significant role of epistatic effects (Table 4). It should be noticed that in this combination – as one of those studied – the empirical and expected means for the F_1 generation (Table 3) as well as the degree of dominance h_1 (Table 3) indicated additive action of genes conditioning plant height in F_1 generation. In the F_2 generation, these means (Table 3) and the dominance coefficient h_2 (Table 2) suggested dominance of short stem. Relations between the empirical and expected means in the F_2 generation, however, pointed out to an essential role of epistasis, which in combination with the scaling test results (Table 4) would suggest the existence of nonallelic interactions in that combination. A similar contradiction between the scaling test results and genetic parameters associated with epistasis was found by ŁAPIŃSKI and PARZYSZEK (1982) in one of the analysed combinations of interlinear rye hybrids. These contradictions most probably result from difficulties connected with a precise determination of some types of nonallelic interactions. Nonsignificance of the parameters [i] and [j] determining interaction of homozygous loci and that of homozygous and heterozygous loci, respectively, should not indicate the lack of nonallelic interaction of that type since these parameters depend on the coefficient r of gene distribution in the parental forms (KACZMAREK et al. 1984). The parameter [j] may be equal to zero also when r = 0. In this connection it is impossible to draw conclusions on the lack of nonallelic interaction of that

type, because there is no method to estimate this coefficient on the basis of segragating generations. The parameter [i] is equal to zero, when the the product kr^2 (number of loci × coefficient of gene distribution) occurring in the numerator of an equation for that parameter is equal to unit. Thus, if the parameter [i] is equl to zero, it is also impossible to draw conclusions about the lack of epistatic interaction of that type (KACZMAREK et al. 1984). As mentioned before, the parameter [h] also appeared to be nonsignificant in the combination Uniwersalne 145 × P-52. The lack of dominance was also indicated by the previously discussed relation between empirical and expected means of the F_1 generation and by the coefficient of dominance h_1. However, a significant role of dominance was indicated by the value of the coefficient h_2 (Table 2). These contradictions are probably concerned with the effects of nonallelic interactions of the type [i] and [j], which could exist, but have not been revealed. In the combination of the line Uniwersalne 145 with the breeding lines P-2, P-9 and P-30 the effects of dominance and homozygotes × homozygotes and homozygotes × heterozygotes interaction effects affected reduction in plant height, whereas its increase resulted from the interaction heterozygotes × heterozygotes. As mentioned before, this situation in the combination P-2W × P-2 was the reverse. Similar signs for the mentioned parameters as in the combination of Uniwersale 145 with short-stem "P" genotypes (except [j] parameter) were also obtained by ŁAPIŃSKI and PARZYSZEK (1982). JEDYŃSKI and KACZMAREK (1986) observed positive values of the parameters [h] and [i] and negative values for the parameters [l] in most combinations. The parameters [h] and [l] differed in signs in all studied cross combinations, indicating a duplicate character of nonallelic interactions.

As follows from the literature review, the number of short-stem carriers in rye is relatively large, but only few of them distinguish by desirable agronomic traits and by the known mechanism of plant height inheritance, which has a negative influence on the effectiveness of these forms utilization in breeding and is the main cause of a comparatively low contribution of short-stem varieties under cultivation. First of all forms with a monogenic control of short-stem are used in breeding. The most common of them is the form EM-1, especially in the former USSR. Forms with a polygenic determination of short-stem are less interesting to the breeders. But in the last years also the latter forms have been successfully used in breeding, which is proved by results of heterosis breeding in the FRG. The short-stem genotypes "P" belong to the last group and simultaneously they distinguish by a desirable level of some agronomic traits (IZDEBSKI 1987, 1988a, b), which permits to suggest that they constitute a valuable initial material, especially for heterosis breeding.

Conclusions

The trait of short-stem in four studied short-stem genotypes was determined polygenically. The "P" genotypes appeared to be genetically distinct in comparison to the known genotypes with a monogenic determination of short stem. A digenic model of interallelic interactions appeared to be insufficient to explain genetic basis of short stem in the "P" genotypes.

Plant height in these genotypes may be determined by both interactions of a higher order or gene linkages and a joint action of these factors. The inheritance of plant height in hybrids from crossing the above genotypes with tall-stem inbred lines concerned all types of gene action. Nonallelic interactions were of a duplicate character. Direction of the action of genes controlling plant height in a given short-stem genotype may significantly depend on the choice of its parental form.

Plant height in the studied hybrids was determined first of all by genetic factors, which was indicated by high values of heritability coeffcients in a broad sense. Significance of the additive effects and nonallelic interaction of the type [i] indicates a possibility of obtaining non-segregating forms with a varied plant height as a result of selection.

When using P-9 genotype in breeding short-stem cultivars, the influence of the direction of crossing should be taken into consideration.

REFERENCES

ANTROPOV V.I., ANTROPOVA V.F. (1936). Rozh – *Secale* L. Kulturnaya flora SSSR. 2: 1-95.

BAUER F. (1979). Sostojanie vozdelyvaniya i selektsii rzhi v VNR. Seminar "Genetika i selekciya rzhi". IHAR Radzików: 45-47.

CHUDOERKO V. (1979). Problemy selektsii intensivnych sortov ozimoj rzhi v usloviyakh vostochnoj lesostepi Ukrainy. Seminar "Genetika i selektsiya rzhi". IHAR Radzików: 88-92.

De VRIES J.N., SYBENGA J. (1984). Chromosomal location of 17 monogenically inherited morphological markers in rye (*Secale cereale* L.) using the translocation tester set. Z. Pflanzenzüchtg. 92: 117-139.

ELANDT R. (1964). Statystyka matematyczna w zastosowaniu do doświadczalnictwa rolniczego. Warszawa, PWN.

FEDOROV W.S., SMIRNOV V.G., SOSNICHINA S.P. (1970). Genetika rzhi (*Secale cereale* L.). Soobshchenije X. Charakter nasledovaniya karlikovosti. Genetika 6, 3: 5-17.

GROCHOWSKI L. (1975). Hodowla krótkosłomych i karłowatych form żyta. Prace Zesp. Bad. Hod. Żyta w 1974 r. IHAR Radzików: 85-97.

GROCHOWSKI L. (1982). Transgressivnaya selektsiya karlikovykh rzhi. Tag.-Ber. Akad. Landwirtsch.-Wiss. DDR, Berlin 198: 401-405.

HOFF J.C., KOLP B.J., BOHNENBLUST K.E. (1973). Inheritance of coleoptile length and culm length in crosses involving olesen's dwarf spring wheat. Crop Sci. 13: 181-184.

IZDEBSKI R. (1987). Charakterystyka krótkoźdźbłowych form żyta wyselekcjonowanych z materiałów kolekcyjnych. Biul. IHAR 161: 77-89.

IZDEBSKI R. (1988a). Ocena potencjalnej wartości rolniczej czterech krótkoźdźbłowych form żyta otrzymanych z materiałów kolekcyjnych. Roślinne zasoby genowe i synteza materiałów wyjściowych dla hodowli. Materiały z Sympozjum, Radzików 1985. Zeszyty Problemowe IHAR. Radzików 1988.

IZDEBSKI R. (1988b). A rapid seedling test for gibberellic acid response in rye. Proccedings of the EUCARPIA Genetic Resources Section. Symposium on Methods of Biochemical Evaluation of Germplasm Collections, 19-20 June 1986: 174-181.

JEDYŃSKI S., KACZMAREK J. (1986). Efekty epistatycznego działania genów u żyta. II Sympozjum "Genetyka ilościowa roślin uprawnych". Wrocław, 21-22 maja 1986: 5-6.

KACZMAREK J. (1985). Heterosis structure in rye population (Secale cereale L.). Genet. Pol. 26: 243-253.

KACZMAREK Z., SURMA M., ADAMSKI T. (1984). Parametry genetyczne – ich interpretacja i sposoby wyznaczania. Listy Biometryczme XXI(1): 3-20.

KEDROV-ZICHMAN O.O., SZAREPO T.I., BEL'KO N.B. (1985). Otsenka nasleduemosti osnovnykh khozyajstvennykh priznakov rzhi v sisteme diallel'nykh skrechchivanij. Dokłady Akademii Nauk BSSR XXIX (8): 750-751.

KOBYLJAŃSKI V.D. (1971). Novyj istochnik korotkostebel'nosti dlya selekcii nepolegayushchej rzhi. Vestn. Skh. Nauki (Mosc.) 9: 58-62.

KOBYLJAŃSKI V.D. (1973). Geneticheskiye osobennosti korotkostebel'nosti rzhi. Tr. Prikl. Bot. Genet. Sel. 49(3): 97-108.

KOBYLJAŃSKI V.D. (1975). Genetic resources of world's rye collection for solving of more important breeding problems. Hod. Rośl. Aklim. Nas. 19, 5/6: 439-446.

KOBYLJAŃSKI V.D. (1982a). Osnovnye problemy selektsii ozimoj rzhi v SSSR i perspektivy ich rezheniya. Tag.-Ber. Adad. Landwirtsch.-Wiss. DDR, Berlin 198: 31-46.

KOBYLJAŃSKI V.D. (1982b). Rozh. Geneticheskiye osnovy selektsii. "Kołos" Moskwa: 271.

KOMENDA K., KOMENDA B., KOMENDA-RONKA J. (1982). Nasledujemost nekotorykh priznakov rzhi (Secale cereale L.). Tag.-Ber. Akad. Landwirtsch.-Wiss. DDR, Berlin 198: 181-183.

KONDRATENKO F.T., GONCHARENKO A.A. (1973). Puti povyshenya efektivnosti selektsii ozimoj rzhi. Sel. i Semen.: 28-33.

KONDRATENKO F.T., GONCHARENKO A.A. (1974). Rezultaty izucheniya gibridov ozimoj rzhi, poluchennykh s uchastiem mutanta EM-1. Sel. i Semen. 6: 15-18.

KUBICKA H. (1987). Zmienność występująca w liniach wsobnych żyta ozimego (Secale cereale L.) i analiza genetyczna wybranych cech. Praca doktorska, SGGW-AR.

KUNAKBAEV S.A. (1969). Formoobrazovatel'nyj protsess u ozimoj rzhi. Tr. Bashkirsk. N.-In.-ta sel'skogo Chozyajstva, Ufa, vyp. 3.

ŁAPIŃSKI M. (1976). Estimates of heterosis efects and combining ability of seven inbred lines of rye (Secale cereale L.) in diallel crosses. Genet. Pol. 17: 293-308.

ŁAPIŃSKI M., PARZYSZEK B. (1982). Nonallelic interaction in inheritance of some quantitative traits in interlinear hybrids of rye (Secale cereale L.). Genet. Pol. 23(1-2): 21-40.

MADEJ L., WARZECHA R. (1977). Informacja o nowym źródle karłowatości u żyta. Prace Zesp. Bad. Hod. Żyta w 1976 r. IHAR Radzików: 23-26.

MAHMUD I., KRAMER H.H. (1951). Segregation for yield, height, and maturity following a soybean cross. Agron. J. 43: 605-609.

MATHER K., JINKS J.L. (1977). Introduction to Biometrical Genetics. London, Chapman and Hall Ltd.

MATHER K., JINKS J.L. (1982). Biometrical Genetics. The study of continuous variation. Third edition. London, New York. Chapman and Hall.

MELZ G., NEUMAN H., MÜLLER H., STURM W. (1984). Genetical analysis of rye (*Secale cereale* L.). 1. Results of gene localization on rye chromosomes using primary trisomics. Genet. Pol. 25: 111-115.

NALEPA S., GRZESIK H. (1975). Inheritance of dwarfing and some characters in the mutants of Zeelandzkie rye. Hod. Rośl. Aklim. Nas. 19, 5/6: 531-535.

PATYNA H., GROCHOWSKI L. (1978). Inheritance of selected quantitative traits in rye (*Secale cereale* L.). Genet. Pol. 19: 487-493.

PETR F.C., FREY K.J. (1966). Genotypic correlations, dominance, and heritability of quantitative characters in oats. Crop Sci. 6: 259-262.

PLARRE W., FISHER V. (1975). Analysis of a diallel cross in inbred lines of rye. Hod. Rośl. Aklim. Nas. 19, 5/6): 391-401.

RUENBAUER T. (1978). Dziedziczenie długości słomy w mieszańcach populacyjnych odmian i rodów żyta. Hod. Rośl. Aklim. Nas. 2/3: 151-163.

RUENBAUER T., KUBARA-SZPUNAR Ł., ŁOŚ T. (1981). Genes controlling quantitative traits in rye (*Secale cereale* L.). Genet. Pol. 22: 397-410.

RUENBAUER T., KUBARA-SZPUNAR Ł., PAJĄK K. (1983). An interesting mutation of pleiotropic character induced by fast neutrons in rye (*Secale cereale* L.). Genet. Pol. 24: 319-325.

RYBA V. (1975). Breeding of short-stem rye at Chlumec Plant Breeding Station. Hod. Rośl. Aklim. Nas. 19, 5/6: 537-539.

SCHLEGEL R., MELZ G., METTIN D. (1986). Rye cytology, cytogenetics and genetics-current status. Theor. Appl. Genet. 72: 721-734.

SYBENGA J., PRAKKEN R. (1962). Gene analysis in rye. Genetica 33: 95-105.

TARKOWSKI Cz. (1984). Genetyka, hodowla roślin i nasiennictwo. PWN, Warszawa.

VELIKOVSKY V. (1979). Nauchno-issledovatel'skaja rabota v oblasti genetiki i selekcii rzhi v ČSSR. Şeminar "Genetika i selektsiya rzhi. IHAR Radzików: 114-118.

VELIKOVSKÝ V., MACHÁN F. (1982). Evaluation of combining ability in short-strawed rye strains using method of incomplete diallel cross. Tag.-Ber., Akad. Landwirtsch.-Wiss. DDR, Berlin 198: 417-429.

WĘGRZYN S. (1972). Zastosowanie modeli genetyczno-matematycznych do przewidywania postępu w hodowli roślin. Zesz. Probl. Post. Nauk Roln. 125: 109-118.

WĘGRZYN S., FABIJANOWSKI J. (1980). Sprawozdanie z badań genetycznych nad żytem. Prace Zesp. Hod. Żyta w 1979 r. IHAR Radzików: 17-20.

WĘGRZYN S., GROCHOWSKI L. (1978). Zmienność fenotypowa i genotypowa dla kilku cech w populacjach żyta diploidalnego. Hod. Rośl. Aklim. Nas. 22: 165-178.

WINKEL A. (1979). Aktual'nyje problemy selektsii intensivnoj rzhi v GDR. Seminar "Genetika i selekcija rzhi". IHAR Radzików: 119-123.

WOLSKI T., PIETRUSIAK A., TYMIENIECKA E., MĄCZYŃSKA L., SZOŁKOWSKI A. (1980). Wstępne wyniki krzyżowania wstecznego żyta z karłem dominującym EM-1 w SHR Dańków-Laski i Choryń. Biul. IHAR 5: 6-11.