PLANT BREEDING AND SEED SCIENCE
Volume 47 (no. 1/2) 2003

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DIALLEL ANALYSIS OF AGRONOMIC TRAITS IN WINTER RYE

ABSTRACT

An analysis of combining ability of rye, based on F_1 generation hybrids, was performed in order to select lines of high effects of general combining ability which are useful for creation of population and synthetic varieties as well as hybrids giving high effects of specific combining ability. The main aim of the present paper was to recognize the actions of genes responsible for quantitative traits and combining ability of rye inbred lines on the basis of F_1 and F_2 hybrids analysis.

The study material included 56 F_1 generation hybrids obtained though diallel–cross with 8 parent lines as well as 56 F_2 generation hybrids crossed with 8 parent lines.

A genetic analysis of generation F_2 yields results and GCA estimates which substantially correspond with those obtained for generation F_1. The closest results were obtained for plant height, ear length and 1000–grain weight. For cultivation purposes, an analysis of generation F_2 will be reliable and the selection based on it successful. Most of the studied lines were found to essentially influence the effects of general combining ability. The most recommendable is the line SMH–49 whose progeny was characterized both by shortened leaves and increased 1000–grain weight and the weight of grains per ear.

Key words: diallel cross, general combining ability, hybrids analysis, specific combining ability, syntetic varieties

INTRODUCTION

Rye is one of the most difficult objects for genetic and breeding studies. This is caused by allogamy, self–incompatibility and dependence between heterozygosity and productivity, which arises as a result of the inter–chromosomal gene interaction.

According to the used study material (interline–, intervariety hybrids) frequently different results of effect estimations, connected with the forms of gene action, are obtained. The possession of valuable inbred lines enables their use in heterosis breeding (Bujak *et al.*, 1993, 1993a, 1995b; Kaczmarek and Kadlubiec 1985; Węgrzyn and Madej 1989).

The genetic analysis and evolution of combination abilities in rye is carried out on generation F_1 hybrids in purpose to select lines with high

Communicated by Elisabeth Gunnarsson

effects of general combination ability, useful for creation of population, synthetic, and hybrid varieties. However, the difficulties in obtaining a sufficient number of F_1 hybrid grains for experiments, force the breeders frequently to establish experiments with hybrids of the F_2 generation. As a result of gene recombination the heterosis vanishes in subsequent generations, and it is not known how far the information on combination values in lines used in the breeding programmes are changing.

There are few results on genetic studies of quantitative features in rye, and their results are frequently variable.

The aim of this study was to recognize the combination abilities and the ways of gene action especially these ones responsible for quantitative traits as well combining ability of rye inbred lines on the basis of F_1 and F_2 hybrid analysis.

MATERIAL AND METHODS

The study material consisted of 8 parental inbred lines, *56* F_1 generation hybrids obtained through diallel–cross with 8 parent lines, as well as *56* F_2 hybrids from the same crosses.

The initial material for the crossing programme consisted of 8 lines of winter rye derived by a deep inbred self pollination: *KL–45 (521),* 92 (S_{25}), SMH–49 (S_7), 5/2a (S_{19}), Z–7 (S_{26}), 7/4 (526), DS–23 (S_{21}). Measurements of plant height, productive tillering, uppermost internode, ear length, number of grains per ear, 1000 grain weight and weight of grains per ear, were performed for all normal plants in the plot.

Hybrids and parental forms were point–sown, spaced 20 × 10 cm in a field experiment set up with the randomised blocks method.

General and specific combining ability analyses were carried out with the use of the Griffing's model *(1956a, 1956b)* The following mathematical model for variance analysis was accepted to the general combining ability analysis:

$$x_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + e_{ijkl}$$

Where:

μ — population mean

g_i, g_j — effect of general combining ability (GCA),

s_{ij} — effect of specific combining ability (SCA),

r_{ij} — effect of reciprocal crosses,

e_{ijk1} — error,

n — number of replications.

The null hypotheses on lack of genotype differentiation was verified by means of the F test at significance level of $\alpha = 0.05$ and $\alpha = 0.01$. The significance of effects of combination values was determined by means of the t test.

When the lines are being selected on the basis of GCA effects, there are performed equally the choice including the point of view on numerous features. Therefore of practical meaning is the information on combination values, based on integrated indices in the shape of the associated combination value (ACA), introduced by Savcenko (1980). In rye hybrids the usefulness of these indices was tested by Kaczmarek and Bujak (1993a, 1993b). The ACA index represents the combination ability of the parental form in shape of an integrated complex of features, when crossed with many other parental forms. This index is recognized as the genetic crossing potential. For all seven traits together a mutual index was introduced as a measure of crossing potential, which expresses the associated combination value (ACA), according to the formula:

$$ACA = g_0 + \Sigma b_k g_k$$

Where:
g_0 — estimation of GCA of weight of grains per ear
g_k — estimation of GCA in k–th associated trait,
b_k — regression coefficient between basic and associated trait

RESULTS

The analysis of variance (Table 1) showed a significant variability of the investigated genotypes for all the traits, excluding tillering of plants, in hybrids of F_1 and F_2 generations. For traits showing a significant variability of the investigated genotypes the analysis of variance of combination ability was carried out (Table 2). For all the analysed traits a high significance and specific combination ability was shown. The mean squares of variability of general combination ability (GCA) for

Table 1

The mean squares for analysed quantitative traits of rye from experiments of F_1 and F_2 hybrids

Variability	Generation	DF	Productive tillering	Plant height	Uppermost internode	Ear lenght	Number of grains per ear	1000–grains weight	Weight of grains per ear
Blocks	F_1	2	1.09	161.12	1.51	1.55	32.12	0.83	0.22
	F_2	2	21.12	28.50	13.45	0.12	78.12	0.59	0.50
Genotype	F_1	63	3.89	536.99**	23.96*	4.15*	198.74*	0.66*	0.56*
	F_2	63	3.44	349.77**	17.83*	2.43*	109.26*	0.61*	0.30*
Error	F_1	126	3.48	53.20	0.68	0.68	34.43	0.07	0.06
	F_2	126	2.88	32.32	0.50	0.50	46.72	0.09	0.05

* – significant at $\alpha = 0.05$
** – significant at $\alpha = 0.01$

plant height, length of uppermost internode, ear length, number of grains in ear, and 1 000 grain weight surpass the mean squares of variability of the specific combination ability (SCA). This testifies to the predominance of action of additive genes over non–additive ones in shaping these traits, though the share of the second ones is also significant. The predominance of additive over non–additive forms of gene actions for number of grains per ear is somewhat lower, whereas for weight of grains per ear a slight predominance of non–additive forms of genes in F_1 over additive ones was recorded.

Table 2

The mean squares of combining ability from experiments of F_1 and F_2 hybrids

Variability	Generation	DF	Plant height	Uppermost internode	Ear length	Number of grains per ear	1000–grains weight	Weight of grains per ear
GCA	F_1	7	710.82**	21.82**	5.60**	135.01**	0.64**	0.23**
	F_2		771.21**	23.40**	3.35**	155.26**	1.27**	0.31**
SCA	F_1	28	154.64**	6.49**	1.28**	88.95**	0.26**	0.29**
	F_2		140.10**	8.15**	1.29**	55.32**	0.15**	0.13**
Reciprocal crosses	F_1	28	70.39**	6.06**	0.43**	26.34**	0.07*	0.07
	F_2		60.59**	6.05**	0.60**	28.77	0.24**	0.12**
Error	F_1	126	17.73	2.02	0.22	11.43	0.02	0.02
	F_2		16.16	2.28	0.25	23.36	0.04	0.02

* – significant at $\alpha = 0.05$
** – significant at $\alpha = 0.01$
GCA – general combining ability
SCA – specific combining ability

On the basis of F_2 hybrids the significance of the general and specific combination ability was ascertained (Table 2). The many times higher mean square values of GCA and SCA for plant height, length of the uppermost internode, ear length, number of grains per ear, 1000–grain weight and grain mass from head, indicate to the predominance of additive gene actions over non–additive ones. The influence of reciprocal crossings upon F_2 hybrids was significant for the analysed traits, except of grain number per ear.

The comparison of the obtained mean squares of general and specific combination abilities from the analysis of variance for generations F_1 and F_2, showed a full concordance of their significance. Higher values of GCA over SCA testify to the predominance of additive over non–additive forms of gene acttion. Instead, for grains mass per ear in generation F_1 the non–additive effects were similar to additive gene action. In F_2 additive genes play a higher part in inheriting this trait.

Table 3

Effects of general combining ability (GCA) and association combining ability (ACA) of some inbred lines of rye

Inbred lines	GCA												ACA	
	Plant height		Uppermost internode		Ear length		Number of grains per ear		1000–grains weight		Weight of grains per ear			
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
KL–45	–2.37**	–8.03**	0.73*	–0.81**	–0.40**	–0.63**	–2.22**	–4.87**	0.03	–0.04	–0.06*	–0.17**	–0.21	–0.62
92	–1.84	–1.51	–1.82**	–1.23**	–0.25*	–0.05	–2.46**	–2.03	–0.17**	–0.23**	–0.18**	–0.17**	–0.60	–0.47
SMH–49	–7.31**	–4.39**	–0.42	1.03**	–0.40**	0.08	–0.53	–0.65	0.26**	0.46**	0.13**	0.23**	0.05	0.49
5/2a	–1.54	–2.02*	0.91**	1.03**	–0.12	–0.05	–1.59*	0.81	0.01	0.13*	–0.02	0.11**	–0.07	0.23
1/2/79	10.42**	9.18**	–0.19	0.74*	0.40**	0.24*	0.55	1.62	0.21**	0.21**	0.16**	0.04	0.61	0.42
Z–7	–7.39**	–5.02**	–1.12**	–1.06**	–0.46**	–0.42**	–2.19**	–0.06	0.01	0.05	–0.08*	0.04	–0.46	–0.13
7/4	9.03**	11.73	1.83**	1.59**	–0.05	–0.05	2.75**	3.62**	0.004	–0.15**	0.09**	–0.003	0.48	0.18
DS–23	1.01	0.08	0.07	–1.30**	1.29**	0.89	5.69**	4.81**	–0.37**	–0.43**	–0.03	–0.08*	0.21	–0.09

* – significant at $\alpha = 0.05$
** – significant at $\alpha = 0.01$

Analysing the estimated effects of GCA on the basis of generation F_1 hybrids (Table 3), it is difficult to determine explicitly, which of the investigated lines makes the best component for crossings. For plant height significantly positive effects of GCA, which gives the increase in stem length in progeny, were found in lines 1/2/79 and 7/4. The negative GCA values in lines KL–45, Z–7 and SMH–49 show, that using these lines in crossing programmes there exists the possibility to obtain hybrids of a shortened stem. Lines 7/4, 52a and KL–45 increase significantly the length of the uppermost internode in their progeny, whereas the use of lines 02 and Z–7 for crossing makes them shorten. Lines DS–23 and 1/2/79 significantly increase the ear length, and Z–7, KL–45, SMH–49 and 92 decrease it.

Positive effects in GCA for grain number per ear, on the basis of generation F_1, are found in lines DS–23 and 7/4, negative ones in 92, KL–45, Z–7 and *5/2a*. The weight of 1000 grains is increased in progeny of lines SMH–49 and 1/2/79, and decreased in DS–23 and 92. A significant increase in weight of grains per ear is caused in progeny by lines SMH–49, 1/2/79 and 7/4, whereas lines 92, Z–7 and KL–45 cause its decrease.

The analysis of GCA effects in F_2 hybrids for plant height (Table 3) allows to distinguish the lines KL45, Z–7 and SMH–49, which transmit the ability to reduce stem length to the progeny. Significantly positive values were obtained for lines 7/4 and 1/2/79. The length of the uppermost internode in progeny is increased by lines 7/4, SMH–49, 5/2a and 1/2/70, whereas lines DS–23, 92, Z–7 and KL–45 decrease it. Lines 1/2/79 and DS–23 affect the ear elongation, again lines KL–45 and Z–7 its reduction.

On the basis of evaluation of the F_2 generation the increase of grain number per ear can be expected in hybrids of lines 7/4 and DS–23, whereas a lower grain number in progeny of line KL–45. Lines SMH–49, 1/2/79 and 5/2a showed a favourable action on l000–grains weight and lines DS–23, 92 and 7/4 cause a decrease in this trait. In progeny, the increase of grains mass from ear was recorded in lines SMH–49 and 5/2a, and its decrease in lines KL–45, 92 and 2. DS–23.

When comparing the GCA effects of both the generations, the effects of generation F_1were accepted as standard estimations. The highest concordance of GCA effects in generations $F_1$and F_2 occurred in plant height, length of ear and 1000–grains weight. The lowest concordance of GCA–effects estimation in both the generations was found for grains mass in ear (5 lines showed different estimations). The lack of concordance of GCA effects occurred also in the case of uppermost internode length. From the breeder's point of view it is most important to find genotypes (lines) transmitting their favourable values to subsequent hybrid generations. From among eight studied genotypes only line 5/2a gave discordant results in four traits per seven analysed. In the remaining lines concordant results were observed in the majority of traits.

Particularly worthy of notice is line SMH–49, which, at simultaneous shortening of stem the 1000–grain weight and weight of grains per ear increases in both generations. In regard to ear length line DS–23 showed significant and positive GCA effects and influenced its elongation in both the generations, acquiring at the same time the highest GCA effects for grains number in ear, but it significantly decreased the 1000–grains weight progeny of each generation. Line 7/4 improves the number of grains per ear, increasing simultaneously plant height and stem length in progeny of the generations analysed.

The positive and negative values of GCA estimations hinder in a considerable degree the selection of the genetically best lines. However, it is possible to analyse together several traits, important from the point of view of selection, and to express them in shape of a single index characterising the cross potential of heterosis; this considerably facilitates the choice of the most valuable lines. Such an index is the associatory combination value (ACA), being a measure of the lines crossing potential. In the present paper as basic trait accepted was the grains mass from ear. This index is based on evaluations of relations, measured by correlation coefficients between phenotypic, genetic and additive meanings of the traits and the proper dispersions. This is an important combination value of the particular traits, which depicts the relation between the basic trait and the remaining associated traits. The quantitative evaluation of the associatory combination value can facilitate considerably the choice of the most valuable breeding materials, and can be one of the fragments of the genetic analysis of experiments. When analysing the calculated ACA values for generation Fl it is possible to distinguish the lines 1/2/79, 7/4, DS–23 and SMH–49, for which positive values of this index were obtained (Table 3). The highest complex valuation was obtained for line 1/2/79, and next lines 7/4 and DS– 23, whereas the lowest evaluations were obtained for lines 92 and Z–7, for which in the previous GCA analysis negative evaluation values were obtained for the majority of traits. The associatory combination value of lines, based on generation F_2 hybrids, showed the highest value for SMH–49. This line has been earlier distinguished, on the basis of GCA estimations, as a good component for crossing. Confirmed is also the high complex estimation of line 1/2/79, for which, on the basis of second–generation hybrids, the second highest estimation value was obtained. Like in the previous case, also line 7/4 attained a positive value of this index. The worst estimated lines were KL–45 and 92, in which ACA estimations of the investigated traits showed negative values. The computed ACA values for lines based on F_1 and F_2 generations are concordant. Though the sequence of arrangement in generation F_2 changes somewhat, but lines showing positive combination ability in F_1 confirm it in generation F_2. This analysis can contribute to the improvement of the process of selection, facilitating the choice based on several important breeding traits of the most valuable lines and genders. The choice and connection of lines of high genetic crossing potential values may create a heterosic population or hybrids for practical use.

When analysing the evaluation effects of specific combination value of F_1 hybrids (Table 4) it can be found that from the breeding point of view the most interesting are hybrids characterised by a reduced plant height, and a non–reduced value of the remaining traits. Among such combinations only SMH–49 × DS–23 and SMH–49 × 7/4 can be rated. In most cases observed was an increase in length of straw in generation F_1 hybrids. Worthy of notice is the hybrid 1/2/79 × *5/2a,* in which an increase occurred in all the traits analysed. Moreover, in two hybrids (KL–45 × 7/4 and 7/4 × DS–23) an improvement in most of the investigated traits was recorded. The highest values of SCA effects for grain number in ear were obtained in line DS–23 in combination with 1/2/79 and 7/4.

As a component for crossings from among the analysed lines, line 1/2/79 should be recommended, which improves in hybrids most of the investigated traits, and SMH–49 with a shortened plant height in progeny.

A relatively large variability in size of effects of specific combination value of hybrids was also recorded in generation F_2 (Table 4). A few F_2–generation–hybrid combinations showed significantly negative SCA values for plant height. These are hybrids KL–45 × DS–23, SMH49 × DS–23, and SMH–49 × 7/4. A significant increase in straw length was observed in hybrids KL–45 × SMH–49, 92 × 7/4, 5/2a × 1/2/79, and 1/2/79 × 7/4. An increase in length of the uppermost internode was observed in eight hybrids, its decrease only in two (KL–45 x 5/2a and 92 × DS–23). In hybrids of line 92 with lines KL–45 and 1/2/79, and of line 5/2a with Z–7, 7/4 and DS–23 an increase of ear length was recorded, whereas a significantly shorter ear occurred in hybrids KL–45 × 5/2a and 92 × DS–23. With respect to number of grains in ear there occurred only positive SCA values in hybrids of line DS–23 with lines 5/2a and 1/2/79.

Similarly for 1000–grains weight exclusively positive SCA effects were recorded. A significant increase in 1000–grains weight was found in hybrids 5/2a × 1/2/79 and 5/2a × Z–7, as well as in their reciprocal hybrids. Positive effect values of specific combination value for grains mass from ear occurred in hybrids of lines 5/2a with lines 1/2/79, Z–7, and DS–23; a significantly negative SCA value occurred in hybrid KL–45 × *5/2a*.

In hybrids 5/2a x DS–23 positive effects occurred for plant height, length of uppermost internode and ear length, and for grain weight from ear and grain number in ear. In combination 5/2a × 1/2/79 there appeared an increase in plant height, length of uppermost internode, 1000–grain weight and grain weight in ear, whereas in hybrid 5/2a × Z–7 the length of the uppermost internode and ear increased. There was also an increase in grain mass per ear, and in 1000–grains weight. Progeny of KL–45 × DS–23 as well as SMH–49 × 7/4 belong to the combination of shortened plant height however SMH–49 × DS–23 represents a shortened ear and a lower weight of grains per ear.

Table 4

Effects of specific combining ability of F_1 and F_2 hybrids

Lines	Traits	92		SMH–49		5/2a		1/2/79		Z–7		7/4		DS–23	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Kl–45	a	4.31	0.93	–2.20	2.29*	–0.47	–1.58	5.09	–0.28	1.41	–0.23	8.99**	–0.64	1.31	–2.23*
	b	–0.38	5.37*	–0.58	4.00	0.46	–5.74*	1.08	0.42	0.40	1.12	1.80*	1.12	0.81	–2.46
	c	0.17	0.74*	–0.02	0.22	0.24	–0.63*	0.56**	–0.30	0.08	–0.25	0.52	0.36	–0.37	–0.08
	d	1.01	–0.65	–1.75	–2.03	0.63	–3.25	2.32	0.93	1.73	2.12	4.94*	0.18	–2.32	1.00
	e	0.10	–0.18	–0.13	–0.05	0.01	–0.13	0.32**	0.18	0.04	–0.01	0.22*	0.09	0.11	0.09
	f	0.09	–0.02	–0.15	–0.12	0.03	–0.20*	0.26**	0.15	0.07	0.04	0.31**	0.05	0.01	0.06
92	a			–1.96	0.83	6.54**	–0.5.	10.22**	–0.36	–3.14	0.05	0.11	2.27*	–2.02	–0.81
	b			–1.22	10.86	0.93	1.48	2.64**	–0.08	0.02	1.11	0.33	5.36*	0.52	–6.73**
	c			–0.08	0.89	0.49	–0.46	0.81**	0.86*	0.18	–0.21	0.02	0.28	–0.32	–1.41**
	d			–0.51	3.12	2.04	1.15	4.07	3.34	0.98	–3.46	3.53	4.09	–1.40	–3.09
	e			–0.02	0.01	–0.01	0.05	–0.06	–0.02	0.12	0.15	0.09	–0.16	0.22*	0.02
	f			–0.05	0.10	0.04	0.03	0.09	0.07	0.08	0.01	0.19*	–0.40	0.07	–0.07
SMH–49	a					8.02**	–0.55	2.89	0.74	2.81	0.41	0.28	–2.11**	–5.89**	–2.70**
	b					0.93	–1.26	–0.01	4.03	1.02	–0.63	–0.03	0.11	–1.52	–3.48
	c					0.19	0.14	0.41	0.47	0.28	–0.22	0.37	0.14	0.12	–0.17
	d					3.61	–1.46	2.79	–1.53	1.05	3.15	1.92	2.96	–0.51	–2.46
	e					0.13	–0.05	0.35**	0.03	–0.01	0.25	0.10	0.26	0.13	–0.14
	f					0.23*	–0.02	0.31**	–0.05	0.02	0.18	0.13	0.29*	0.05	–0.04

* – significant at $\alpha = 0.05$
** – significant at $\alpha = 0.01$

Table 4

Effects of specific combining ability of F_1 and F_2 hybrids (continued)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
5/2a	a							6.27**	3.49**	1.24	1.54	1.66	1.63	2.13	1.41
	b							2.39**	5.16*	–0.17	5.11*	0.37	8.48**	0.73	9.14**
	c							0.68**	0.61	–0.19	0.91**	0.54	0.66*	0.45	0.96**
	d							4.69*	3.50	2.94	5.43	–2.00	0.75	1.21	6.06**
	e							0.58**	0.56**	0.11	0.31*	–0.04	–0.04	0.25**	0.22
	f							0.51**	0.42**	0.13	0.34**	–0.13	–0.01	0.19*	0.28**
1/2/79	a									6.56**	0.21	–3.35	2.18*	6.06*	0.83
	b									0.83	6.28**	–0.51	2.78	–0.01	8.69**
	c									0.22	0.36	0.16	0.49	0.22	–0.21
	d									–1.19	1.62	–2.15	–0.31	13.90**	8.75**
	e									0.25*	0.21	0.07	0.07	–0.16	–0.03
	f									0.06	0.08	–0.03	0.05	0.30**	0.21*
Z–7	a											0.31	0.51	2.32	1.26
	b											1.16	4.48	–0.08	–1.10
	c											0.43	0.16	–0.16	–0.03
	d											2.26	4.87	–0.17	2.81
	e											0.17	–0.16	0.04	–0.23
	f											0.19*	0.02	0.03	–0.07
7/4	a													9.25**	0.23
	b													1.31	1.01
	c													0.62*	0.08
	d													8.36**	3.25
	e													0.01	0.04
	f													0.23*	0.05

* – significant at α = 0.05
** – significant at α = 0.01

From the presented effects of specific combination value in hybrids of generation F_2 it results, that for breeding purposes the hybrids of line *5/2a,* with improved values in most of the analysed traits, should be recommended. However, this line, in combination with 1/2/79, transfers an undesirable high stem.

CONCLUSIONS

1. The genetic analysis carried out by means of the Griffing's method revealed a predominance of additive over non–additive forms of gene action in traits of generations F_1 and F_2, except for weight of grains per ear in generation F_1, where the effects of domination were similar to the additive ones.
2. The genetic analysis of generation F_2 yields a high concordance of results and estimations of GCA estimations, which substantially correspond to these, obtained for generation F_1. The closest results were obtained for plant height, ear length and 1000–grains weight. For cultivation purposes, the analysis of generation F_2 shall be reli–able and the selection, based on it, successful.
3. Most of the investigated lines were found to essentially influence the effects of general combining ability. The most recommendable is line SMH–49, of which the progeny was characterised both by shortened stem and increased 1000–grain mass, and grain mass from ear.
4. The associative combining ability enables to determine the crossing potential of lines on the basis of several traits. On the basis of this parameter, lines SMH–49 and 1/2/79, which in generations F_1 and F_2 obtained the highest values of the complex estimation, can be recommended for breeding purposes.

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