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SELECTION OF WINTER RYE (*Secale cereale* L.) INBRED LINES FOR GENERAL AND SPECIFIC COMBINING ABILITY AND ITS RELATIONSHIP WITH VALUABLE TRAITS

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Abstract

Creation of F_1 heterosis hybrids instead of population varieties is an advanced breeding technology since XX century. The rye as a strictly cross-pollinated culture is rather perspective for heterotic breeding. The success depends on the use of rye homozygous lines with high combining ability. The topcrossing allows effective estimates of the best genotypes to be used in synthesis of high heterotic hybrids. This paper is the first characterization of the authors' winter rye unique high-homozygous inbred lines, which are based on three Russian gene pools, with high combining ability intended for breeding programs. The purpose of our researches was to estimate by topcrossing method the general and specific combining ability of winter rye inbred lines. Test crossings in 2016 involved five sterile lines with type Pampas cytoplasm (H-649, H-577, H-842, H-1058, and H-1185), and four male fertile lines (H-451, H-1011, H-1247, and H-1071) as testers. In total, 20 simple F_1 interlinear hybrids were selected. In 2017, the hybrids were studied in plot tests (8 m^2 plots, 3 replications, and 500 grains per 1 m^2). F_1 hybrid yields varied from 5.02 up to 7.90 t/ha vs. 6.50 t/ha yield of population variety Valdai. The highest yield had F_1 (H-649 × H-1011, i.e. 7.9 t/ha that is 21.5 % higher compared to the standard Valdai variety. As a whole, the frequency of F_1 hybrids with high competitive heterosis is 7 of 20 (or 35%). Variation of F_1 productivity is mainly due to different combining ability of their parents. Note, both general and specific combining abilities (GCA and SCA) contribute to a dispersion of productivity trait, thought GCA effects account to 91.1% while SCA only 7.7%. Thence, additive gene effects but not intralocus dominance are the basic genotypic components of productivity trait variance. The obtained GCA/SCA values specify on high enough genetic divergence of the inbred lines used. Sterile analogues of lines H-1185 and H-649, and also of paternal line-tester H-1011 possess high GCA effects. The dwarf lines H-577 and H-1071 show lower general combining ability. High SCA effects are characteristic of the sterile lines H-1058 and H-649, and also the testers H-1071 and H-451. It was revealed that GCA of the used rye lines positively correlates with plant height (r = 0.85±0.10), 1000-grain weight (r = 0.80±0.13) and grain weight per ear (r = 0.64±0.21). These data emphasize the importance of inbred lines' selection for high own performance and combining of high 1000-grain weight and a dwarfism.

Keywords: *Secale cereale* L., winter rye, cytoplasmic male sterility, CMS, tester, homozygous inbred line, F_1 hybrids, general combining ability, GCA, specific combining ability (SCA), yield, 1000-grain weight, grain weight per ear, dwarfism

The choice of parents for crossing is a fundamental problem in the breeding of winter rye F_1 hybrids based on cytoplasmic male sterility (CMS). A clear proof of the presence of cytoplasmic male sterility in the Argentine variety of rye Pampa was presented by N.N. Geiger and F.W. Schnell (Hohenheim University — Universität Hohenheim, Germany) [1], and the first experimental

F_1 hybrids gave the impressive results. In comparison with the parent lines, the average heterosis in grain yield was 39%, in the number of grains in the ear 58%, in the 1000-grain weight 37%, in the plant height 31%, in the number of ears per 1 m^2 10% [2]. This was an incentive for private investment in methodology, biotechnology, and practical hybrid rye breeding, with the result that its share in the structure of the world plantings of this crop exceeded 20% [3]. In recent years, German breeding companies have created a series of improved hybrids that combine high yields with other valuable features (short stem, resistance to lodging, brown rust, and ergot) with improved baking qualities of grain and greater suitability for the production of feed and biogas [4].

At average, the grain yield in F_1 hybrids of winter rye is 15-20% higher than in population varieties [5]. In Germany, from 1982 to 2005, the annual yield increase in population varieties was 30 kg/ha, in hybrid varieties 51 kg/ha (70% higher) [6]. At the same time, the rate of breeding improvement at the hybrid level is much higher than at the population level. In Germany for 26 years (1991-2016) the yield of rye hybrids in the state testing increased by 23.3%, while in the population varieties by 18.1% [4]. In Poland, in the state testing, the yield increase of such varieties compared to the population varied was from 9.8 to 14.5 c/ha, while F_1 hybrids were more resistant to lodging and less affected by brown rust and powdery mildew [7]. In Canada in the areas of traditional cultivation of this crop, the decrease in its areas which lasted for a long time now stopped due to the introduction of the European hybrid varieties [8]. The State Register of Selective Breeding Results of the Russian Federation included five rye hybrids of German selection, the Picasso, Magnifico, Palazzo, KWS PABO (the originator is KWS Lochow GmbH, Germany); Helltop (the originator is Monsanto Saaten GmbH, Germany), and two Ukrainian hybrids (Pervistok and Yuryevets, the originator is the Yuriev Plant Production Institute, Ukraine), but the area under them is small; domestic linear hybrids are absent in the register. In Russia, heterotic breeding of rye with the use of CMS is almost not conducted currently. The exception is provided by the works involving three gene pulls of rye (from Nemchinovka, Saratov, and Kirov) with the use of multiple inbreeding plants from self-fertile populations and saturating crossings to obtain sterile analogues of lines like Pampa [9] using CMS, and the subsequent hybrid breeding (Federal Research Center Nemchinovka).

Evaluation of the genetic properties of homozygous lines with high productivity in interline crossings is the most difficult and costly stage in heterotic breeding. It is proposed to start the determination of the general combining ability (GCA) in the first generation of inbreeding (I_1-I_3), as the probability of line segregation on this trait is very small in the subsequent generations, and it is advisable to exclude them from further testing and self-pollination [10]. It is extremely important because the frequency of lines with high GCA is very low. For example, from 364 hybrid combinations in different types of crossings (polycrossing, topcrossing, variety-to-line crossing, interline crossing), such lines were about 20% [11], and less than 8% when taking into account only economically significant heterosis [12]. The reason is that those inbred lines that are superior to other lines can be genetically related, which reduces the effect of heterosis. Maximum heterosis can be achieved only in crossing genetically different inbred lines [13].

The analysis of F_1 hybrids from diallel crosses gives an objective assessment of the combining ability of parent lines. It is possible to determine the GCA of parent forms with one variety-tester, and the scheme in which a set of breeding valuable inbred lines serves as the tester allows breeders to characterize SCA of parent forms without diallel crossing [14]. The study of five inbred lines of corn as testers showed [15] that the best, in this case, will be the forms with increased yield and high effects of the GCA. Topcrossing as a method of early estimates is considered effective in assessing the combining ability of winter rye lines [16]. It is important to take into account that the choice of the optimal number of testers in determining the GCA is largely influenced by the number of environmental test points in testcrossings [17].

The GCA of inbred lines is used in the selection not only for yield but also for other characteristics. The comparison of 40 simple interline hybrids of winter rye artificially infected with *Fusarium culmorum* (W.G. Sm.) Sacc. showed that the GCA variance on resistance to this pathogen was 10 times higher than the SCA variance [18]. On this basis, it was concluded on the predominance of additive interaction of genes controlling stability, which determined the strategy of selection. Similar data were obtained for winter triticale [19]: a close relationship between the effects of parental GCA and their own productivity, which makes it possible to reliably determine the expected resistance to ear head blight in F_1, was also determined.

The forecast for hybrid power in interline hybrids is of great interest. A prediction is possible both on the basis of the GCA effects and data on the productivity of inbred lines per se [20]. The structurally simple features, by the average value of which in the parent lines it is possible to estimate the expected expression of these features in hybrids, are the most convenient. In relation to complex structural characteristics, such as productivity, the accuracy of such prediction is reduced by the effects of dominance [21].

In the present paper, the unique high-homozygous inbred lines of winter rye, which were obtained on the basis of three domestic gene pulls, were characterized for the first time, and the forms with high combining ability, promising for breeding for productivity and other main economically valuable features (winter hardiness, short stem, 1000-grain weight, etc.) were identified.

The aim of the research is to determine the combining ability of inbred lines of winter rye using test crosses according to the scheme of complete topcrossing and to study the correlation of the obtained effects of the GCA with the main breeding traits.

Techniques. Inbred lines were obtained by multiple inbreeding of plants from hybrid populations derived from crosses between the rye varieties Alpha, Valdai, Voskhod 1, Voskhod 2, Saratovskaya 5, Bezenchukskaya 87, etc. with various donors of self-fertility. The lines were selected for winter hardiness, short and strong stem, ear productivity, 1000-grain weight, resistance to fungal diseases, the falling number and viscosity of the aqueous extract of grain meal. To create the sterile analogs of inbred lines in winter (in greenhouse conditions), the pair backcrossings were conducted by placing the ears of sterile and fertile plants under the same parchment isolator. The source of sterile cytoplasm of the Pampa type was one of the highly sterile inbred lines. The preservation of plants sterility after each backcrossing was controlled visually in the greenhouse and in the field.

When creating the parent lines A and B in the formula of simple hybrid, different gene pulls, unrelated to the synthetics-pollinator C, were used. The parent lines for A were five male sterile lines (N-649, N-577, N-842 N-1058, and N-1185), selected according to the complex of economically valuable traits (winter hardiness, short stem, large-grainy, etc.). Test crosses were carried out in 2016 (experimental field of the Federal Research Centre Nemchinovka, Moscow Province) under topcrossing scheme with four male fertile lines (N-451, N-1011, N-1247, and N-1071) as a paternal form. The resulting 20 interline F_1 hybrids were assessed in 2017 in field tests arranged in 3-fold repetition, with 8.0 m^2 plots and the seeding rate of 500 grains per 1 m^2. The yield was harvested at full ripeness (a Winter-Classic small combine, Wintersteiger AG, Austria).

The effects of the GCA and the SCA of maternal sterile lines and paternal fertile testers were measured using the mathematical evaluation model proposed by Wolf and Litun [22].

Results. The weather conditions during the growing season deviated from the norm significantly. The partial death of plants due to the ice crust had happened in winter. April was abnormally cold, the cold weather also dominated in May, snow and rain fell often, rainfall was record high (88.4 mm at the rate of 52.4 mm). Heavy rains in June had a negative impact on trans-pollination. In July, the weather was also mostly cold and humid: rainfall was 34.6% higher than the rate; 420.3 mm of precipitation fell from April to July total at the rate of 249.5 mm (168.5% of the rate). This led to the lodging of some hybrids, reduction of 1000-grain weight and, as a result, reduced productivity, technological, and baking quality of grain.

In total, more than 2000 homozygous lines were obtained, from which the best for a number of features (winter hardiness, short and durable stem, early ripeness, a well-grained ear, large grain, resistance to fungal diseases, the high falling number, and viscosity of the aqueous extract of grain meal) were selected. On the basis of long-term data from this group, short-stem and valuable in terms of a complex of other features inbred lines were selected, from which sterile analogs were obtained, which were used in the "breeding conveyor" for the synthesis of interline F_1 hybrids based on the CMS of the Pampa type.

1. Yield (t/ha) **of winter rye (*Secale cereale* L.) simple interline hybrids F_1** (field tests, Moscow Province, 2017)

Sterile line	Fertile line (tester)				Average X_i
	H-451	H-1011	H-1247	H-1071	
H-649	7.02*	7.90*	7,03*	6,02	7,00
H-577	5.09	5.98	5,74	5,78	5,65
H-842	5.88	6.50	6,31	6,15	6,21
H-1058	6.89	7.03*	6,01	5,53	6,36
H-1185	7.39*	7.52*	6,89	7,19*	7,24
Average X_j	6.45	6.99	6,39	6,13	6,49
LSD_{05}	0.52				

* The hybrid yield is significantly higher than the average yield in the experiment.

The results of the field test of 20 winter rye interline F_1 hybrids (Table 1) showed 6.49 t/ha average yield in the experiment (6.50 t/ha in the standard population variety Valdai). Seven F_1 hybrids exceeded ($P \geq 0.95$) this standard for competitive heterosis by 0.5-1.4 t/ha (8.0-21.5%). The F_1 hybrid derived from N-649 × N-1011 showed the highest yield (7.90 t/ha), F_1 hybrid of N-577 × N-451 was the lowest in yielding (5.09 t/ha). The maternal sterile line N-1185 was present in the pedigree of the most productive hybrids, and the N-1011 line was present among the paternal testers. The hybrids produced with the participation of the N-577 and N-842 lines were the most low-yielding. The lines N-1185, N-649 and the tester N-1011 mostly gave high-yielding hybrids. The typical feature of these lines was that each of them gave three high-yielding hybrids when crossing with others. It indicates their high combining value. At average, the frequency of F_1 hybrids with significantly increased competitive heterosis in yield was 35% (7 out of 20). The genotype of the maternal lines caused a stronger variation in the yield of hybrids than the genotype of the tester lines.

The variation of yield in the studied hybrids was mainly due to the unequal parental combining ability. According to the results of the variance analysis, three components that affect the variance of yield significantly were found in the yield genotypic variance, i.e. the GCA of sterile lines, the GCA of testers, and the SCA of the combination “line × tester” (Table 2).

2. **Dispersion analysis of the combining ability of the obtained inbred lines of winter rye (*Secale cereale* L.)**

Source of dispersion	SS	df	ms^2	F_{actual}	F_{05}
GCA of sterile lines	6.49	4	1.62	54.0	2.6
GCA of tester lines	1.92	3	0.64	21.3	2.9
SCA	2.27	12	0.19	6.3	2.0
Residual	0.97	38	0.03		

N o t e. GCA is general combining ability, SCA is specific combining ability.

It is important to note the relatively large variance of sterile maternal lines GCA (ms^2 = 1.62), and tester lines GCA (ms^2 = 0.64) compared to the variance of the SCA (ms^2 = 0.19). By summing up the variances, it can be found that the share of the GCA effects is 91.1% of the whole yield variability of the studied hybrids, and the SCA is 7.7% only. Consequently, the main component of the genotypic variance for yield is the additive interaction of genes, but not the intralocus dominance. The large value of the variances ratio (GCA/SCA) indicates the sufficiently high genetic divergence of inbred lines taken for crossing [23].

3. **Effects of general and specific combining ability** (GCA and SCA) **in the obtained sterile inbred lines and fertile lines of rye (*Secale cereale* L.) testers** (field tests, Moscow Province, 2017)

Line	GCA effect (g_i)	SCA effect (S^2_{ij})				ΣS^2_{ij}	σ^2_{Si}
		H-451	H-1011	H-1247	H-1071		
Sterile lines:							
H-649	0.50*	0.05	0.42	0.15	–0.62	0.58	0.173*
H-577	–0.84*	–0.52	–0.16	0.19	0.49	0.57	0.017
H-842	–0.28	–0.29	–0.21	0.20	0.30	0.26	0.067
H-1058	–0.13	0.57	0.17	–0.26	–0.48	0.65	0.197*
H-1185	0.75*	0.19	–0.22	–0.27	0.30	0.25	0.063
H-451	–0.04						
H-1011	0.50*						
H-1247	–0.10						
H-1071	–0.36*						
S^2_{ii}		0.72	0.32	0.24	1.03		
σ^2_{Si}		0.158*	0.058	0.038	0.235*		
			σ^2_{Si} = 0.134				
			σ^2_{Si} = 0.122				
Error Edg_i (lines)	0.156						
Error Edg_i (testers)	0.136						

* The indicator value is statistically significant at $p \leq 0.05$.

In the experiments, the studied lines had both positive and negative estimates for GCA. The sterile lines N-1185 and N-649 were characterized by the high GCA effects on yield; the short-stem line N-577 had significantly lower GCA (Table 3). Among the fathers-testers, the best GCA was in the N-1011 line, the worst in the N-1071 line (see Table 3). The F_1 hybrids involving these lines varied in yield greatly.

The crossing scheme used in this experiment made it possible to compare the lines not only for the GCA but also for the SCA and to assess the contribution of the heterosis effect to the yield potential for each pair of parents. If the heterosis value in the resulting combination is much higher than can be expected from the GCA value of the line, then such a line has a high SCA. The SCA indicator allows us to determine the use of which lines will give F_1 hybrids with the highest yield. Among the studied lines, the N-649, N-1058, N-1071, and N-451 showed significantly high SCA.

It should be noted that in the selection of inbred lines, their productivity is an important landmark. Miedaner et al. [24], studying the relationship between the manifestation of eight traits of productivity in inbred lines and testcrosses, concluded that the selection of lines per se at the phenotypic level is important at all stages of hybrid breeding. It is noted that genotypic correlations (r_g) become weaker as the structure of the trait becomes more complex. The authors found the highest correlations ($r_g > 0.7$) for plant height, 1000-grain weight, as well as for the falling number and starch content [24]. According to the data of this experiment (Table 4), the sterile lines N-649 and N-1185, as well as the fertile tester line N-1011, which showed the highest estimates for the GCA as compared to the low-combination line N-577, were distinguished by a relatively long stem (from 86 to 97 cm vs. 78 cm), a larger grain (1000-grain weight is 24.4-30.0 g vs. 21.5 g) and a productive ear (grain weight per ear is 0.79-1.15 g vs. 0.62 g).

4. Productivity traits and their correlation with the effects of general combining ability (GCA) **in the obtained sterile inbred lines and fertile tester lines of rye (*Secale cereale* L.)** (field tests, Moscow Province, 2017)

Line	GCA effect	Plant height, cm	Weight, g		Grain and flour		
			1000 grains	grains per ear	falling number, s	protein content, %	grist water extract viscosity, cP
H-649	0.50	86	24.4	0.79	112	14.9	8.3
H-577	–0.84	78	21.5	0.62	261	12.8	10.3
H-842	–0.28	82	22.9	0.93	228	14.4	5.5
H-1058	–0.13	84	26.3	1.08	126	13.0	3.8
H-1185	0.75	95	29.5	1.15	234	12.8	8.5
H-451	–0.04	81	22.8	0.73	265	14.3	3.6
H-1011	0.50	97	30.0	1.12	116	13.7	9.4
H-1247	–0.10	80	22.8	0.63	222	13.1	6.2
H-1071	–0.36	79	23.0	0.71	173	13.7	3.8
Correlation coefficient (*r*) of GCA effect with the trait:							
		0.85*	0.80*	0.64*	–0.42	0.20	0.23

* The indicator value is statistically significant at $p \leq 0.05$.

In the experiment, we revealed close relationship between the GCA and some important breeding characteristics. For example, the high-confidence ($p \leq 0.05$) positive correlation between the estimates of the GCA lines and the plant height ($r = 0.85 \pm 0.10$), 1000-grain weight ($r = 0.80 \pm 0.13$) and the grain weight per ear ($r = 0.64 \pm 0.21$) was identified. It is important to note that the presence of conjugation between the GCA and plant height is undesirable, since long-stem lines are not suitable for hybrid breeding. However, the selection improvement of lines on this basis is generally achievable, especially if intensive and large-scale selection for the compatibility of the traits of large grain size and short stem is used. These features are characterized by a high coefficient of heritability; therefore, the selection of them per se among the used lines will allow being more confident to predict the best interline hybrids. The possibility of effective forecasting the productivity of simple interline rye hybrids based on the particular features of parental forms is also noted by other researchers [25, 26]. According to the latest data [3], in Germany, as a result of intensive breeding, modern self-pollinated rye lines exceed the productivity of the first inbred forms by 5-8 times, which accordingly affected the productivity of commercial hybrids. Due to breeding improvements of the parent forms, modern hybrid rye reached the level of such leading crops as maize and wheat in terms of yield.

Thus, according to the results of the field test of 20 topcross F_1 hybrids, 7 promising combinations were identified, which demonstrated significantly high competitive heterosis in yield. The highest yield had the simple F_1 hybrid N-649 × N-1011 (7.90 t/ha, that is the 21.5% excess compared to the standard variety Valdai). The sterile lines N-1185, N-649 and the tester-pollinator N-1011 also showed a high general combining ability in yield; therefore, they can be effectively involved in hybrid breeding. The observed variances ratio of

GCA/SCA indicates a significant genetic divergence of the crossed inbred lines. The GCA effects positively correlate with plant height, 1000-grain weight, and the grain weight per ear. The correlation analysis allows us to conclude about the possibility of early prediction of the combining ability of inbred rye lines for the compatibility of large grain size and short stem.

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