

A.A. Torop, V G.Dedyayev, V V Tschaykin V VDokuchaev

Agricultural Research Institute of Central-Chernosem Area Talovaya, Voronezhskaya oblast,
397463, Russia

THE RESULTS OF RYE BREEDING IN THE CENTRAL-CHERNOSEM REGION OF RUSSIA

ABSTRACT:

Winter rye in the Central-Chernosem Region of Russia carries out the role of the «insurance culture». To carry out this role, winter rye should have varieties with genetic protection against unfavorable conditions, which might threaten the potential productivity. For that new genetic sources were created. On the basis of the created breeding material new varieties with better (than earlier created) resistance to severe weather conditions, were developed

Key words. winter rye, breeding resistance to severe conditions new sources for breeding.

SHORT COMUNICATION

Winter rye in the Central-Chernosem Region of Russia was the basic food culture in the 1950s of the last century. Its sowing areas were approximately equal to 2 mln ha. But the development of winter-hardy and productive varieties of winter wheat caused decrease of winter rye acreage in this region in the 1960s, despite of significant growth of potential productivity of some new created cultivars (Fig. 1)

Nowadays the winter rye in the Central-Chernosem Region carries out a role of the «insurance culture» which can contribute to the harvest in case of the severe weather conditions. Significant areas of the crop are used for green forage as well. Acreage fluctuates between 300000 and 500000 ha.

To carry out the role of the insurance culture, winter rye should have varieties with genetic protection against unfavorable conditions! factors, which might threaten the potential productivity. Among such factors in our region there are lodging, different diseases and drought. The low resistance of cultivated rye varieties to lodging was the basic reason for reduction of rye acreage in the region. This drawback was eliminated only due to using a gene *Hi (Dw-1)*, discovered by the pro-

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professor V. D. Kobylansky. The gene, when used in the selection process, allowed creating varieties with short-stem. Due to this, many new rye varieties with lodging resistance and high real productivity were developed. Our institute was one of the first to carry out this project. We created new varieties with lodging resistance, such as Talovskaya 12, Talovskaya 15. Table 1 illustrates the effectiveness of these new short-stem varieties.

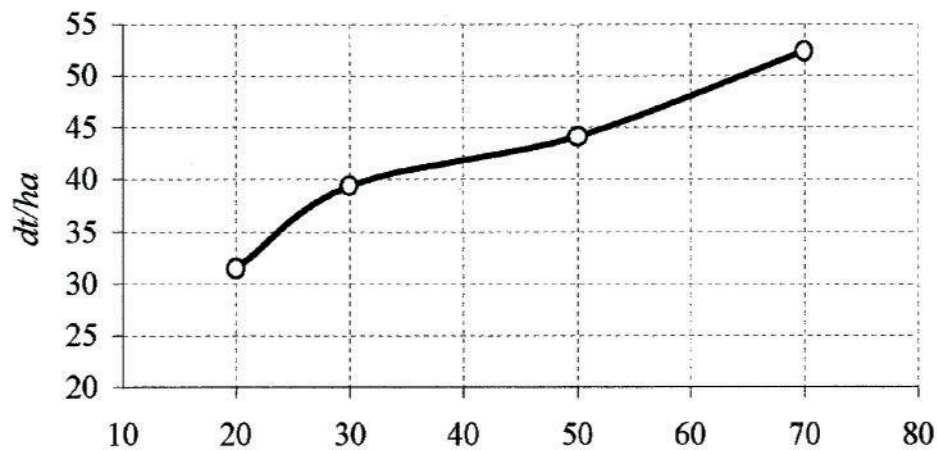


Fig. 1 The contribution of breeding into increase of efficiency potential of winter rye in the Central Chernosem Region of Russia

The basic parameters of winter rye varieties in competitive test

Table 1

Year	Yield [t × ha ⁻¹]			Score for the lodging resistance evaluation according to the 5-point scale		
	Kharkovskaya 60	Talovskaya 12	Difference	Kharkovskaya 60	Talovskaya 12	Difference
1976	4.10	4.50	0.40	2.85	3.64	0.79
1977	3.73	4.22	0.49	3.35	4.39	1.04
1978	6.54	6.63	0.09	3.30	4.47	1.17
1979	7.42	7.53	0.11	3.57	4.62	1.05
1980	3.77	6.22	2.45	3.08	4.76	1.68
1981	5.50	6.14	0.64	3.92	4.54	0.62
1982	4.69	6.66	1.97	2.58	4.78	2.20
1983	5.69	6.69	1.00	3.54	4.63	1.09
Average	5.18	6.07	0.89	3.27	4.48	1.21
%	100	117.2	17.2	100	137.0	37.0

As a result, lodging resistance of the new variety increased up to 1.21 points (37%) and its productivity has increased with 17.2%. The essen-

tial increase of its productivity was in high humidity years (1980 and 1982), when the productivity amounted accordingly 65% and 42%.

It is well known that rye belongs to farm crop with stem type of photosynthesis. Shortening of the stem up to 30–35% caused a serious concern of disease protection of new varieties (Table 2). With regard to this at the second stage of our work the basic attention was given to creation of varieties resistant to leaf (in the first place) and stem diseases. For this the perennial rye variety Derzhavinskaya 29 was used with simple and effective infectious backgrounds and finally two new varieties (Talovskaya 29 and Talovskaya 33), resistant to lodging and diseases, were created. The new rye varieties have higher and more stable productivity during the periods of epiphytotoy, when their productivity is about 40% or more (judging by the grain mass of one ear, the criteria which is influenced mostly in case of a disease – Table 2).

Table 2
The comparative characters of winter rye varieties with various resistance to diseases

Variety	Natural background		Artificial infectious background					Grains per ear [%]
	Yield [t × ha ⁻¹]	**Lodging resistance	*Susceptibility on:			Weight [g]		
			Rust		Powdery mildew	Grains per ear	1000–grain weight	
			brown	stem				
Talovskaya 15	4.78	4.52	3.04	2.84	1.64	1.08	24.8	67.0
Talovskaya 29	4.85	4.35	1.34	0.98	1.18	1.52	32.2	69.4
Difference	0.07	-0.17	-1.70	-1.86	-0.46	0.44	7.4	2.4
In %	1.5	-3.9	-55.9	-65.5	-28.0	40.7	29.8	3.6

Susceptibility on diseases: from 0.0 to 3.6 points

Resistance to lodging according to scale 1–5 points

In the Central Chernosem Region the significant decrease of winter rye productivity is mainly due to droughts. In regard to this at the 3rd stage of our work the attention was given to creating short–stem varieties resistant to diseases and droughts. So the hybridization involved the modern varieties, developed by the Saratov selection group, and our rye forms with vertical leaves. At the same time some other more valuable sources of lodging, disease and drought resistance, were created also from this material. Their characteristics are given in Table 3. With the use of these sources the new selection material was created. Its characteristics are given in Table 4.

The Table 4 illustrates that the new selection material has preserved the previous level of productivity potential and disease resistance, but obviously demonstrates the higher level of drought resistance. It can preserve the level of its productivity in severe weather conditions. However, the potential productivity itself has not increased.

To increase potential productivity we created the plant with changed architectonics: with short stalks, vertical big leaves, larger ear and

Table 3
Sources of winter rye selection improvement

Attribute	Talovskaya 15 (standard)	Population 52	Population 57	Population 32	Population 56	HK-1205	HK-1192 k/st	Selection from Talovskaya 29
Logging resistance coefficient Seko*	0.35	0.29	0.28	0.25				
Drought resistance [scale 1-5 points]	-	20.6	25.0	40.0				
Susceptibility to powdery mildew [%]	3.67				4.72	4.12	4.00	
Susceptibility to brown rust [%]	17.5							0.2
Susceptibility to stem rust [%]	85.8							4.2
Susceptibility to stem rust [%]	98.0							15.0

* - excess above the standard

Table 4
Characteristics of new breeding material within the years 1944 - 1996

Variety	Yield [t x ha-1]	An artificial infectious background				Grains per ear [%]		
		*Susceptibility on		Weight [g]				
	**Lodging resistance	Rust brown	stem	Powdery mildew	1000-grain weight			
Talovskaya 15	5.0	4.96	3.15	3.11	0.60	1.09	26.0	65.2
Talovskaya 29	5.16	4.87	1.32	1.25	0.40	1.62	33.5	67.5
New material	5.08	5.0	1.65	1.52	0.50	1.60	33.7	68.5

Susceptibility on diseases: from 0.0 to 3.6 points

Resistance to lodging according to scale 1-5 points

grain and other. This will allow to create a new population of rye plants with optimal optical and biological organization of sowing.

The study of photosynthetic features of the most interesting rye forms has revealed some interesting characteristics (Table 5). They (Population 56 with vertical leaves; Population 54 with large leaves; Population 57 with short stem) are found to have a photosynthetic surface of bigger size and often contain more chlorophyll, which proves their bigger potential of productivity.

Table 5
The area of photosynthetic surface and amount of chlorophyll plants of various morphological types during the ripening period of grain (1998, 1999)

Variety/population	Ear		Leaves		Stem	Leaves vagina
	Area [cm ²]	Amount of chlorophyll [mg × g ⁻¹]	Area [cm ²]	Amount of chlorophyll [mg × g ⁻¹]	Amount of chlorophyll [mg × g ⁻¹]	Area [cm ²]
Talovskaya 15 [std]	53.3±1.45	0.30	17.6±1.26	0.87	0.46	135.1±5.17
Population 54	54.3±1.0	0.38	29.5±1.26***	1.10	0.58	153.0±3.71**
Population 56	57.3±1.09*	0.45	25.4±1.47***	1.19	0.40	161.7±4.68***
Population 57	60.9±1.12***	0.46	37.0±1.26***	1.24	0.50	175.3±4.48***
LSD _{0.05}		0.04		0.21	0.11	

*, **, *** – significant at $\alpha = 0.05, 0.01$ and 0.001 respectively
std – standard

The creation of highly productive rye varieties is impossible without using short–stem forms. However, there is always a contradiction between the height of a plant and its efficiency. Yet we managed to “break the tradition” and developed short–stem (80–105 cm in comparison with usual 110–140 cm of Talovskaya 15 which is adjusted for the region) highly productive populations.

It has resulted into essential architectonics change of a plant. The assimilation surface of the sprout has decreased whereas the assimilation surface of the leaves and, the ear especially, has largely increased. Due to this, their role during ripening has considerably increased, which allows the short–stem plant to form a productive ear with help of multiflowered ear and larger grains.

Effective results are achieved through creation of short–stem rye forms with larger, vertical leaves. On the basis of the created breeding material new varieties with better, than earlier created, resistance to severe weather conditions (Table 6).

Variety Talovskaya 35, which is being tested, is characterized by vertical leaves and due to this drought resistance. It is resistance and to lodging. Another variety, Talovskaya 36, which is also being tested at present, is characterized by 3 most valuable features: resistance to lodging, drought and the most harmful diseases.

Table 6
The characteristics of perspective winter rye bonitation (competitive test within the years 1997–1999)

Variety	Resistance to										
	Yield		Lodging		Droughts		Brown rust		Stem rust		Frost resistance [%]
	Difference from standard [t/ha]	According to scale [points]	Difference from standard [t/ha]	According to scale [points]	Difference from standard [t/ha]	According to scale [points]	Susceptibility [%]	Difference from standard [t/ha]	Susceptibility [%]	Difference from standard [t/ha]	
Talovskaya 15*	5.37	4.08	-	3.60	-	70.7	-	68.3	-	60.1	
Talovskaya 33**	5.08	4.00	-	3.56	-	24.7	-	19.3	-	64.0	
Talovskaya 35	5.52	4.16	0.08	4.52	0.92	72	1.5	50.0	-18.3	52.9	
Talovskaya 36	5.43	4.35	0.35	4.10	0.54	43.3	18.6	38.7	19.4	61.5	

* standard for Talovskaya 35

** standard for Talovskaya 36

Table 7
Polyploid influence on productivity and green mass quality

Parameter	Percent from initial diploid	
	Diploid	Tetraploid
Yield of green mass [dt/ha]	476.0	542.0
Yield of hay [dt/ha]	79.0	88.8
The amount of fodder units per 1 kg	0.727	0.732
Amount of energy exchange [MJ]	9.15	9.19
The amount of fodder units collected from 1 ha	58.6	65.6
Amount of energy exchange per 1 ha [103 MJ]	73.7	82.4
Raw fiber [dt]	9.45	10.93

Efficiency of genes used in winter rye breeding

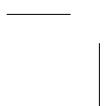
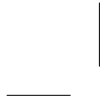
Table 8

Genes used in breeding	Result of breeding	Effect of genes used in the breeding
<i>Dw 1 (Hl)</i>	Talovskaya 12 Talovskaya 15	Increase yield with 15–20% and increase of resistance to lodging with 35–40%
<i>Dw 1 (Hl), Pm, Lr1-Lrn, Sr</i>	Talovskaya 29 Talovskaya 33 Talovskaya 36	Good resistance to lodging and increase of productivity within epiphitoty with 45–50%
<i>Dw 1 (Hl), Sl</i>	Talovskaya 35	Good resistance to lodging and increase of resistance todrought with 25%
<i>Dw 1 (Hl), al (el), mul</i>	Strain 1193	Good resistance to lodging and increase of amount of energy exchange in hay with 5% and number of seeds with 35–40%

For creation of varieties for green mass production tetraploid forms were used. They are found to be better in comparison with diploid forms in relation to productivity and quality of green mass (Table 7). Using these forms a new variety, Savala Tetra, was created and recommended to use.

Another perspective tendency in selection of varieties for green mass production is the combination in one variety of dominant short–stem feature (gene *Hi*), vertical arrangement of leaves (gene *a1* or *S1*) and gene of multiflowered ear (gene *mul*). It allows to create (see strain 1193 in Table 8) highly productive, lodging resistant varieties with high quality of green mass and good seed yield. They can also function as suitable components when mixed with winter vetch.

Table 8 illustrates the efficiency of different genes used in selection procedure with winter rye in our institute.



A.-M. Tomerius, H. H. Geiger

Institute of Plant Breeding, Seed Science and Population Genetics (350), University of
Hohenheim, 70593 Stuttgart, Germany

INFLUENCE OF QUANTITATIVE-GENETIC AND ECONOMIC PARAMETERS ON THE EFFICIENCY OF CMS-LINE DEVELOPMENT IN RYE

ABSTRACT

Model calculations were conducted to optimize and compare alternative schemes of CMS-line development in hybrid rye breeding on the basis of their expected selection gain per year assuming a fixed annual budget. Selection gains are predicted using current estimates of the relevant quantitative-genetic and economic parameters. Two alternative schemes are dealt with here. The first scheme (STD) represents a standard procedure in present-day second-cycle breeding. The second scheme (POP) is especially suited for population material that has not undergone intense inbreeding and selection yet. We:

- (i) give the optimum dimensioning of the schemes and their relative efficiency,
- (ii) study the effect of alterations in the dominance variance, the genotype \times environment-interaction variance, and the budget, and
- (iii) assess how deviations from the optimum dimensioning affect the selection gain.

Assuming identical genotypic variances, scheme STD is clearly superior to POP. It should thus always be used for second-cycle material. If, however, the population material used with scheme POP offers larger genotypic variances than the second-cycle material, POP becomes competitive. Changes in genetic and economic parameters affect the dimensioning but not the ranking of the schemes. Deviations from the optimum dimensioning only slightly reduce the selection gain as long as they are not too severe. This is shown for suboptimum numbers of testers and locations. All in all, the results demonstrate the importance of optimizing breeding schemes with respect to genetic, technical, and economic aspects.

Key words: hybrid rye breeding, line development, model calculations, optimization

INTRODUCTION

Since the release of the first hybrid varieties in Germany in 1984, the importance of hybrid rye has steadily increased (Geiger and Miedaner, 1999). In Germany, hybrids are currently grown on about 60% of the rye acreage. They are highly attractive for the grower mainly due to their superior yields, as experienced in many European countries (Madej, 1996).

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In hybrid rye breeding, seed-parent and pollinator lines are developed from the two genetically divergent gene pools 'Petkus' resp. 'Carsten'. Inbred-line development comprises selection for line performance *per se* followed by selection for combining ability to the respective opposite gene pool. Cytoplasmic-genic male sterility (CMS) is employed as hybridizing mechanism for the production of testcrosses as well as commercial seed. The schemes presently used for inbred-line development basically follow proposals of Geiger (1982, 1985). They have evolved according to the experiences accumulated in the last twenty years, but their further optimization remains a challenge for the breeder. A theoretical study comparing two strategies for the selection of pollen-parent lines in rye was carried out by Wilde (1996). This paper presents results of model calculations aiming at the optimization of seed-parent line development in hybrid rye breeding (Tomerius, 2001). Alternative breeding schemes are optimized and compared on the basis of their expected selection gain per year under the assumption of a fixed annual budget. Here we:

- (i) give the optimum dimensioning and relative efficiency of two alternative breeding schemes,
- (ii), assess the effect of alterations in the underlying quantitative-genetic as well as economic parameters, and
- (iii) investigate how deviations from the optimum dimensioning affect the expected selection gain.

METHODS

Breeding schemes investigated

Two alternative schemes for the development of seed-parent lines are investigated in this paper. The first scheme, STD, represents a standard procedure in present-day second-cycle breeding (Fig. 1). First, inbred lines in the second generation of selfing (S_2L) are evaluated *per se*. CMS analogues of the selected candidates are then developed by repeated backcrossing concurrently to the continued selfing process. Testcross performance is assessed at two successive stages using topcrosses of the CMS analogues of S_4L in backcross generation BC_1 resp. of S_6L in BC_2 with testers from the pollinator pool. Finally selected lines are used to produce experimental hybrids. With scheme STD one cycle of CMS-line development requires eleven years.

At the beginning of a hybrid breeding program – or if the genetic variability for a trait has been exhausted in a second-cycle breeding program — line development has to be based on populations that have not undergone continued selfing before or which have been established by introgressing population breeding materials into second-cycle materials. Such populations carry a high mutational load of deleterious recessive genes. Consequently, the proportion of inbred lines with acceptable agronomic appearance is very low. Intense selection for *per se*

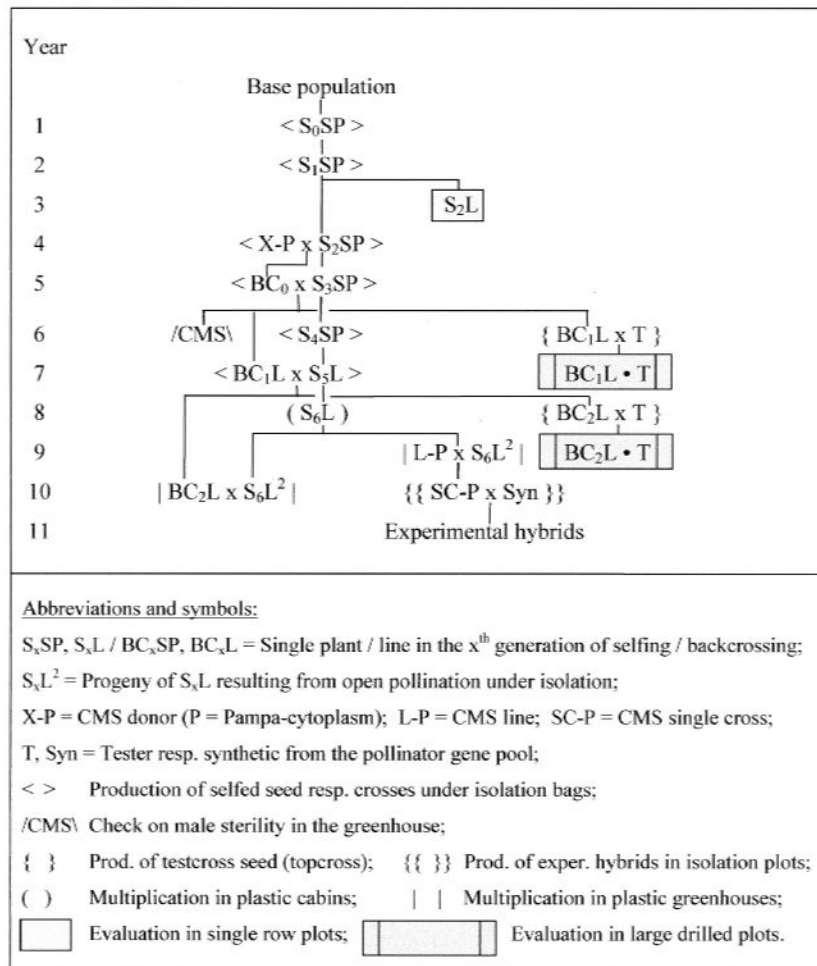


Fig. 1 Flow chart of the breeding scheme STD

performance is thus necessary before the development of CMS analogues and the evaluation of testcrosses is economically justifiable. Here, scheme POP is used to study the development of CMS–lines from population material (Fig. 2). Evaluation of line performance is carried out at two successive stages employing S₁L and S₂L. Testcross evaluation corresponds to scheme STD. One cycle of POP is two years longer than that of STD since advancing the lines by selfing and I or backcrossing is postponed until a positive selection decision has been reached in S_i and S₂ to avoid labour and expenses for candidates that are not worth being continued.

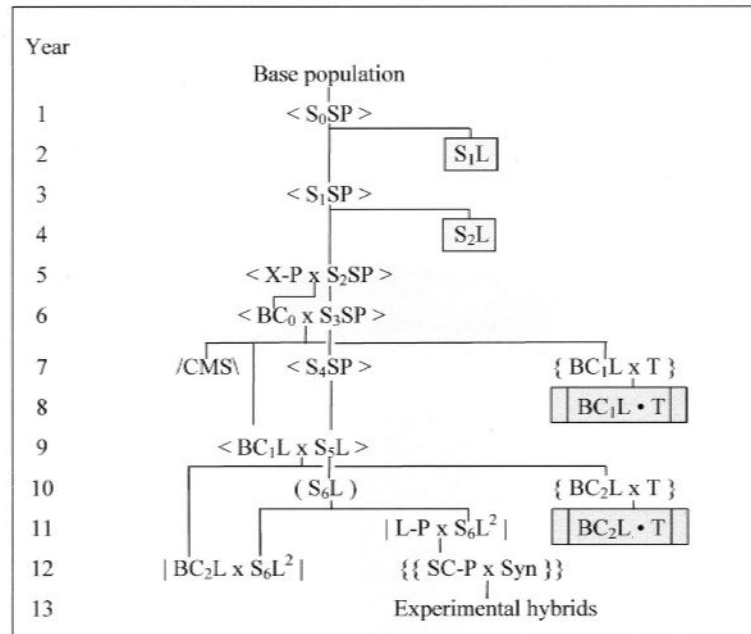


Fig. 2 Flow chart of the breeding scheme POP (for explanation of abbreviations and symbols – see Fig. 1)

Optimization of the breeding schemes

A detailed description of the model calculation approach can be found in Tomerius (2001). Briefly, the breeding schemes are optimized and compared on the basis of their expected selection gain per year. To calculate the expected gain from multistage selection, the formulae of Cochran (1951) as extended by Utz (1969) are employed. Prediction of selection gain rests on quantitative-genetic parameters estimated from breeding experiments, current testcross series, and official variety trials (Tomerius, 2001). The costs of the individual breeding activities are based on data provided by German hybrid rye breeders. The influence of different genetic and economic situations on the optimum dimensioning and relative efficiency of the schemes is investigated by varying the relevant parameters. Optimization is carried out under the restriction of a fixed budget to guarantee a fair comparison of the schemes and to reflect the economic constraints present. The standard budget is 200,000 per year. Assuming that a new line-development cycle starts every year, the annual budget — spent on all cycles running in parallel — equals the budget available for one entire cycle of a given scheme.

The selection criterion employed in the model calculations is an index comprising plant height, thousand-kernel weight, and resistance

to lodging, sprouting, and leaf rust when selecting for line performance *per se*. In testcross evaluation the index additionally comprises grain yield as the most important trait. The optimization criterion is the sum of the selection gains per year in line performance and general combining ability (GCA) weighed in the ratio of 1: 3 to reflect the importance of combining ability in hybrid breeding.

Optimum values are determined for the number of test units, testers used to assess GCA, and test locations at each selection stage. It is assumed that the lines *per se* are evaluated in unreplicated trials at no more than three locations while testcross trials always employ two replicates. The number of finally selected candidates is fixed at three.

RESULTS AND DISCUSSION

Optimum dimensioning of scheme STD under standard assumptions

Under standard assumptions for the genetic and economic parameters it would be optimum with scheme STD to evaluate 2683 S_2L *per se* at three locations and select 188 of them for further advancement (Table 1). CMS analogues of S_4 –lines (in BC_1) are then crossed to one tester and performance of the testcrosses is assessed at four locations. At the next stage, testcrosses of the 21 best S_6 –lines (in BC_2) with three testers are evaluated at eleven locations. Finally, the three best lines are selected to develop experimental hybrids. This standard variant of scheme STD will serve as a reference for all comparisons in the following. Its relative gain in the optimization criterion is set to 100%.

Influence of changes in the genetic and economic parameters

Since breeding programs may differ considerably with respect to the underlying genetic and economic parameters, it is important to study the impact of alterations in these parameters on the optimization results. In the following we investigate the influence of (i) the relative size of the dominance variance, (ii) the magnitude of genotype \times environment–interaction, and (iii) the available budget on the optimum dimensioning and the selection gain of scheme STD. Results show that the relative size of the dominance variance mainly affects the optimum number of testers

(Table 1). With increasing dominance variance, the importance of specific combining ability (SCA) increases. The breeder consequently needs more testers to assess the candidates' GCA. Since the budget is limited, fewer candidates and test locations can thus be employed. As a result, the expected selection gain is reduced despite the adjusted optimum dimensioning. With less dominance variance, on the other hand, the number of testers can be reduced in favour of the number of candidates and locations and the achievable selection gain increases.

Table 1

Optimum dimensioning and relative selection gain of breeding scheme STD under various assumptions for the underlying genetic and economic parameters

Scheme	Assumptions	CL	Test	N	T	L	G[%]
STD	Standard	11	LP	2683	–	3	100.0
			TP ¹	188	1	4	
			TP ²	21	3	11	
STD	Dmominance variance doubled	11	LP	2689	–	3	76.5
			TP ¹	144	2	3	
			TP ²	19	5	9	
STD	Dominance variance halved	11	LP	2798	–	3	111.6
			TP ¹	198	1	4	
			TP ²	20	2	14	
STD	G × E variance doubled	11	LP	2513	–	3	91.7
			TP ¹	171	1	5	
			TP ²	20	3	13	
STD	G × E variance halved	11	LP	3449	–	2	106.4
			TP ¹	207	1	3	
			TP ²	24	3	9	
STD	Budget = 100000 per year	11	LP	1256	–	3	90.4
			TP ¹	99	1	4	
			TP ²	15	2	9	
STD	Budget = 300000 per year	11	LP	4335	–	3	105.1
			TP ¹	270	1	4	
			TP ²	27	3	13	

CL – cycle length [years],

N – number of candidates,

T – testers, L – locations,

G – gain in the optimization criterion relative to that of the STD standard variant,

LP – line performance,

TP¹ – testcross performance 1st test,

TP² – testcross performance 2nd test,

G × E – genotype × environment interaction

The magnitude of genotype × environment –interaction (G × E) variances mainly affects the optimum number of locations (Table 1). With larger G × E variances, the optimum number of locations is increased to account for the reduction of the heritability. The number of candidates is consequently reduced and the selection gain decreases. With lower G × E variances, the opposite effect is observed: fewer locations are needed at all selection stages so that more candidates can be evaluated and the achievable selection gain increases.

Alterations in the available budget predominantly influence the optimum number of candidates while the optimum evaluation intensity

remains quite stable (Table 1). Assuming half the standard budget (i.e. 100,000), the number of candidates at all selection stages is severely reduced. The relative selection gain amounts to 90% of the STD standard variant. With a budget of 300000, more candidates are evaluated at all stages. The relative selection gain under this assumption is 105%.

Influence of deviations from the optimum dimensioning

As outlined above, the optimum numbers of testers at the two testcrossing stages are low under standard assumptions and moderate to high if large dominance variances are assumed (see Table 1). The impact of deviations from the optimum numbers of testers determined in the model calculations is now studied for scheme STD. Assuming standard genetic variances, the expected selection gain is hardly affected as long as the numbers of testers do not deviate too much from the optimum (Fig. 3). A relative efficiency below 99% results only if:

- (i) one tester is used at both testcrossing stages or
- (ii) three testers are used at the first testerossing stage.

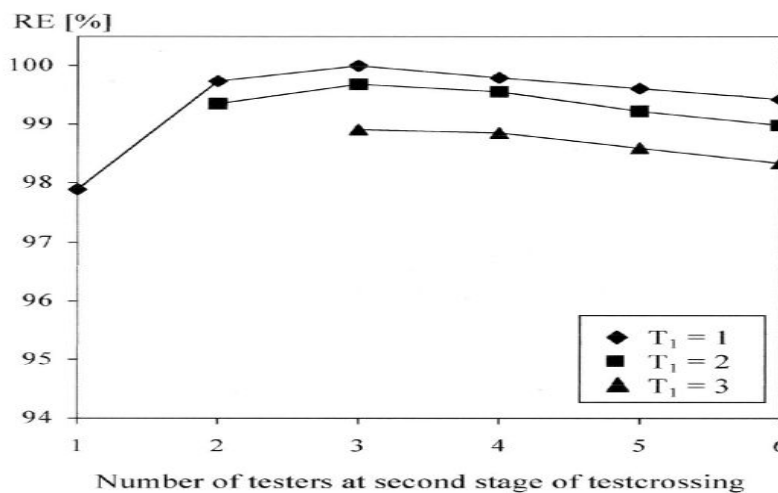


Fig. 3 Relative efficiency (RE – percentage of respective optimum variant) of scheme STD as a function of the number of testers at the second stage of testcrossing (T₂) and standard dominance variances (Restriction: T₂ ≥ T₁)

With increasing numbers of testers, the number of candidates and locations at all evaluation stages decreases (data not shown). A different relationship is observed if doubled dominance variances are assumed. In this case, the expected selection gain is markedly reduced if too few testers are used, especially if only one tester is used at the first stage (Fig. 4). With two or three testers at the first testcrossing stage and four to six testers at the second testcrossing stage, the expected selection gain is always maximized.

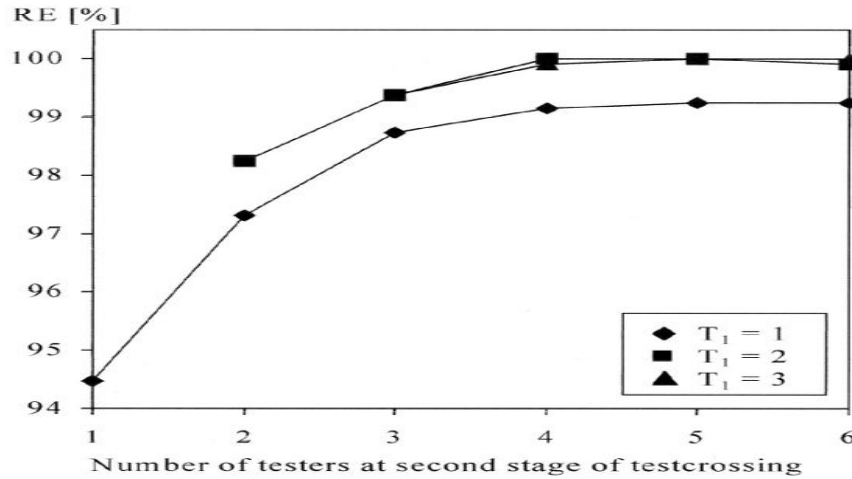


Fig. 4 Relative efficiency 9RE – percentage of respective optimum variant) of scheme STD as a function of the number of testers at the second stage of testcrossing (T_1) and doubled dominance variances (Restriction: $T_2 \geq T_1$)

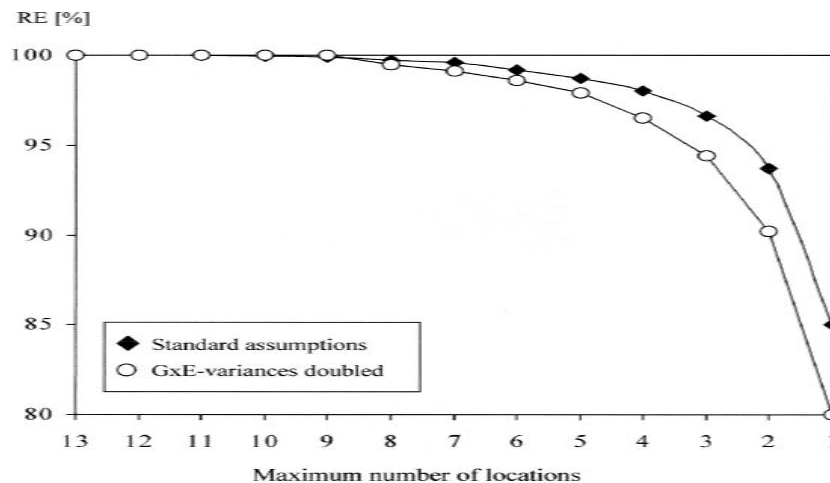


Fig. 4 Relative efficiency 9RE – percentage of respective optimum variant) of scheme STD as a function of the maximum number of available locations (Restriction: number of locations is not allowed to decrease from one evaluation stage to the next)

Another important aspect is the number of locations available in a breeding program. For various reasons their number may be much lower than the optimum number determined in the model calculations, particularly at the final evaluation stage. Assuming standard genetic parameters, the expected selection gain of scheme STD decreases by only 2% in the range of eleven (i.e. the optimum number determined) to four locations available (Fig. 5). Below four locations, the selection gain decreases much stronger. If only a single location would be employed at

each selection stage, the selection gain would be reduced by 13%. The number of replicates for testcross evaluation was allowed to increase with the decreasing number of locations for this particular purpose. For only one location at each selection stage, three replicates would be optimum at the first testcrossing stage and five replicates at the second testcrossing stage. The number of candidates and testers is increased, too (data not shown). A stronger decrease of selection gain is observed if large $G \times E$ variances are assumed (Fig. 5).

Comparison of schemes STD and POP assuming different amounts of additive variance in the base population

Table 2

Scheme	Additive variance	CL	Test	N	T	L	G[%]
STD	Standard = 100%	11	LP	2683	–	3	100.0
			TP ¹	188	1	4	
			TP ²	21	3	11	
POP	Standard = 100%	13	LP ¹	3816	–	1	86.5
			LP ²	1091	–	3	
			TP ¹	180	1	4	
			TP ²	21	3	11	
POP	125%	13	LP ¹	3744	–	1	98.7
			LP ²	1064	–	3	
			TP ¹	189	1	4	
			TP ²	20	3	11	
POP	150%	13	LP ¹	3934	–	1	109.6
			LP ²	1095	–	3	
			TP ¹	198	1	4	
			TP ²	21	2	12	

CL – cycle length [years],
 N – number of candidates,
 T – testers, L – locations,
 G – gain in the optimization criterion relative to that of the STD standard variant,
 LP – line performance,
 LP¹ – line performance, 1st test,
 LP² – line performance, 2nd test,
 TP¹ – testcross performance 1st test,
 TP² – testcross performance 2nd test,

Comparison of schemes STD and POP

Under standard assumptions, the optimum dimensioning of scheme POP differs from that of the standard scheme only with respect to selection for line *per se* performance (Table 2). A large number of S₁–lines is first evaluated at a single location. Roughly the 30% best S₂–lines are then evaluated more precisely at three locations. Testcross evaluation is identical to the standard scheme except for a slightly lower number of BC₁L–testcrosses. The expected selection gain of POP in the optimization criterion is only 86.5% of the STD standard variant due to the two years longer breeding cycle. When working with population

material, however, the additive variance in the base population is often larger than in a second-cycle program. As a consequence, the relative merit of scheme POP increases. Assuming e.g. a 25% higher additive variance, the efficiency of POP is 99% of the STD standard variant despite the longer breeding cycle (Table 2). With 50% higher additive variance, POP would even be superior to STD by 10%. The usefulness of a base population, however, depends not only on its genetic variance and the selection gain resulting therefrom, but also on the population mean (Schnell, 1983). With respect to line *per se* performance, the mean of genetically broader populations will usually be much lower than that of second-cycle populations. Yet, with regard to combining ability the difference is not necessarily that large. Roux *et al.* (2001) found that seven (out of a set of 19) genetic resources investigated showed comparable combining abilities as adapted population materials when crossed to two elite CMS-testers. Under such circumstances the development of inbred lines from genetically broader population material may well be competitive.

The influence of changes in the genetic and economic parameters and of deviations from the optimum number of testers and locations on scheme POP is very similar to that described for scheme STD (data not shown).

CONCLUSIONS

1. Results demonstrate the usefulness of model calculations for evaluating the efficiency of alternative breeding schemes. Scheme STD should always be used for second-cycle material since it is clearly superior to POP due to the shorter breeding cycle. When working with population material, the breeder has to use scheme POP since he needs to spend more time and labour on identifying the lines that are worth testing for GCA. The extended cycle length of scheme POP may be counterbalanced, however, by a larger additive variance in the base population, so that line development from population material by scheme POP and from second-cycle material by scheme STD may be equally successful in practice.
2. The optimum dimensioning of a breeding scheme clearly depends on the underlying genetic and economic parameters. Knowledge of such parameters as the relative size of the dominance variance or the genotype \times environment-interaction variance in present breeding materials is thus crucial for the breeder to choose an appropriate dimensioning.
3. According to the results, only one tester should be used at the first testcrossing stage except if the dominance variance is very large. Yet, employing two testers instead of one hardly affects the expected selection gain but increases the security of testcross seed

production and offers the possibility to choose testers specifically suited for different trait complexes such as grain yield, quality or disease resistance. The use of two testers already at the first stage of testerossing may therefore be advisable in many situations. Assuming a limited number of test locations, the expected selection gain is not severely reduced as long as five or six locations are employed at the final selection stage.

ACKNOWLEDGEMENTS

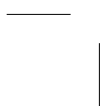
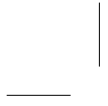
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P. Wilde, J. Menzel, B. Schmiedchen

Lochow-Petkus GmbH, 29303 Bergen, Germany (email wilde(ä-lochow-petkus.de)

ESTIMATION OF GENERAL AND SPECIFIC COMBINING ABILITY VARIANCES AND THEIR IMPLICATIONS ON HYBRID RYE BREEDING

ABSTRACT

Effects and variances of general (GCA) and specific (SCA) combining ability have been estimated from two experiments. For the first experiment (EXP I) 19 homozygous lines originating from the Petkus pool were crossed with two *CMS* single cross testers derived from the Petkus pool (intra-pool test crosses) and with two testers from the Carsten-Danko pool (inter-pool test crosses), respectively. In the year 2000 grain yield was measured at 5 locations in Germany. The second experiment (EXP II) comprised a factorial of inter-pool crosses by using 4 homozygous *CMS* Petkus pool lines as seed parents and 6 Carsten-Danko lines as pollen parents. The respective 24 inter-pool crosses were evaluated for grain yield on several locations in 1996 and 1998.

In EXP I GCA-variance of candidate lines (4.7 —5.9 q/ha) was estimated to have a similar size as SCA-variance. Possible reasons for an overestimation of SCA-variance are extreme divergence between testers, insufficient removal of inbreeding effects in the intra-pool test crosses and bias due to SCA \times year interaction-variance. The use of intra-pool testers should be restricted to breeding material where inbreeding due to consanguinity between testers and candidate lines is either absent or will evenly affect test cross performance of all candidates.

In EXP II GCA-variances for female 9.2 q/ha² and male 2.4 q/ha lines were much higher than SCA-variance. Repeatability for GCA-effects over different environments was medium ($r=0.67$), whereas for SCA-effects it was low ($r=0.13$). Selection intensity for yield should therefore be moderate, if based on a single year of testing only. Selection of parental components for hybrids and prediction of hybrid performance should mainly base on GCA-effects. Alternative to the use of factorial crosses test crosses with testers representing the opposite pool are recommended. Testing for SCA-effects and for SCA \times environment interaction-effects can be a valuable diagnostic tool, to become aware of strengths and weaknesses of the elite material used to build new hybrids. SCA-tests should therefore be performed by using highly divergent environments.

Key words: *CMS* cross testers, general combining ability (GCA), homozygous lines of rye, hybridrye breeding, specific combining ability (SCA)

INTRODUCTION

Hybrid rye breeding aims to detect inbred lines, which excel by a high performance in their crosses. When developing candidate lines their partner lines in the final hybrid are not known in most cases and no direct tests for the hybrid performance are feasible. Therefore selection

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must base on indirect selection criteria during line development. By intensive selection on line *per se* performance high heritable traits are improved. By test crosses the breeder aims to identify candidate lines showing excellent general combining ability (GCA) effects for low heritable traits such as yield.

In most breeding programs (Geiger, 1982) lines belonging to the seed parent pool are top crossed by using their near isogenic *CMS* analogues lines. This allows to cross them easily with a male tester, usually a synthetic derived from the pollen parent pool. Lines belonging to the pollen parent pool are outcrossed to *CMS* single cross testers which are regarded to be representative for the seed parent pool. Yield tests of the test crosses grown over several locations and at least one year allow to reduce the number of candidate lines considerably and to focus on the most promising fraction. For final evaluation and for identifying hybrid combinations elite lines from the seed and pollen parent pool can be crossed in a factorial way. This procedure also allows to estimate specific combining ability effects (SCA) of given crosses of elite lines.

In this paper we report about general combining ability effects and their variances when crossing a line population to testers originating from different heterotic pools (EXP I). When developing seed parent lines the breeder may be motivated to replace the normally used opposite pool testers by testers, which have been derived from the seed parent pool, too. After outcrossing S2- or S3- candidate lines on such testers, their **intra-pool test crosses** allow to test for yield in a much earlier stage of line development and to save time and costs. Thus, they might be a valuable alternative to the traditionally used **inter-pool test crosses** based on more or less isogenic *CMS* analogues of the candidate lines.

Further, we evaluate a factorial cross of seed and pollen parent lines (EXP. II) with regard to their GCA- and SCA-effects and their respective variances.

MATERIALS AND METHODS

Experiment I:

As candidate line population we used 19 homozygous lines from the Petkus pool. From these lines the male fertile version in the Normal-cytoplasm (N-L) and their respective *CMS* analogues (P-L) were available. The latter were obtained by backcrossing the male fertile version to a donor plant for the Pampa cytoplasm over at least five generations. In 1998 the N-L were outcrossed to two *CMS* single cross testers (T1 and T2) developed also from the Petkus pool. T1 and T2 were chosen to be unrelated to each other. Both testers were selected by pedigree analysis to have either no or only distant ancestors in common with the candidate lines. Thus, biases due to inbreeding effects in the **intra-pool test crosses** should be kept as low as possible. In case candidate lines and testers had ancestors in common, adjusted yield (Y_{adj})

was calculated from observed yield data (Y_{obs}) and from the inbreeding coefficient (F) (Falconer and Mackay, 1996) of the test crosses as derived from pedigree data. The formula:

$$Y_{adj} = \frac{Y_{obs}}{1 - 0.7 \times F}$$

assumes an inbreeding minimum of 30 % of the heterozygote performance (Wricke, 1973) and a linear relationship between degree of heterozygosity and performance level. In test crosses with T1 inbreeding coefficients ranged between $0 < F > 0.03125$ for 3 candidate lines, whereas in test crosses with T2 F was calculated to range between $0.0625 < F > 0.0859$ for 7 candidate lines and for the rest of the lines $0 < F > 0.0469$. In 1997 and 1999 the P-L were used as seed parents to produce **inter-pool test crosses** with two other testers (T3 and T4). Both testers were derived from Carsten-Danko breeding populations, which are used in our hybrid program as pollen parent pool. T3 was an inbred line in S2-L generation and T4 is a synthetic developed of two inbred lines in S3-L generation. T3 and T4 are unrelated to each other.

In the year 2000 yield plots (5 m^2) of the test crosses were grown at five locations in Northern and Eastern Germany with two replications/location. The experiment was laid out as a split plot design with lines as main units and tester \times line-combinations as sub-units.

Experiment II:

Experiment II comprised 24 factorial inter-pool crosses between the CMS analogues of four homozygous inbred lines from the Petkus pool and six S2-L from the Carsten-Danko pool. The lines represent actual breeding material and most of them are parental components in registered hybrids. The inter-pool crosses were grown in seven environments (i.e. 3 and 4 locations in Northern and Eastern Germany in the years 1996 (Erfurt, 1997) and 1998, respectively) with two replications/location.

For brevity, in the following only grain yield data (q/ha) are presented.

RESULTS AND DISCUSSION EXPERIMENT I:

Means of the **inter-pool test crosses** (71.3 q/ha) surpass those of the **intra-pool test crosses** (62.8 q/ha) for about 8 q/ha. Because all testers have been comparably preselected for combining ability, superiority of **inter-pool test crosses** can be attributed to heterotic increase due to combining divergent gene pools. With regard to their ability to differentiate between candidate lines a slight advantage for the Carsten testers compared to the Petkus testers can be stated. On the other hand intra-pool test cross results are less impeded by masking effects such as

genotype \times location interaction and error effects. This finding can be explained by two reasons:

First, sowing in autumn 1999 suffered from unfavourable weather and soil conditions and seed quality severely influenced germination rate at the different locations. **Intra-pool test cross** seedlings could benefit from excellent seeds grown on their heterozygous seed parents (Ti and T2). In contrast, **inter-pool test cross** grains suffered from bad seed quality caused by the homozygous *CMS* analogues serving as seed parents (Table 1).

Table 1
Estimates of means, variance components and heritability (h^2) for yield (q/ha) in the test cross series with 19 Petkus pool lines (EXP. 1)

Parameter	Origin of testers							
	Petkus				Carsten-Danko			
	T1		T2		T3		T4	
Mean	62.8		62.8		73.3		69.4	
σ_t^2	18.8**	$\pm 4.6^{\S}$	6.9**	$\pm 3.4^*$	14.0**	± 6.7	8.2**	± 4.1
σ_{tp}^2	14.3**	± 3.1	11.6**	± 3.1	27.5**	± 5.8	27.5**	± 3.7
σ_e^2	8.3	± 1.2	12.6	± 1.9	13.4	± 2.1	13.4	± 1.4
h^2 [%]	74.5		65.7		67.2		64.6	

σ_t^2 – genetic component

σ_{tp}^2 – genotype \times location interaction

σ_e^2 – error variance component

\S – standard error of the respective variance component estimate

*, ** – estimates are significant at probability level $P=0.05$ and $P=0.01$ respectively

Secondly, the exceptionally high σ_{tp}^2 estimate for T3 test crosses is in accordance with other experiments showing a rather low environmental stability of T3. Moreover, because T3 is an inbred line, the respective test crosses are genetically more narrow based than those of the three other testers. Genetic structure however is known to influence buffering capacity of experimental hybrids (Becker and Leon, 1988).

On the other hand, **intra-pool test crosses** can be sensitive to another source for masking genotype effects: In contrast to **inter-pool test crosses** they are male sterile and seed set therefore depends on a sufficient pollen cloud provided by neighbouring plots. This may become a bottleneck if grown at the border of the experimental field or in case of unfavourable weather conditions during flowering period. Heritability is one of the components and key factors of the expected genetic gain (Falconer and Mackay, 1996). With regard to this parameter first choice would be to use Ti ($h^2=74.5\%$) for test crosses.

As already mentioned intra-pool test crosses were adjusted for inbreeding effects. (Fig. 1). If combining ability to the mean of the two opposite pool testers T3 and T4 is regarded as target criterion, effectiveness of adjustment can be studied. The phenotypic correlation of test cross means with Ti to the mean of test crosses with T3 and T4

($r_{adj.}=0.68$) is scarcely influenced by inbreeding effects, because there were only three candidate lines showing slight consanguinity to the tester. In contrast, correlation of test crosses with T2 ($r_{unadj.}=0.46$) could be improved considerably by adjustment ($r_{adj.}=0.61$). The adjustment above described is simple to calculate, but it's efficiency depends on:

- (i) correct pedigree data which are not always available under practical conditions,
- (ii) the size of sampling effects with regard to the contribution of the ancestors genome to the candidate and tester genome,
- (iii) a linear relation between hetero- and homozygous performance.

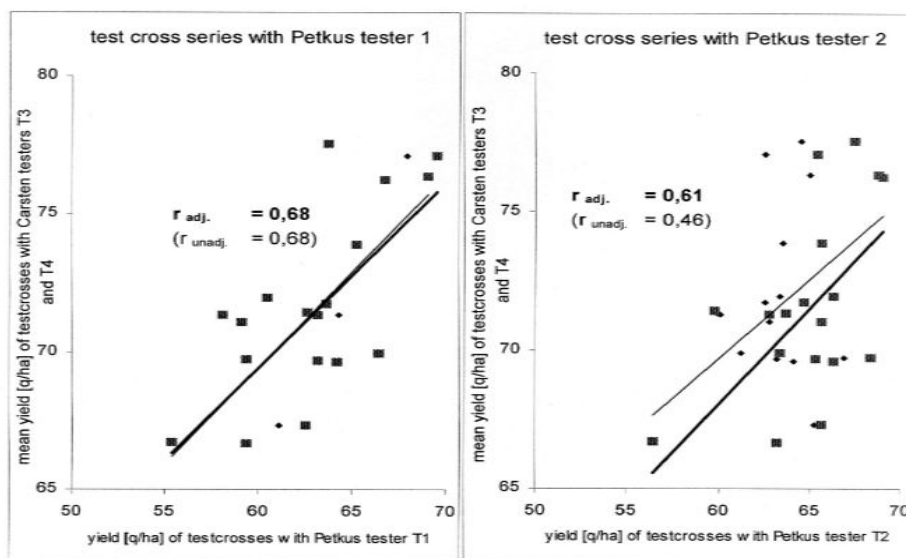


Fig. 1 Phenotypic correlation of test crosses with intra-pool testers T1 and T2 to the mean of test crosses with opposite pool testers T3 and T4 (Experiment I). Squares and diamonds – adjusted and unadjusted values respectively

The present experiment offers no possibility to examine in how far a better adapted adjustment would influence the association between ultra and inter-pool test cross series. The phenotypic correlation of test cross means with T1 to the mean of test crosses with T3 and T4 ($r_{adj.}=0.68$) is comparable in size to the corresponding correlation between the test cross series with the opposite pool testers T3 and T4 ($r=0.63$). This results demonstrates, that test crosses with unrelated **intra-pool testers** can be useful to test candidate lines for GCA to the opposite pool. On the other hand, results with related testers such as T2 clearly show, that **intra-pool testers** may become a pitfall leading to a rather inaccurate gca estimation of the candidate lines, if no adequate adjustment for inbreeding effects is possible.

As can be seen (Table 2) from the high variance between testers ($\sigma^2_T=21.4$ q/ha) use of all testers allows to test candidate lines on an ex-

tremely divergent genetic background. This variance is mainly due to origin of testers, as becomes obvious when testers are grouped according to their pools. Compared to estimates in the literature (Kolasińska and Wegrzyn, 1998; for review see also Tomerius, 2001) the size of SCA-variance relative to GCA-variance is rather high. In contrast to the 1:1 relation between SCA- and GCA-variance found in our experiment most estimates in the literature attribute much lower values to SCA-variance. Possible reasons for our deviating results are: extreme divergence of testers (in case of all four testers), insufficient removal of inbreeding effects (in case of Petkus testers) and narrow versus broad based tester (in case of Carsten testers). Anticipating results from Experiment II, it should be realised, that in a one-year-experiment estimators of SCA-variance can be severely biased upwards by SCA \times year interaction variance.

Table 2
Estimates for variance components and heritability (h^2) for yield (q/ha) with the test crosses grouped according to the origin of the tester

Parameter	Origin of testers					
	PET + CAR		PET		CAR	
σ^2_T	21.4**	$\pm 14.1^{\S}$	62.8	± 1.5	73.3	± 6.1
σ^2_{GCA}	4.7*	± 3.2	6.9**	± 3.1	14.0**	± 4.6
σ^2_{SCA}	5.0**	± 1.2	11.6**	± 1.8	27.5**	± 2.1
$\sigma^2_{GCA \times E}$	15.9**	± 3.2	12.6	± 2.8	13.4	± 4.5
$\sigma^2_{SCA \times E}$	1.9**	± 0.6	65.7	± 0.9	67.2	± 1.2
h^2	47.5		39.4		42.4	

σ^2_T – tester component

σ^2_{GCA} – general combining ability component

σ^2_{SCA} – specific combining ability component

$\sigma^2_{GCA \times E}$ – interaction of general combining ability with environment

$\sigma^2_{SCA \times E}$ – interaction of specific combining ability with environment

\S – standard error of the respective variance component estimate

*, ** – estimates are significant at probability level $P=0.05$ and $P=0.01$ respectively

For practical breeding purposes the following conclusions can be drawn:

- (i) The use of intra-pool testers for testing candidate lines from the seed parent pool should be restricted to recurrent selection programmes or to **breeding populations**, which have been derived from self incompatible base populations. In all these cases consanguinity between testers and candidate lines will be either absent or will evenly affect test cross performance of all candidates.
- (ii) In contrast, with **second cycle material** from the seed parent pool it will be hard to avoid distortion caused by considerable variance of inbreeding effects due to consanguinity between candidate lines and testers. Therefore, in this case use of testers from the opposite pool is crucial for an unbiased GCA-estimation.

(iii) If **early testing procedures** are intended with second cycle material from the seed parent pool *CMS* testers have to be developed from the pollen parent pool. This however can become a tedious work, because restorer genes have to be removed completely for the sake of a reliable male sterility of the *CMS* testers.

Experiment II

Regarding GCA-effects on the basis of seven environments (Table 3) the variability among seed parent lines is mainly caused by line F3 and F4 showing highly significant positive and negative effects, respectively. In comparison, variability on the pollen parent side was smaller and mainly due to line M4 and M5. SCA-effects were generally found to be less important than GCA-effects and showed higher standard errors.

Table 3

General combining ability(GCA) and specific combining ability (SCA) for yield (q/ha) of a factorial cross of 4 seed parent (F1-F4) and 6 pollen parent lines (M1-M6) estimated over 7 environments (EXP. II)

Line	M1	M2	M3	M4	M5	M6	GCA _F
	SCA						
F1	1.8	1.1	-1.5	-0.7	-1.3	0.7	-0.6
F2	-1.1	0.9	-0.6	-0.6	0.3	1.0	1.1
F3	-0.2	-1.2	0.2	0.5	-0.1	0.9	3.4
F4	-0.5	-0.9	2.0	0.8	1.1	-2.6	-4.0
GCA _M	-0.5	-0.8	1.8	-2.4	2.7	-0.8	0.6

Corresponding standard errors (SE):
 GCA-effects: 0.78 q/ha and 1.09 q/ha for seed and pollen parent lines respectively
 SCA-effect: 1.24 q/ha

Testing environments in the years 1996 and 1998 were rather different, with a high yield average (77.4 q/ha) in the first year and a rather poor yield level 55.9 q/ha) in the second year, which was due to unfavourable weather conditions. Thus, dependence of GCA- and SCA-estimators on different environmental conditions can be studied.

GCA-effects revealed a medium correlation (Fig. 2) over years ($r=0.67$), whereas SCA-effects proved to be rather inconsistent ($r=0.13$).

If estimated over both years genetic variation among inter-pool crosses (Table 4) could almost exclusively be attributed to GCA-variance. Large differences, however, were found for this parameter between female and male lines (9.2 vs. 2.4 q/ha).

Beside limited precision in parameter estimation there are two genetic reasons to explain this discrepancy.

(i) The elite female and male lines used for the experiment do not reflect variability in the unselected seed and pollen parent pool, respectively, but represent the remaining variability after two stages of selection on GCA-effects. Thus, differences in intensity of selection will also influence parameter size.

- (ii) Variability between female lines is expected to be higher, because they are almost completely homozygous, whereas male lines have been inbred only up to 52-L generation.

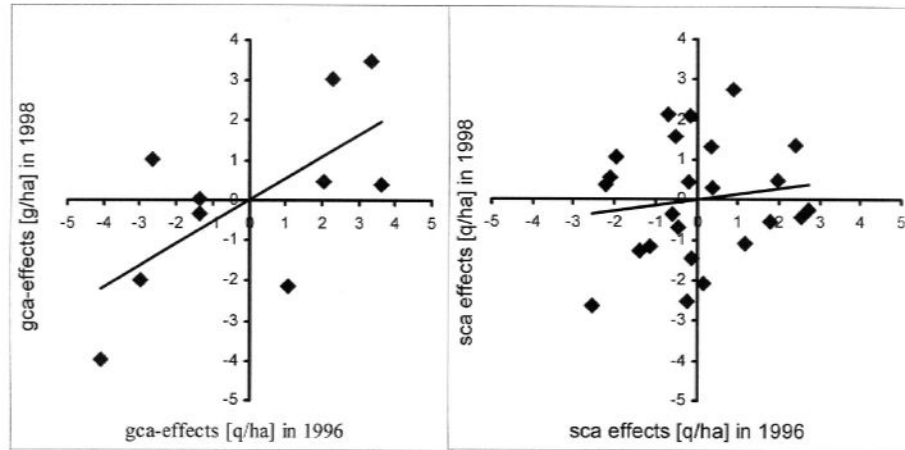


Fig. 2 Relationship between GCA-effects and SCA-effects [q/ha] estimated in 1996 (3 locations) and 1998 (4 locations) – Experiment II

Variance components and heritability (h^2) for yield (q/ha) estimated over seven environments (Experiment II)

Table 4

Parameter	Female	⇐Lines⇒	Male
σ^2_{GCA}	9.2** ±6.2§		2.4* ±1.9
σ^2_{SCA}		0.44 ±0.77	
$\sigma^2_{GCA \times E}$	2.0* ±1.2		4.9** ±1.9
$\sigma^2_{SCA \times E}$		5.34** ±1.76	
h^2_{GCA}	93.8		66.4

Abbreviations – see the legend of the Table 2

In comparison with GCA-variance SCA-variance was of almost negligible size and showed a high standard error. As already pointed out in Fig. 2 interaction with environments played an important role in our experiment leading to highly significant $\sigma^2_{GCA \times E}$ (male lines) and $\sigma^2_{GCA \times E}$ variances. Consequently, heritability estimators were found to be medium to high for GCA-effects and very low for SCA-effects (data not shown). Jenkins (1934) developed methods to predict hybrid performance depending on estimation of GCA- and SCA- effects. An application of his method B could be to use the performance of the single crosses measured in the first environment for the prediction of their performance in a second environment. In this case prediction bases on GCA- and SCA-ef-

fects. Method C is differing from method B by using only GCA-effects for prediction. In Fig. 3 both methods are compared. In the first case single cross performance in 1998 is predicted by using single cross performance in 1996. In the second case forecast of hybrid performance in 1998 bases exclusively on GCA-effects as estimated in 1996. Both methods can be regarded as equivalent with regard to their ability to predict single cross performance. Due to rather precise estimation of GCA-effects method C can compete with method B, which should be superior, if SCA-effects are important and could be estimated with high accuracy.

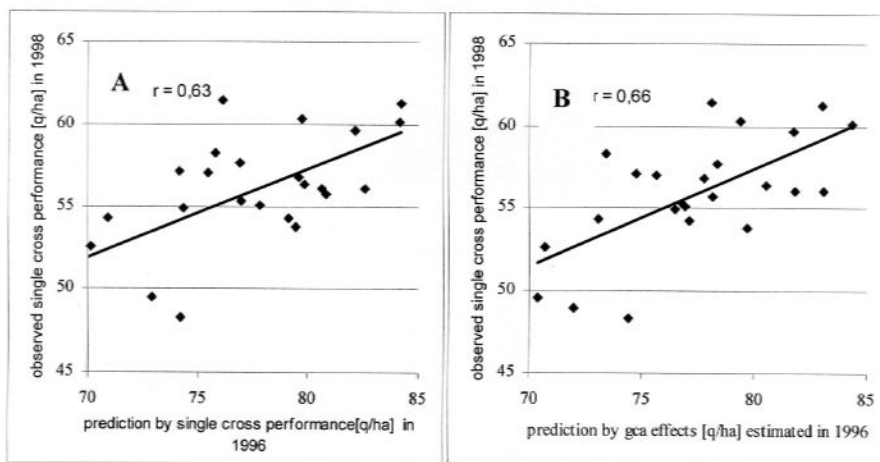


Fig. 3 Prediction of single cross performance in 1998 by using single cross performance (A) and parental GCA-effects (B) in 1996, respectively (Experiment II)

CONCLUSIONS

The following conclusions can be drawn for practical breeding programs:

- (i) Selection of parental components for hybrids and prediction of hybrid performance should mainly base on GCA-effects, because precision of prediction is at least equivalent to other methods taking also SCA-effects into account.
- (ii) For GCA-tests 2–3 testers chosen for a good representation the opposite pool should be used. Compared to factorial crosses of inbred lines costs for seed production will be lower and testing efficiency will be superior.
- (iii) Selection intensity for yield should be moderate if based on a single year of testing, only. Reliability of results can considerably be improved by applying multi-stage selection procedures (Wilde, 1996, Tomerius, 2001) over subsequent years.

- (iv) Estimating SCA-effects and their variances will be justified only at the end of the breeding process, where a very small number of line crosses has to be tested.
- (v) Testing for SCA-effects and for SCA \times environment interaction-effects can be a valuable diagnostic tool, to become aware of strengths and weaknesses of the elite material used to build new hybrids. SCA-tests should therefore be performed by using highly divergent environments.

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