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 × 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).

Communicated by Elisabeth Gunnarsson

In hybrid rye breeding, seed–parent and pollinator lines are devel–oped from the two genetically divergent gene pools 'Petkus' resp. 'Carsten'. Inbred–line development comprises selection for line per–formance *per se* followed by selection for combining ability to the re–spective 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 in–bred–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 chal–lenge 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 al–
      ternative breeding schemes,
  (ii), assess the effect of alterations in the underlying quantita–
      tive–genetic as well as economic parameters, and
  (iii) investigate how deviations from the optimum dimensioning af–
      fect 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 evalu–ated *per Se*. CMS analogues of the selected candidates are then devel–oped 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 ma–terials. Such populations carry a high mutational load of deleterious recessive genes. Consequently, the proportion of inbred lines with ac–ceptable agronomic appearance is very low. Intense selection for *per se*
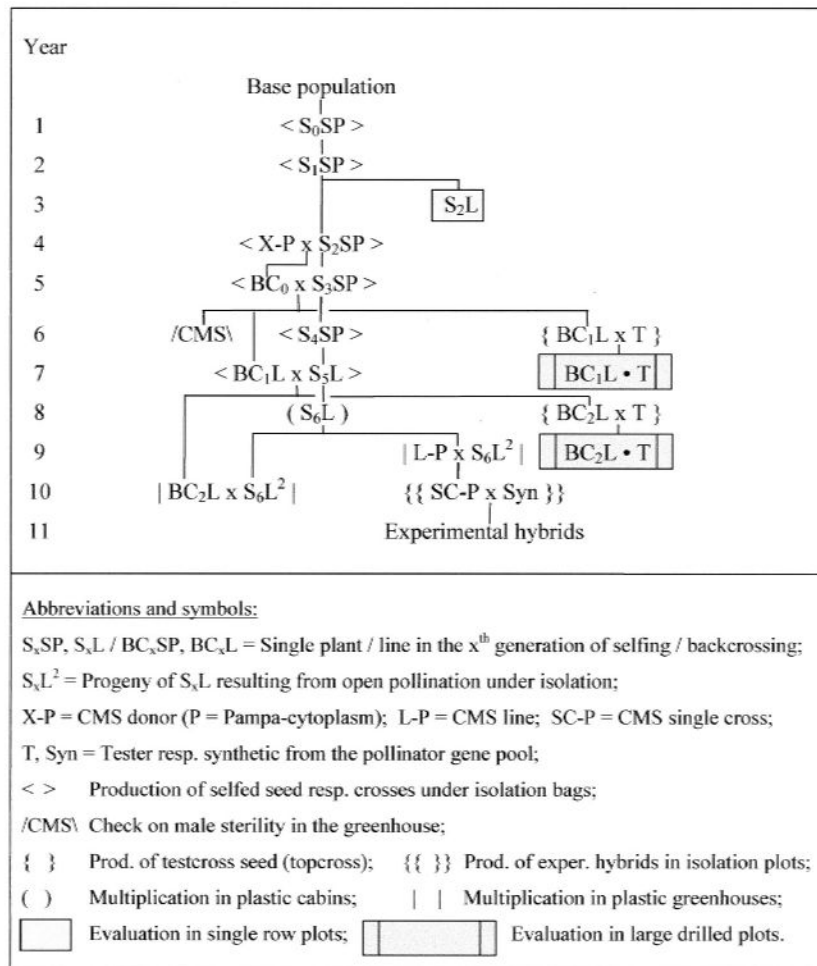
Fig. 1 Flow chart of the breeding scheme STD

performance is thus necessary before the development of CMS ana–logues 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 S_1L and S_2L. Testcross evalua–tion 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 back–crossing is postponed until a positive selection decision has been reached in Si and S2 to avoid labour and expenses for candidates that are not worth being continued.
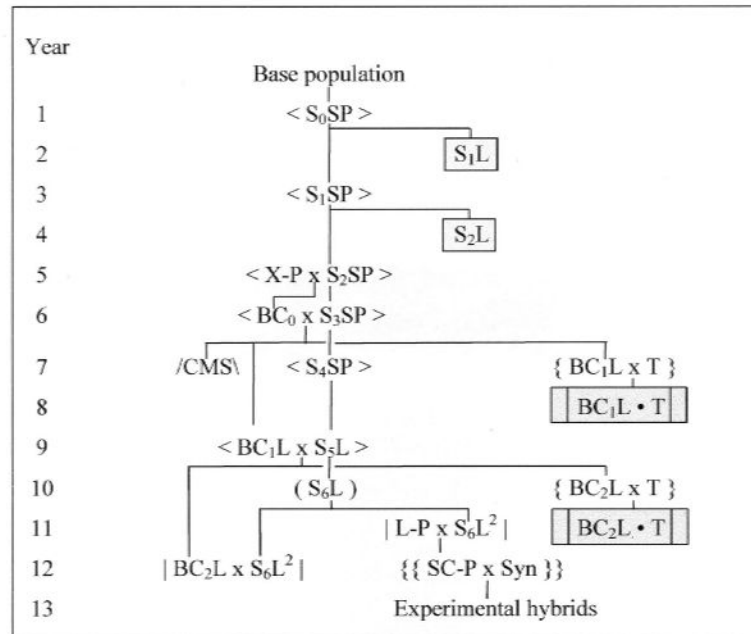
Fig. 2 Flow chart of the breeding scheme POP (for explanation of abreviations and symbols – see Fig. 1)

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 vari–ety trials (Tomerius, 2001). The costs of the individual breeding activi–ties 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 in–dex 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 combin– ing 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 as– sumed 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 parame– ters 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 (Ta– ble 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 follow– ing. 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 re– sults. In the following we investigate the influence of (i) the relative size of the dominance variance, (ii) the magnitude of genotype × envi– ronment–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	Dmominnance 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,
TP[1] – testcross performance 1st test,
TP[2] – testcross performance 2nd test,
G × E – genotype × environment interaction

The magnitude of genotype × environment –interaction (0 × E) vari–ances 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 candi–dates 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 eval–uated and the achievable selection gain increases.

Alterations in the available budget predominantly influence the op–timum 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 stan–dard variant. With a budget of 300000, more candidates are evalu–ated 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 af–fected 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

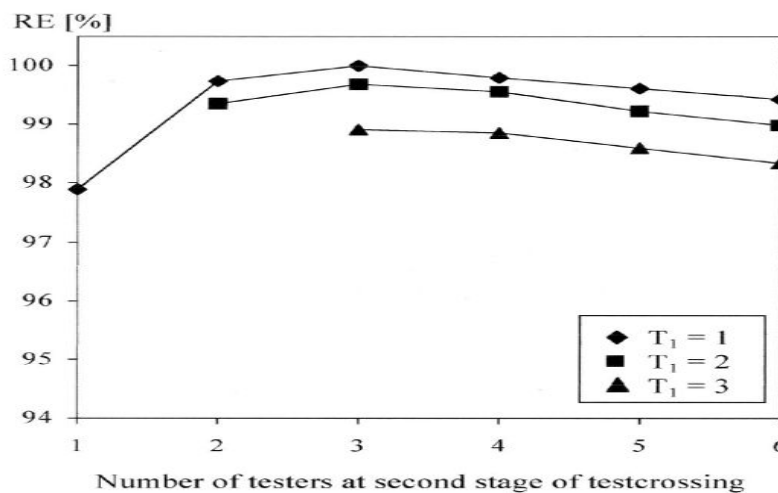(ii) three testers are used at the first testerossing stage.

Fig. 3 Relative efficiency 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 <u>standard dominance variances</u> (Restriction: $T_2 \geq T_2$

With increasing numbers of testers, the number of candidates and lo–cations 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.
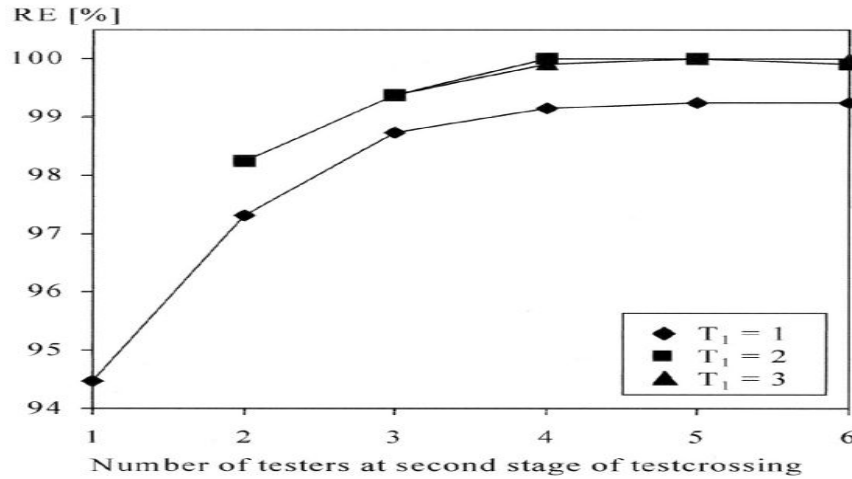
Fig. 4 Relative efficiency 9RE – percentage of respective optimum variant) of scheme STD
as a function of the number of testers at the second stage of testcrossing (T_1)
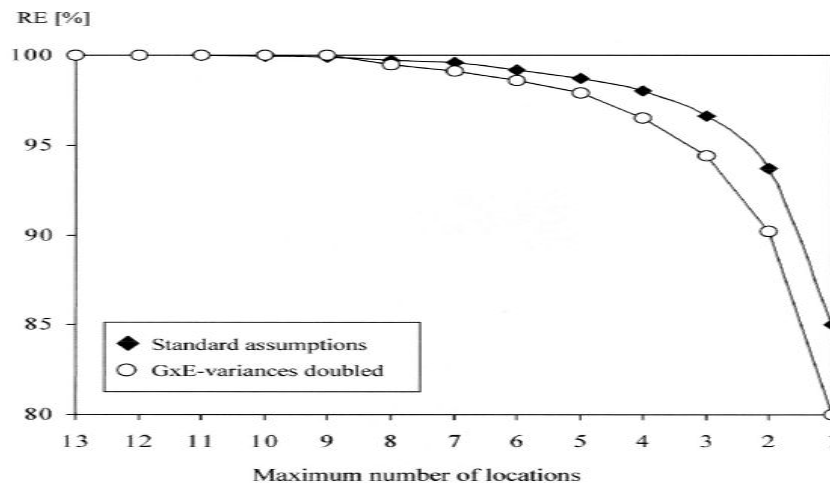and <u>doubled dominance variances</u> (Restriction: $T_2 \geq T_2$)

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 sec–ond testcrossing stage. The number of candidates and testers is in–creased, too (data not shown). A stronger decrease of selection gain is observed if large $G \times E$ variances are assumed (Fig. 5).

Table 2

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

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,
LP^1 – line performance, 1st test,
LP^2 – line performance, 2nd test,
TP^1 – testcross performance 1st test,
TP^2 – 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 se–lection for line *per se* performance (Table 2). A large number of S_1–lines is first evaluated at a single location. Roughly the 30% best S_2–lines are then evaluated more precisely at three locations. Testcross evalua–tion is identical to the standard scheme except for a slightly lower number of BC_1L–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 of–
ten larger than in a second–cycle program. As a consequence, the rela–
tive 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 ge–
netic variance and the selection gain resulting therefrom, but also on
the population mean (Schnell, 1983). With respect to line *per se* perfor–
mance, 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 investi–
gated showed comparable combining abilites as adapted population
materials when crossed to two elite CMS–testers. Under such circum–
stances the development of inbred lines from genetically broader pop–
ulation 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 de–
   velopment 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 × environment–interaction variance in present
   breeding materials is thus crucial for the breeder to choose an ap–
   propriate 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 ex–
   pected 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. As–suming a limited number of test locations, the expected selection gain is not severely reduced as long as five or six locations are em–ployed at the final selection stage.

ACKNOWLEDGEMENTS

Note: The underlying doctoral dissertation (Tomerius, 2001) can be downloaded as a pdf–file under www.um–hohenheim.delublopus/volltexte/200 1110

REFERENCES

Cochran W.G. 1951. Improvement by means of selection. 2nd Berkeley Symp. Math. Stat. Prob., p. 449–470.

Geiger H.H. 1982. Breeding methods in diploid rye *(Secale cereale* L.). In*:* Tag.Ber. 198 Akad. Landw.–Wiss. DDR, Berlin, p. 305–332.

Geiger H.H. 1985. Hybrid breeding in rye *(Secale cereale* L.). In: Proc. Part I. Eucarpia Meeting of the Cereal Section on Rye, Svalöv, Sweden, p. 23 7–265.

Geiger H.H., Miedaner. T. 1999. Hybrid rye and heterosis. In: Proc. CIMMYT Symposium on the Genetics and Exploitation of Heterosis in Crops, Aug 17–22, 1997, Mexico City, Mexico, p. 439–450.

Madej L.J. 1996. Worldwide trends in rye growing and breeding. Vortr. PflanzenzUchtg., 35*,* 1–6.

Roux S.R., Miedaner, T. Geiger H.H., Knopf E., Wilde P., Wortmann H. 2001. Combining ability vs. population performance of genetic resources in rye. In*:* Proc. Eucarpia Meet–ing of the Cereal Section on Rye, Radzików, Poland.

Schnell F.W., 1983. Probleme der Elternwahl — Em Uberblick. In Bericht über die Arbeitstagung 1983 der Arbeitsgemeinschaft der Saatzuchtleiter in Gumpenstein, Osterreich, p. 1–11.

Tomerius A–M., 2001. Optimizing the development of seed–parent lines in hybrid rye breeding. Doctoral dissertation, Univ. Hohenheim, Stuttgart.

Utz H.F., 1969. Mehrstufenselektion in der PflanzenzUchtung. Doctoral dissertation, Univ. Hohenheim, Stuttgart.

Wilde P., 1996. Multi–stage selection for combining ability among pollen parent lines in hy–brid rye breeding. Vortr. Pflanzenzuchtg., 35, 15–25.