

# Optimization of DH-line based recurrent selection procedures in maize under a restricted annual loss of genetic variance

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**Abstract** Doubled haploid (DH) lines are increasingly being used in commercial hybrid maize (*Zea mays* L.) breeding. They allow for various quantitative genetic and logistic advantages provided that they are implemented in efficient and optimally allocated breeding procedures. In the present study, a new software was applied to optimize two recurrent selection (RS) schemes for hybrid maize breeding based on DH lines under a restricted annual budget and an upper limit for the relative annual loss of genetic variance. This software maximizes the expected gain from selection in general combining ability by means of quantitative genetic model calculations. Optimization results are compared for one, two, and three stages of testcross selection under different assumptions regarding the evaluation of lines per se and the annual budget. Results show that the optimum allocation of technical and budget resources to the individual steps of an RS program and the efficiency of alternative RS procedures are decisively determined by the number of selection stages. Under standard assumptions, one-stage selection was superior to two- and three-stage selection. Thus, shortening the length of an RS scheme considerably increases its efficiency. By intercrossing

a reduced number of selected lines for starting a new RS cycle, the short-term response to selection may be increased, but the population size and, thus, the selection limits in the long run are diminished. Therefore, fair comparisons of alternative RS procedures require to define the intended time span for maximizing the genetic gain from RS and to restrict the relative annual loss of genetic variance accordingly.

**Keywords** Doubled haploid lines · Effective population size · Expected genetic gain · Long-term selection · Optimum allocation

## Introduction

The use of doubled haploid (DH) lines is increasingly replacing the traditional development of inbred lines in commercial hybrid maize (*Zea mays* L.) breeding. The use of DH lines features several quantitative genetic and operational advantages including: (1) Maximum genetic variance in line per se and testcross trials, (2) high reproducibility of early-selection results, (3) simplified logistics. High cost savings are possible due to reduced expenses for the selfing program, handling of seed batches, and for maintenance breeding (Röber et al. 2005). Yet, the success of employing DH lines depends on the choice of an efficient breeding procedure and the optimum allocation of technical and budget resources to the

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individual breeding steps in order to maximize the genetic gain from selection.

Quantitative genetic model calculations are a useful tool to optimize breeding procedures. Based on quantitative genetic principles and estimates of genetic parameters, model calculations allow the breeder to determine the optimum number of candidate lines, testers, testing locations, and replicates at each testcross selection stage by maximizing the expected gain from selection.

In hybrid maize breeding, the aim of recurrent selection (RS) is to improve the general combining ability (GCA) of the breeding population with respect to one or several so called ‘opposite’ pool(s), and testers are chosen accordingly. Since the aim of both RS and hybrid parent line development is to improve GCA, RS constitutes an integral part of hybrid breeding. The long-term progress achievable by the latter fully depends on the genetic advance in RS. In addition to this advance, the breeder can capitalize on specific combining ability (SCA) when selecting among experimental hybrids in the final phase of a breeding program.

Genetic response to selection for a quantitative trait is a function of the selection accuracy, the selection intensity, and the variation of the gain criterion in the population (Falconer and Mackay 1996). In plant breeding, selection is generally practiced as a cyclical long-term procedure of population improvement. The breeder therefore has to keep the decay of genetic variance caused by random drift and selection in narrow limits in order to preserve enough variation for subsequent RS cycles.

In order to limit the decline of genetic variance, the effective population size ( $N_e$ ) should not fall below a minimum level, since the decline per RS cycle is proportional to  $1/(2N_e)$  (Crow and Kimura 1970). However, limiting  $N_e$  restricts the selection intensity and, thus, the achievable short-term response to selection. Hence, the breeder has to find a compromise between maintaining genetic variance in the long run and maximizing short-term selection response (Robertson 1960; Wei et al. 1996). Bouchez and Gallais (2000) addressed this problem by comparing alternative RS procedures on the basis of the same effective size of the population of intercrossed plants. Other authors (Strahwald and Geiger 1988; Schipprack 1993; Borchard 1995), who optimized breeding procedures in barley, millet, and sugar beet,

respectively, proposed to equally restrict the relative *annual* loss of genetic variance when comparing the merits of alternative breeding strategies. This approach allows fair comparisons among procedures with differing cycle lengths.

Comparisons between alternative breeding procedures, in addition, require restrictions regarding the available annual budget. To meet this restriction, the cost of the whole breeding procedure has to be accounted for. A first approach to consider the cost was made by Utz (1969), who used the number of testcross plots in the yield trials as cost units. Longin et al. (2006) additionally introduced ‘plot equivalents’ for the cost of the DH line production. However, this does not allow for a detailed consideration of the expenses of individual breeding steps according to the specifics of alternative breeding procedures. Borchard (1995) and Tomerius (2001) first employed detailed cost accounting when optimizing breeding procedures for sugar beet and rye, respectively.

The objective of this study is to compare the optimum allocation and the response to one-, two-, and three-stage testcross selection of two hybrid maize RS schemes based on DH lines. The criterion for optimizing the RS procedures is a maximum expected annual gain in the GCA of the breeding population with respect to an opposite gene pool under the restriction of a given annual budget and an upper limit for the relative annual loss of genetic variance. Different scenarios are compared regarding the expenses for evaluating lines per se, the available annual budget and the decay of genetic variance. All optimizations were performed with MBP (version 1.0), a new software package for optimizing DH-line based breeding procedures by means of quantitative genetic model calculations (Gordillo and Geiger 2007a).

## Materials and methods

### Recurrent selection schemes

In the following, a ‘breeding population’ represents a gene pool (heterotic group) of a hybrid maize breeding program. It is assumed that crosses are made every year to start a new selection program such that the whole population is subdivided into

multiple, timely staggered, subpopulations. Thus, every year a new RS cycle is started in a different subpopulation and the number of staggered subpopulations is equal to the cycle length in years. Moreover, it is assumed that an equal number of lines from each of the staggered subpopulations is intercrossed in order to start a new RS cycle. Thus, the effective number of intercrossed lines corresponds to the number of selected lines per RS cycle times the total number of staggered subpopulations. This corresponds to a maximum degree of subpopulation interlinking.

Two alternative RS schemes based on DH lines are compared. Scheme 1 (Fig. 1a) comprises the following steps:

1. Creating new variation by intercrossing selected lines (recombination units) from the gene pool under consideration to produce single crosses. To start a new RS cycle, each of the  $n$  selected parent lines is intercrossed at random with 1 up to  $n - 1$  of the remaining lines.
2. In vivo haploid induction in generation  $S_0$ .
3. Chromosome doubling of haploid seedlings and selfing of the resulting DH plants in generation  $D_0$  in order to produce the first DH line generation ( $D_1$ ).
4. Evaluation of  $D_1$  lines in single-row observation plots and, in parallel, seed multiplication by selfing to produce  $D_2$  lines.
5. Production of testcross progenies with one or more testers from an opposite gene pool. Testers are assumed to be single crosses between unrelated homozygous lines at all selection stages.
6. Evaluation of the testcross performance of  $D_2$  lines in multi-environment yield trials.

Scheme 1 requires 3, 4, or 5 years for one, two, or three stages of testcross selection, respectively. With one-stage testcross evaluation, selection is based on field tests in a single year. With two-stage selection, field tests are continued in a second year with a subset of the best lines selected at the first stage. Likewise, the lines to be tested at the third stage are selected from the second.

In Scheme 2 (Fig. 1b), intercrossing of selected parents and in vivo haploid induction of  $S_0$  plants are performed in the same season. Further, testing of lines per se is carried out in parallel to the

first testcross evaluation. Testcrosses for the first selection stage are produced on  $D_1$  instead of  $D_2$  lines. The cycle is 1 year (two seasons) shorter than in Scheme 1.

### Quantitative genetic and economic parameters

Standard values of all relevant variance components were estimated from testcross data of several samples of Central European inbred and DH lines made available by collaborating breeding companies (Gordillo and Geiger 2004). The following estimates were obtained:  $\sigma_{A_{GY}}^2 = 29.0$ ,  $\sigma_{D_{GY}}^2 = 9.0$ ,  $\sigma_{A_{DMC}}^2 = 3.8$ , and  $\sigma_{D_{DMC}}^2 = 0.39$ , where  $A$  and  $D$  refer to additive and dominance effects and  $GY$  and  $DMC$  to grain yield ( $dt \cdot ha^{-1}$ , where  $dt = 10^{-1} t$ ) and dry matter content (%), respectively. Predictions of the response to selection were based on the relative size of the variance components  $\sigma_t^2$ ,  $\sigma_{ty}^2$ ,  $\sigma_{tl}^2$ ,  $\sigma_{tyl}^2$ , and  $\sigma_e^2$  designating the variances of the genotypic, genotype  $\times$  year interaction, genotype  $\times$  location interaction, genotype  $\times$  year  $\times$  location interaction, and error effects. The underlying ratio of variance components is  $\sigma_t^2:\sigma_{ty}^2:\sigma_{tl}^2:\sigma_{tyl}^2:\sigma_e^2 = 1:0.6:0.6:0.8:1.1$  for grain yield and  $1:0.15:0.15:0.34:0.47$  for dry matter content.

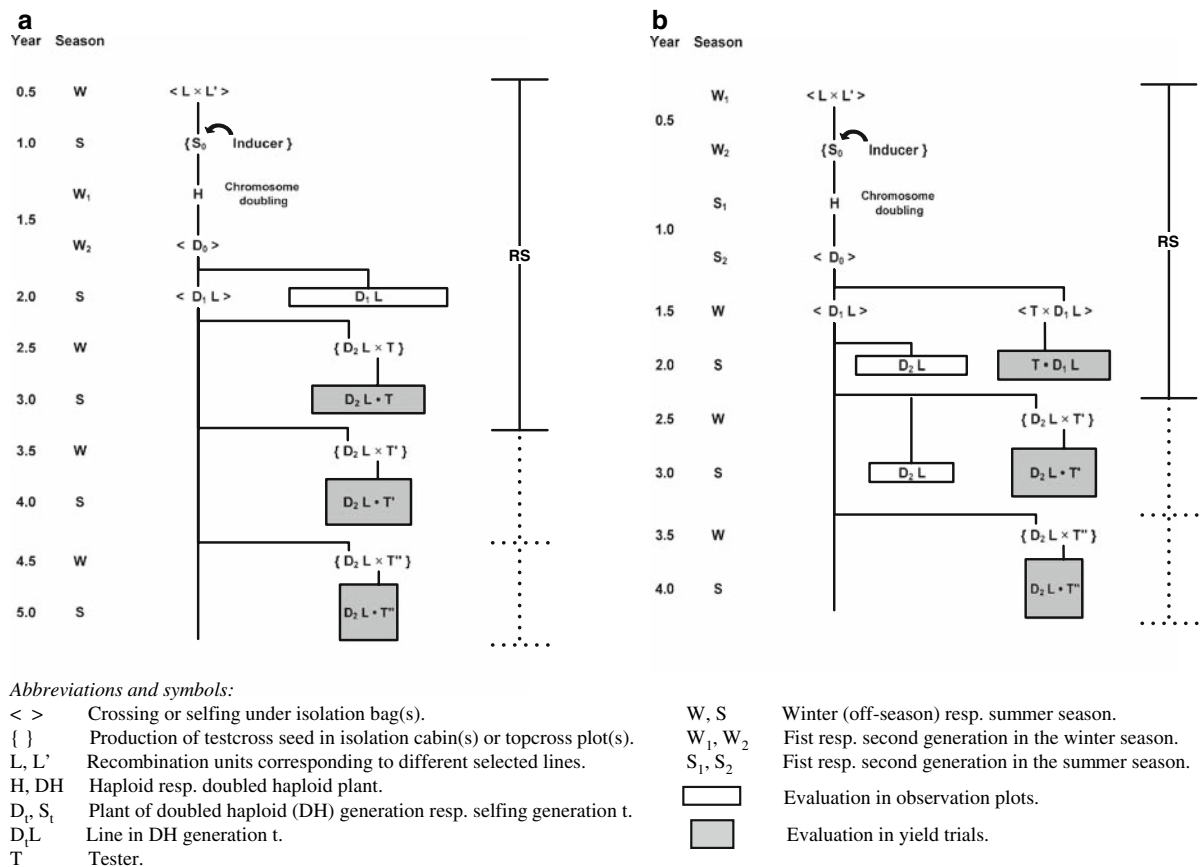
Labor costs of each breeding step (e.g. cost of selfing one entry, developing one  $D_1$  line, or evaluating a testcross progeny in one field plot) as well as haploid induction parameters were also estimated from data provided by collaborating breeders. The underlying economic parameter estimates are average values corresponding to breeding programs in Europe and North America.

### Genetic model

In the present study, a test unit corresponds to the testcross progeny of a DH line with a given set of testers. The phenotypic variance of the test units refers to entry means and is defined as

$$\sigma_x^2 = \sigma_t^2 + \sigma_{ty}^2 + \frac{\sigma_{tl}^2}{L} + \frac{\sigma_{tyl}^2}{L} + \frac{\sigma_e^2}{LRT}, \quad (1)$$

where  $L$  denotes the number of test locations,  $R$  the number of replicates, and  $T$  the number of testers. At all selection stages, 1-year testing is assumed. The



**Fig. 1** Flow charts of two alternative recurrent selection schemes based on doubled haploid maize lines: **(a)** Scheme 1, **(b)** Scheme 2

parameter  $\sigma_t^2$  is defined according to Griffing (1956) as

$$\sigma_t^2 = \sigma_{GCA}^2 + \sigma_{SCA}^2/T, \quad (2)$$

where  $\sigma_{GCA}^2$  and  $\sigma_{SCA}^2$  are the general and specific combining ability variances, respectively. The expectation of  $\sigma_{GCA}^2$  and  $\sigma_{SCA}^2$  is defined in terms of additive ( $\sigma_A^2$ ) and dominance variance ( $\sigma_D^2$ ) in analogy to Kempthorne's (1957, p. 455) formula for estimating the covariance between full sibs of inbred parents, assuming that epistatic and maternal effects are absent. For testcross progenies of DH candidate lines,

$$\sigma_{GCA}^2 = \frac{1}{2} \sigma_A^2 \text{ and } \sigma_{SCA}^2 = u_{VW} \sigma_D^2, \quad (3)$$

where  $u_{VW}$  is the probability that the two alleles at a random locus in a random individual V are identical by descent to those in another individual W of the

same testcross progeny. If the tester is a homozygous line,  $u_{VW} = 1$ , and if it is a single cross,  $u_{VW} = 0.5$ .

It is assumed that  $N_{DH:C}$  DH lines from each of  $N_C$  crosses enter the testcross evaluation stage. Accordingly, the genotypic variance between DH-line testcrosses ( $\sigma_{t_{DH}}^2$ ) is subdivided into components due to crosses ( $\sigma_{t_c}^2$ ) and DH lines within crosses ( $\sigma_{t_{DH:C}}^2$ ). The total genotypic variance between test units is calculated according to Borchard (1995) as

$$\sigma_{t_{DH}}^2 = \frac{N_{DH:C}(N_C - 1)}{N_{DH:C}N_C - 1} \sigma_{t_c}^2 + \sigma_{t_{DH:C}}^2.$$

#### Gain criterion

The gain criterion is the GCA of the selected lines according to a base index (Brim et al. 1959; Williams

1962) composed of the testcross performance for grain yield and grain dry matter content:

$$I = b_{GY}x_{GY} + b_{DMC}x_{DMC},$$

where  $b_{GY}$  and  $b_{DMC}$  refer to the index weights for grain yield and dry matter content, respectively, and  $x_{GY}$  and  $x_{DMC}$  denote the corresponding means of the test units. The trait weights ( $b_{GY} = 1.0$  and  $b_{DMC} = 2.5$ ) assumed herein correspond to those applied in statutory maize trials in Germany.

As commonly practiced in hybrid maize breeding, we assume that the traits considered in line selection (e.g. ideotype traits or resistances) differ from those targeted in testcross selection. Moreover, we assume that there is no genotypic correlation between the former and the latter and, therefore, no correlated response in testcross performance is accounted for. However, the cost for testing lines per se is calculated and subtracted from the total budget. Thus, the budget remaining for the evaluation of the testcross performance is diminished. In the present paper, the fraction of lines selected for performance per se ( $\alpha_{LP}$ ) is assumed to be 0.25, 0.50, or 0.75.

#### Prediction of selection gain

The gain in GCA from one stage of index selection for grain yield is computed by

$$G(GCA_{GY}|I) = i\rho_{I,GCA_{GY}}\sigma_{GCA_{GY}} = i\frac{cov_{I,GCA_{GY}}}{\sigma_I}$$

$$G(GCA_{GY}|I) =$$

$$i\frac{b_{GY}\sigma_{GCA_{GY}}^2 + b_{DMC}cov_{GCA_{GY},DMC}}{\sqrt{b_{GY}^2\sigma_{x_{GY}}^2 + b_{DMC}^2\sigma_{x_{DMC}}^2 + 2b_{GY}b_{DMC}cov_{x_{GY},DMC}}}$$
(4)

where  $i$  is the selection intensity,  $\rho_{I,GCA_{GY}}$  and  $cov_{I,GCA_{GY}}$  are the correlation coefficient and covariance, respectively, between the index value and GCA for grain yield,  $\sigma_{GCA_{GY}}$  is the standard deviation of GCA for grain yield,  $\sigma_I$  is the standard deviation of the index,  $cov_{GCA_{GY},DMC}$  is the covariance between the GCA effects for grain yield and grain dry matter content, and  $cov_{x_{GY},DMC}$  is the phenotypic covariance between grain yield and dry matter content. The expected gain in GCA for grain dry matter content is estimated analogously. The gains in grain yield and

grain dry matter content sum up to the total genetic gain:

$$G(GCA_{Total}|I) = b_{GY}G(GCA_{GY}|I) + b_{DMC}G(GCA_{DMC}|I).$$

To predict the gain from multi-stage selection, exact formulae derived by Cochran (1951) for two stages and extended by Utz (1969) to three stages are applied. The general formula for the selection gain from  $m$  selection stages is

$$G_m = \frac{1}{\alpha} \sum_{s=1}^m \rho_{I,GCA_s} z_s I_{ms} \sigma_{GCA_s},$$

where  $\alpha$  is the final selected fraction,  $\rho_{I,GCA_s}$  is the correlation between the index value and GCA at selection stage  $s$ ,  $z_s$  is the ordinate of the univariate normal distribution at the truncation point  $k_s$  of selection stage  $s$ , and  $I_{ms}$  is the incomplete area of the standardized  $(m-1)$ -variate normal integral. Uni-, bi-, and trivariate normal integrals or alternatively their lower truncation limits are determined by numerical methods (Utz 1969; Tomerius 2001). It is assumed that lines are selected according to the evaluation results at the selection stage under consideration, i.e. no information from previous selection stages is accounted for.

For calculating the selection intensity, an infinite population size is assumed although, in reality, the population size is finite. However, comparisons have shown that the two assumptions (finite versus infinite population size) result in negligible differences regarding the optimum allocation and the expected selection gain (Cochran 1951; Utz 1969).

#### Prediction of the effective population size

The prediction of  $N_e$  is based on formulae of Santiago and Caballero (1995), which account for the cumulative effect of selection on the extent of genetic drift. Assuming that timely staggered subpopulations are improved and the distribution of the number of DH lines per parental cross combination is random,  $N_e$  for a given trait  $T$  can be calculated from the following equation:

$$N_{eT} = \frac{N \cdot S}{(1+F)(1+Q_T^2 C_T^2)},$$

where  $T$  refers to grain yield and grain dry matter content,  $N$  is the number of parent lines,  $F$  is their

inbreeding coefficient,  $S$  accounts for the number of interlinked subpopulations (equivalent to the cycle length in years, if every year a new breeding cycle is started and each of the staggered subpopulations contributes an equal number of recombination units),  $C_T^2$  refers to the variation in the selective advantage of the individual crosses for trait  $T$ , and  $Q_T^2$  is a parameter accounting for the corresponding cumulative effect of selection. In the present study, DH lines are used as recombination units so that  $F = 1$  and

$$N_{eT} = \frac{N \cdot S}{2(1 + Q_T^2 C_T^2)}. \quad (5)$$

$C^2$  is approximated by  $C^2 \approx i^2 \rho_{FS}^*$  (Milkman 1978; Santiago and Caballero 1995), where  $\rho_{FS}^*$  is the asymptotic value of the intraclass correlation of full sibs (lines within a cross). The procedure of estimating  $\rho_{FS}^*$  is described in the appendix. Testcross performance is based on effects of the gametes produced by the candidate lines. Hence, testcross performance is inherited like a trait without dominance so that  $Q$  can be approximated by  $2/(2 - G_r)$ , where  $G_r$  is the proportion of genetic variance remaining after selection. Under an infinitesimal model of gene effects,  $G_r = 1 - \lambda \rho_{I,GCA}^*$  (Bulmer 1980; Santiago and Caballero 1995), where  $\lambda = i(i - k)$  and  $\rho_{I,GCA}^*$  is the asymptotic correlation between the index value and GCA.

The relative annual loss of genetic variance for a given trait  $T$  is calculated as

$$\Delta\sigma_{gT}^2 = 1/(2N_{eT}Y), \quad (6)$$

where  $Y$  denotes the RS cycle length in years. The weighted values for grain yield and dry matter content sum up to

$$\Delta\sigma_g^2 = w_{GY}\Delta\sigma_{gGY}^2 + w_{DMC}\Delta\sigma_{gDMC}^2,$$

where  $w_{GY}$  and  $w_{DMC}$  denote the relative importance of grain yield and dry matter content, respectively (Barwick and Henzell 2005). For grain yield,

$$w_{GY} = b_{GY}\sigma_{GCA_{GY}} / (b_{GY}\sigma_{GCA_{GY}} + b_{DMC}\sigma_{GCA_{DMC}}).$$

The relative importance of dry matter content is calculated analogously. In the present study, all breeding procedures are compared under the same restriction regarding the upper limit for  $\Delta\sigma_g^2$ .

## Optimization procedure

All breeding procedures were optimized by using the software package MBP (version 1.0). The optimization procedure follows an  $n$ -dimensional grid search approach suggested by Tomerius (2001). The optimum number of crosses, testers, test units, locations, and replicates at each testcross selection stage is first calculated for a selectable number of recombination units. If the upper limit for the relative annual loss of genetic variance ( $\Delta\sigma_{g\max}^2$ ) is exceeded, the optimization procedure is re-started with a higher number of recombination units. The contrary occurs if  $\Delta\sigma_g^2$  falls below the specified upper limit. This procedure is repeated until the lowest number of recombination units complying with the  $\Delta\sigma_{g\max}^2$  restriction is found. The budget considered for optimizing the testcross selection phase is reduced according to the cost of developing and evaluating DH lines.

## Results

### Optimum allocation

For both RS schemes and an annual budget of €500,000, the number of recombination units ( $N_{RU}$ ) required to comply with the upper limit for the relative annual loss of genetic variance ( $\Delta\sigma_{g\max}^2$ ) sharply decreases as the number of testcross selection stages is increased (Table 1). In Scheme 1, the number decreases roughly to one third and in Scheme 2 to one fourth when employing three-stage instead of one-stage selection. The selected fraction in the line per se test ( $\alpha_{LP}$ ) hardly influences the number of required recombination units. The number of recombination units can be lowered considerably if  $\Delta\sigma_{g\max}^2$  is relaxed from 0.01 to 0.02 or 0.05 (Table 2). This allows for a larger selection intensity and, thus, for a higher genetic gain. Furthermore, an increase in  $\Delta\sigma_{g\max}^2$  hardly influences the optimum allocation at the first testcross selection stage, but leads to a noticeable reduction of the number of tested lines and an increase in the number of testers and test locations at advanced testcross stages (Tables 1 and 2).

As the number of selection stages rises, the optimum number of DH lines at the first testcross selection stage increases, while the number of test



**Table 1** Optimum allocation for recurrent selection Schemes 1 and 2 with one, two, and three stages of testcross selection and respective genetic gain for different selected fractions in lineper se evaluation ( $\alpha_{LP}$ ), assuming an annual budget of €500,000 and an upper limit for the relative annual loss of genetic variance ( $\Delta\sigma_{g_{\max}}^2 \leq 0.01$ )

| Scheme | $\alpha_{LP}$ | No. of stages | $N_{RU}^b$ | Optimum allocation <sup>c</sup> |         |         |         |         |         |         |         |         | Genetic gain <sup>d</sup> |          |
|--------|---------------|---------------|------------|---------------------------------|---------|---------|---------|---------|---------|---------|---------|---------|---------------------------|----------|
|        |               |               |            | $N_1^*$                         | $N_2^*$ | $N_3^*$ | $T_1^*$ | $T_2^*$ | $T_3^*$ | $L_1^*$ | $L_2^*$ | $L_3^*$ | per cycle                 | per year |
| 1      | 0.25          | 1             | 29         | 2129                            | –       | –       | 1       | –       | –       | 10      | –       | –       | 9.41                      | 3.14     |
| 1      | 0.25          | 2             | 15         | 2433                            | 102     | –       | 1       | 3       | –       | 5       | 21      | –       | 11.84                     | 2.96     |
| 1      | 0.25          | 3             | 9          | 2549                            | 138     | 23      | 1       | 2       | 5       | 4       | 15      | 24      | 13.35                     | 2.67     |
| 1      | 0.50          | 1             | 30         | 3045                            | –       | –       | 1       | –       | –       | 9       | –       | –       | 9.75                      | 3.25     |
| 1      | 0.50          | 2             | 16         | 3901                            | 129     | –       | 1       | 3       | –       | 4       | 20      | –       | 12.32                     | 3.08     |
| 1      | 0.50          | 3             | 9          | 4317                            | 342     | 31      | 1       | 2       | 5       | 2       | 11      | 25      | 13.95                     | 2.79     |
| 1      | 0.75          | 1             | 31         | 3723                            | –       | –       | 1       | –       | –       | 8       | –       | –       | 9.90                      | 3.30     |
| 1      | 0.75          | 2             | 17         | 5242                            | 163     | –       | 1       | 3       | –       | 3       | 18      | –       | 12.52                     | 3.13     |
| 1      | 0.75          | 3             | 9          | 5799                            | 296     | 30      | 1       | 2       | 5       | 2       | 11      | 23      | 14.20                     | 2.84     |
| 2      | 0.25          | 1             | 53         | 1144                            | –       | –       | 1       | –       | –       | 6       | –       | –       | 7.42                      | 3.71     |
| 2      | 0.25          | 2             | 25         | 1635                            | 183     | –       | 1       | 3       | –       | 2       | 16      | –       | 10.26                     | 3.42     |
| 2      | 0.25          | 3             | 13         | 1831                            | 366     | 44      | 1       | 2       | 4       | 1       | 9       | 24      | 11.92                     | 2.98     |
| 2      | 0.50          | 1             | 58         | 2289                            | –       | –       | 1       | –       | –       | 6       | –       | –       | 8.26                      | 4.13     |
| 2      | 0.50          | 2             | 26         | 2868                            | 174     | –       | 1       | 3       | –       | 3       | 16      | –       | 11.07                     | 3.69     |
| 2      | 0.50          | 3             | 14         | 3087                            | 311     | 38      | 1       | 2       | 4       | 2       | 12      | 25      | 12.80                     | 3.20     |
| 2      | 0.75          | 1             | 61         | 3158                            | –       | –       | 1       | –       | –       | 7       | –       | –       | 8.74                      | 4.37     |
| 2      | 0.75          | 2             | 27         | 4373                            | 213     | –       | 1       | 2       | –       | 3       | 18      | –       | 11.52                     | 3.84     |
| 2      | 0.75          | 3             | 14         | 4841                            | 288     | 40      | 1       | 2       | 4       | 2       | 10      | 23      | 13.28                     | 3.32     |

<sup>a</sup> Lines are visually selected in unreplicated observation plots across two locations<sup>b</sup> Number of recombination units required to comply with the upper limit for the annual loss of genetic variance<sup>c</sup>  $N_j^*$ ,  $T_j^*$ ,  $L_j^*$  denote the optimum number of lines, testers (single crosses), and test locations, respectively, used at testcross selection stage  $j$ . In Scheme 2,  $N_1^*$  only includes testcrosses pertaining to the selected fraction ( $\alpha_{LP}$ ) in the parallel line per se test. The optimum number of replicates is one at each testcross selection stage. The maximum number of test locations is restricted to 25<sup>d</sup> Expected genetic gain from index selection involving grain yield and dry matter content

locations decreases for all cases considered. One tester is optimal at the first testcross stage for all procedures, except for the one-stage selection procedure of Scheme 1 with  $\Delta\sigma_{g_{\max}}^2 = 0.05$ , where two testers are optimal.

The selected fraction in the line per se test ( $\alpha_{LP}$ ) has a major influence on the optimum number of test units at the first testcross stage, especially for Scheme 2 (Table 1). Strong per se selection increases the cost per DH line entering the testcross phase. As a consequence, fewer test units can be evaluated. This effect is larger in Scheme 2 with line per se evaluating in parallel to the first testcross selection stage. Thus, a portion ( $1 - \alpha_{LP}$ ) of lines with superior combining ability but insufficient per se performance has to be culled in Scheme 2. This means that the effective number of test units lies below the number of entries included in the first stage of testing for

combining ability. On the other hand, the fraction  $\alpha_{LP}$  exerts a comparatively small effect on the optimum number of testers and test locations at all testcross selection stages.

At the second and third testcross selection stage, a strongly reduced number of test units is evaluated with an increased number of testers and test locations. In contrast to the first selection stage, the optimum number of test units at the second and third stages is higher in Scheme 2 than in Scheme 1.

### Genetic gain from selection

In all cases considered, the genetic gain per cycle increases as the number of selection stages rises. Compared to the one-stage selection procedure of Scheme 1 with  $\Delta\sigma_{g_{\max}}^2 \leq 0.01$ , the gain per cycle is on

**Table 2** Optimum allocation for recurrent selection Schemes 1 and 2 with one and two stages of testcross selection and respective genetic gain for different upper limits for the relativeannual loss of genetic variance ( $\Delta\sigma_{g_{\max}}^2 \leq 0.01$ ) assuming a selected fraction in the line per se test ( $\alpha_{LP}$ ) of 0.5 and an annual budget of €500,000

| Scheme | $\Delta\sigma_{g_{\max}}^2$ | No. of stages | Optimum allocation <sup>b</sup> |         |         |         |         |         |         |           | Genetic gain <sup>c</sup> |  |
|--------|-----------------------------|---------------|---------------------------------|---------|---------|---------|---------|---------|---------|-----------|---------------------------|--|
|        |                             |               | $N_{RU}^a$                      | $N_1^*$ | $N_2^*$ | $T_1^*$ | $T_2^*$ | $L_1^*$ | $L_2^*$ | per cycle | per year                  |  |
| 1      | 0.02                        | 1             | 16                              | 2879    | –       | 1       | –       | 10      | –       | 10.47     | 3.49                      |  |
| 1      | 0.02                        | 2             | 9                               | 3892    | 90      | 1       | 4       | 4       | 22      | 13.20     | 3.30                      |  |
| 1      | 0.05                        | 1             | 7                               | 1935    | –       | 2       | –       | 9       | –       | 11.43     | 3.81                      |  |
| 1      | 0.05                        | 2             | 4                               | 3935    | 60      | 1       | 5       | 4       | 25      | 14.28     | 3.57                      |  |
| 2      | 0.02                        | 1             | 32                              | 2106    | –       | 1       | –       | 7       | –       | 9.06      | 4.53                      |  |
| 2      | 0.02                        | 2             | 14                              | 2910    | 132     | 1       | 3       | 3       | 20      | 12.00     | 4.00                      |  |
| 2      | 0.05                        | 1             | 15                              | 1951    | –       | 1       | –       | 8       | –       | 10.00     | 5.00                      |  |
| 2      | 0.05                        | 2             | 6                               | 2895    | 83      | 1       | 4       | 3       | 25      | 13.17     | 4.39                      |  |

<sup>a</sup> Number of recombination units required to comply with the upper limit for the annual loss of genetic variance<sup>b</sup>  $N_j^*$ ,  $T_j^*$ ,  $L_j^*$  denote the optimum number of lines, testers (single crosses), and test locations, respectively, used at testcross selection stage  $i$ . In Scheme 2,  $N_1^*$  only includes testcrosses pertaining to the selected fraction ( $\alpha_{LP}$ ) in the parallel line per se test. The optimum number of replicates is one at each testcross selection stage. The maximum number of test locations is restricted to 25<sup>c</sup> Expected genetic gain from index selection involving grain yield and dry matter content

average 26% and 43% larger for the two- and three-stage procedures, respectively (Table 1). The increase is even larger in Scheme 2. Here, the gain per cycle is 34% and 56% larger for the two- and three-stage procedures, respectively, than for the one-stage procedure.

However, when considering the gain per year, which is the criterion to be maximized in the present study, one-stage selection is the most efficient procedure, irrespective of the breeding scheme (Table 1). While the differences in the annual gain between one-, two-, and three-stage selection are relatively small in Scheme 1, the superiority of one-stage over two- and three-stage selection amounts to 12% and 29%, respectively, in Scheme 2. The relative merits of one-, two-, and three-stage selection procedures are only slightly influenced by the annual budget and their rankings remain unaltered (Fig. 2). The maximum annual response to selection is larger for Scheme 2 than for Scheme 1, irrespective of the number of selection stages, the selected fraction in the per se test and the annual budget (Fig. 2). The response curves show a decreasing slope as the budget increases, illustrating a diminishing return on investment. Consequently, raising the budget may turn out to be less rewarding than keeping the annual budget but switching over to a superior RS procedure. For instance, switching over from one-, two-, or three-stage selection in RS Scheme 1 to one-stage selection in RS Scheme 2 leads to a much

higher increase in the annual genetic gain than doubling or quadruplicating the budget in Scheme 1. A similar result is obtained when changing over from three-stage to one-stage selection in Scheme 2.

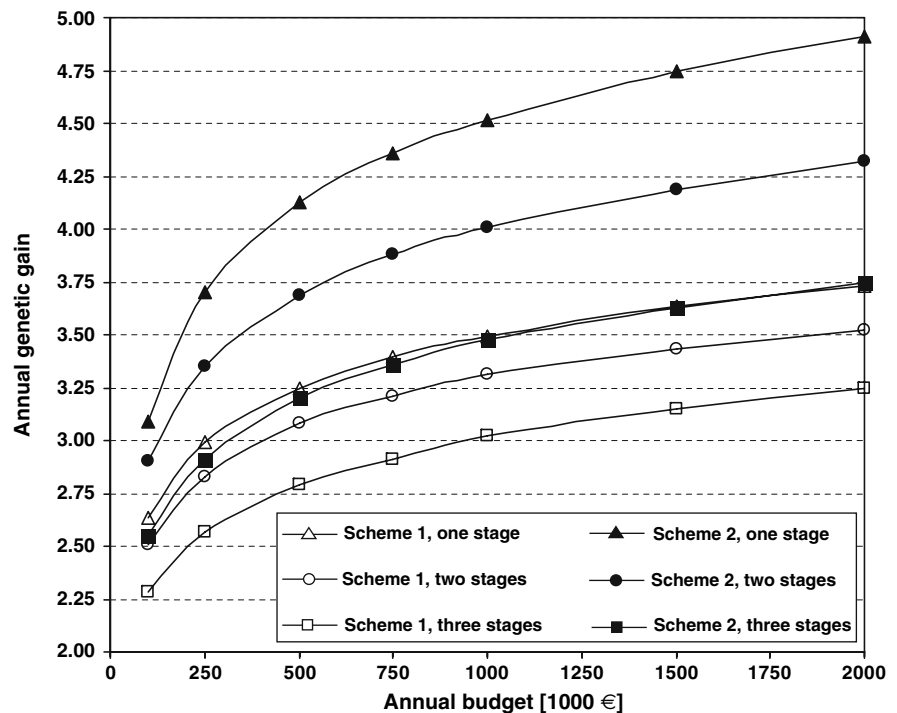
## Discussion

### Evaluation of lines per se

In commercial maize breeding, lines are commonly evaluated per se for traits with a high heritability. Usually, no line selection for grain yield is carried out since, in general, a low genotypic correlation exists between line and testcross performance for this highly heterotic trait (Hallauer and Miranda 1981). This correlation is even smaller when lines are evaluated in the off-season. In accordance with this, the evaluation of lines per se is not considered in predicting the gain in testcross performance, but it is regarded as a matter of expense. Thus, the expenses per DH line effectively entering the testcross evaluation phase rise as the fraction of lines selected in the per se test ( $\alpha_{LP}$ ) is diminished. The efficiency of RS for GCA is affected by varying the intensity of line per se selection to a larger extent if lines are evaluated in parallel to the testcrosses as in Scheme 2. Yet, this does not alter the ranking of the selection procedures compared.



**Fig. 2** Annual genetic gain from one, two, and three stages of testcross selection for recurrent selection Schemes 1 and 2 as a function of the annual budget. The genetic gain refers to index selection for grain yield and dry matter content



#### Factors influencing the response to selection

For all cases considered herein, the maximum gain per cycle increases with the number of selection stages (Tables 1 and 2). This is mainly due to the higher selection intensity achievable with multi-stage selection. Although the response to multi-stage selection can be increased if information from foregoing selection stages is used, in commercial breeding this is usually not the case. This situation is assumed in the present model calculations. Moreover, previous theoretical studies showed that considering test results of foregoing years hardly increases the expected genetic gain and does not change the ranking of alternative selection procedures (Wricke and Weber 1986). In addition to this, the advantage of using information from previous selection stages becomes negligible at high selection intensities (Utz 1969).

The main disadvantage of multi-stage selection is the unavoidable increase in cycle length resulting in a decrease of the genetic gain per unit of time. Therefore, the one-stage procedures of Schemes 1 and 2 are more efficient than the two- and three-stage procedures although they had higher expected genetic gains on a per-cycle basis.

The one-stage procedure of Scheme 2 turned out to be superior to all versions of Scheme 1 even if the budget of Scheme 1 was doubled or quadruplicated. Thus the choice of an adequate breeding procedure may be more crucial than enhancing the annual budget. Interestingly, Scheme 2 shows the highest efficiency although the test of lines per se is carried out in parallel rather than prior to the first testcross evaluation stage. This is in agreement with results from Tomerius (2001), who studied alternative breeding schemes for the development of seed-parent lines in hybrid rye. The author found that shortening the length of the breeding cycle resulted in a higher annual genetic gain, although this involved an increased labour input per test unit.

Bouchez and Gallais (2000) compared the potential of RS using testcrosses of doubled haploids compared with testcrosses of  $S_0$ ,  $S_1$ , or  $S_2$  plants for an annual crop like maize. Their results showed that the cycle length has a greater effect on the efficiency of an RS scheme than the heritability and the selection intensity. As in the present study, the highest annual gains were obtained from short-cycle selection schemes.

In contrast, model calculations of Strahwald (1988) on RS in barley revealed a superiority of rather long multi-stage selection procedures. There are two main reasons for this deviating result: First, the cycle length

of the compared procedures varied between 4 and 8 years. Therefore the *relative* increase in cycle length when adding a further selection stage was much smaller than in the present cases, where the shortest cycle lasts only 2 years. Secondly, Strahwald (1988) assumed a relatively low annual budget resulting in small numbers of test units, allowing only a weak selection intensity. This deficit had to be compensated by a highly accurate evaluation procedure, which could only be achieved in multi-stage yield trials.

In model calculations aiming at optimum breeding plans for the development of sugar beet inbred lines, Borchard and Geiger (1997) also found a superiority of multi-stage over one-stage selection procedures. According to the author this was mainly due to the expected increase of the genotypic variance in higher inbred generations and to the higher accuracy of selection at the advanced selection stages. In the present study dealing with DH lines, the maximum possible genotypic variance is available already at the first selection stage. This may be an additional reason for the superiority of the short-cycle selection procedures obtained herein for both RS schemes.

In the present study, the expected genetic gain is calculated as a function of pertinent quantitative genetic parameters. The latter were estimated from a broad range of experiments with Central European breeding populations (Gordillo and Geiger 2004). In order to study the validity of our optimization results, the impact of varying the relative size of the genotype  $\times$  environment interaction and error variances from extremely low to extremely high values was studied for Scheme 2 in another investigation (Gordillo and Geiger 2007b). Results showed that the relative size of the variance components may considerably influence the optimum allocation of resources and the height of the expected genetic gain. However, it does not alter the ranking of the compared RS procedures. This is in agreement with previous results of Borchard (1995) and Tomerius (2001).

The number and type of testers also influence the response to selection. In the present study, the gain criterion is the GCA of a breeding population to an opposite heterotic pool. In this context, SCA acts as masking effect (see (1) and (2)) and, thus, reduces the correlation between selection index and GCA ( $\rho_{I,GCA}$  (4)). The masking effect of SCA can be reduced, on the one hand, by raising the number of testers (2). This inevitably increases the cost per test unit and

consequently reduces the number of lines that can be evaluated. On the other hand, the SCA variance can be reduced by using genetically broader testers such as double crosses or synthetics. Broadening testers leads to a reduced contribution of the SCA variance to the testcross variance (see (3)) and, hence, increases the agreement between selection and gain criterion.

Although genetically narrow testers lead to the lowest expected response to selection, they prevail in commercial breeding since they represent potential hybrid parents. The best testcross can therefore directly be transferred into the final phase of variety testing. A further advantage of using pure lines and single crosses as testers is that they produce a homogeneous gametic array. This increases the uniformity of the testcrosses and avoids bias due to assortative mating.

As a pragmatic compromise, we consider single cross testers as most recommendable. On the one hand, they furnish a higher expected gain in GCA than using pure line testers and, on the other hand, still meet the above practical requirements. The MBP (version 1.0) software allows the user to specify the tester type (pure line, single cross, double cross, or synthetic) separately for each testcross selection stage.

### Long-term response to selection

RS as described in the present paper can readily be integrated into the procedure for the development of hybrid parent lines (Hallauer and Miranda 1981). In RS, the breeder has to ensure a minimum  $N_e$  in order to preserve enough variation for subsequent selection cycles. In contrast, in the development of hybrid parent lines, a smaller fraction of superior lines is selected, i.e. a higher selection intensity is achieved. Moreover, the selection of hybrid parent lines may be based on more evaluation stages than the RS procedure, which allows for a higher precision in the estimation of the genetic value of lines. Yet, the genetic gain in line development builds up on the performance level of the breeding population, which is determined by the cumulative genetic gain from RS. In the long run, the efficiency in RS becomes the main factor determining the genetic gain in the development of hybrid parent lines.

Relaxing the  $\Delta\sigma_{g_{\max}}^2$  restriction from 0.01 to 0.02 or 0.05, considerably lowers the required number of recombination units allowing the breeder for an increased selection intensity and, thus, a higher short-

term genetic gain (Table 2), but will reduce the long-term response.

Under an infinitesimal model of gene effects and assuming no gametic-phase disequilibrium and constant phenotypic variance, the response to selection in generation  $t$  can be calculated according to Robertson's (1960) classic theory of selection limits as

$$G(t) = \left(1 - \frac{1}{2N_e}\right)^t G(1),$$

where  $G(1)$  is the response after the first selection cycle (Walsh 2004). Noting that

$$\sum_{j=1}^t \left(1 - \frac{1}{2N_e}\right)^j = 2N_e \left[1 - \left(1 - \frac{1}{2N_e}\right)^{t+1}\right] - 1,$$

the total cumulative response at generation  $t$  becomes

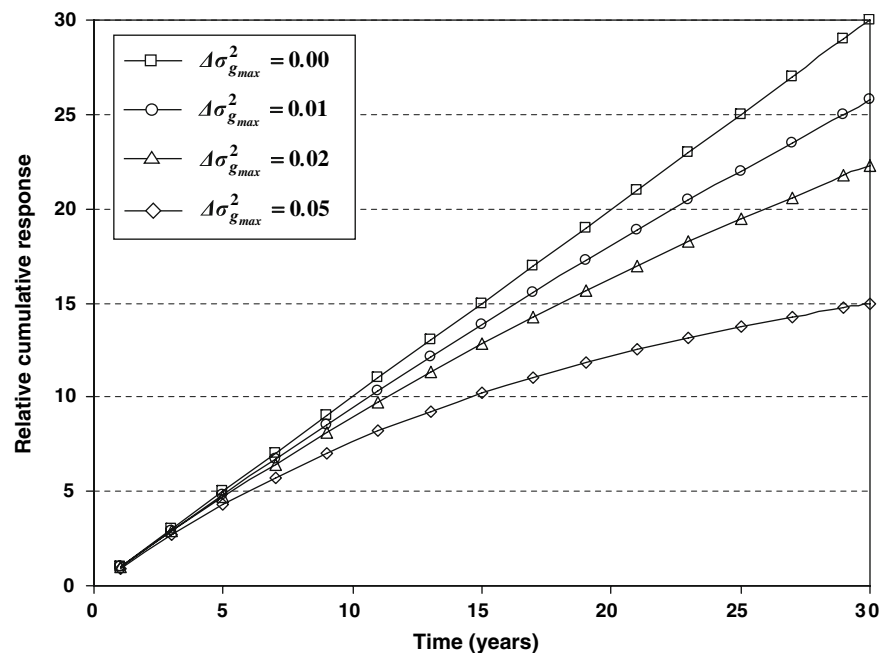
$$G_{cum}(t) = \left\{ 2N_e \left[1 - \left(1 - \frac{1}{2N_e}\right)^{t+1}\right] - 1 \right\} G(1). \quad (7)$$

In the present study, one generation corresponds to one RS cycle and the generation interval is equivalent to the RS cycle length, which may vary considerably among breeding schemes. Therefore, it is more meaningful to express the cumulative selection response as a function of the number of years instead of generations. This is achieved by substituting  $N_e$  with the *annual* effective population size defined as  $N_{ey} =$

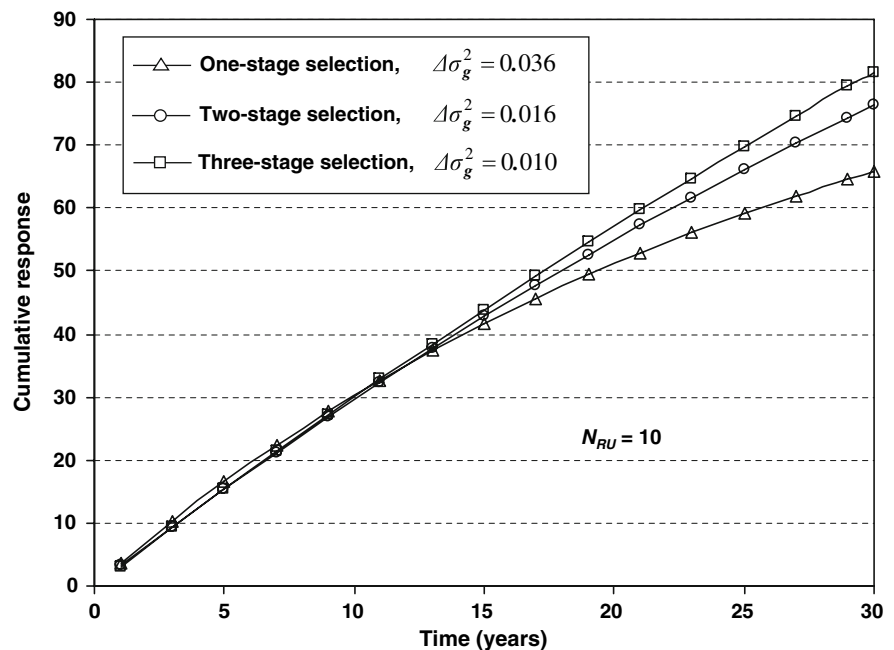
$1/(2\Delta\sigma_{g_{max}}^2)$  and  $G(1)$  with the annual genetic gain in the first selection cycle in Eq. 7. On this basis, the relative cumulative genetic gain over years is compared for different values of  $\Delta\sigma_{g_{max}}^2$  in Fig. 3. Herein, it is shown that the stringency of the  $\Delta\sigma_{g_{max}}^2$  restriction should be assessed according to whether short-, medium-, or long-term selection shall be optimized. For instance, if a time span of 5–10 years is considered, a relative annual loss of genetic variability of 0.05 may be acceptable. If the time span is extended to about 15–20 years, an adequate value of  $\Delta\sigma_{g_{max}}^2$  may be 0.02 and, finally, for longer time spans, an upper limit of 0.01 appears recommendable.

Without restricting the annual loss of genetic variance, no fair comparison between alternative selection procedures is possible. An example is given in Fig. 4, in which the cumulative response to one-, two-, and three-stage selection in Scheme 1 is presented over a time span of 30 years, when the number of recombination units is fixed at ten. One-stage selection then reduces the genetic variance by 3.6% per year, two-stage selection by 1.6%, and three-stage selection by 1%. As can be seen from Fig. 4, one-stage selection shows the highest cumulative selection response during the first 10 years. Thereafter, multi-stage selection gradually becomes more efficient. After 30 years, the cumulative response of one- and two-stage selection is already 24% and 7%,

**Fig. 3** Cumulative genetic response to selection over years relative to the annual genetic gain after one cycle of selection, based on Robertson's (1960) classic theory of selection limits assuming an infinitesimal model of gene effects and different upper limits for the relative annual loss of genetic variance ( $\Delta\sigma_{g_{max}}^2$ )



**Fig. 4** Cumulative genetic response to selection over years for the one-, two-, and three-stage procedures of Scheme 1, assuming a fixed number of recombination units ( $N_{RU} = 10$ ). The cumulative response refers to the gain from index selection for grain yield and dry matter content and is calculated according to Robertson's (1960) classic theory of selection limits assuming an infinitesimal model of gene effects



respectively, lower than that of three-stage selection. In contrast, if the same limit for the relative annual loss of genetic variance is applied to the three procedures, one-stage selection proves to be superior irrespective of the time span and the value for  $\Delta\sigma_{g_{\max}}^2$  considered.

Walsh (2004) studied the consequences of the assumptions underlying Robertson's (1960) theory of selection limits. The author showed that Robertson's formula slightly overestimates the genetic gain in early generations since it ignores gametic-phase disequilibrium. On the other hand, the coefficient of heritability is underestimated since Robertson also assumes a constant phenotypic variance. Interestingly, these two opposing biases largely cancel out leading to very similar results of the formula proposed by Robertson (1960) and those of a full prediction model according to Walsh (2004). This is in agreement with results of Wei et al. (1996), who illustrated the effect of accounting for gametic-phase disequilibrium, changes in phenotypic variance, and mutation in the prediction of the cumulative genetic response, also assuming an infinitesimal model.

In conclusion, DH-based recurrent selection is a highly effective tool to improve the GCA in maize gene pools. As a negative consequence of this high efficacy, the genetic variation is rapidly exploited if  $N_e$  is not kept at an adequate level. The MBP software, for the first time, allows to determine  $N_e$  as

a function of the joint action of random drift and selection. Setting the same upper limits for the relative annual loss of genetic variance, our model calculations show that one-stage selection procedures are superior to multi-stage procedures and that high-input, short-cycle RS procedures are most efficient. We suggest to optimize breeding procedures under the restriction of an upper limit of 0.01–0.02 for the relative annual loss of genetic variance in RS projects planned for a period of 15–30 years.

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## Appendix

Derivation of the asymptotic intraclass correlation between full sibs ( $\rho_{FS}^*$ )

Under an infinitesimal model of gene effects, selection induces a gametic-phase disequilibrium, which leads to a reduction of genetic variance. The remaining

proportion of genetic variance after truncation selection for a normally distributed trait is  $G_r = 1 - \lambda h^2$  (Bulmer 1980), where  $h^2$  is the heritability of the trait and  $\lambda = i(i - k)$ . The gametic-phase disequilibrium is reduced to one half with one generation of random mating. An asymptotic value for the genetic variance is then reached, when the reduction of variance due to selection is balanced by the increase of variance from random mating following selection (Wricke and Weber 1986; Gomez-Raya and Burnside 1990). As a consequence, the intraclass correlation between full sibs ( $\rho_{FS}$ ) also declines in the course of RS cycles until an asymptotic value for the genetic variance is achieved (Santiago and Caballero 1995).

Gomez-Raya and Burnside (1990) derived the following expression for the asymptotic additive variance resp. for the asymptotic heritability:

$$\sigma_A^{2*} = \frac{2\sigma_A^2(1 - h^2)}{1 - 2h^2 + \sqrt{1 + 4h^2\lambda(1 - h^2)}} \quad (8)$$

and

$$h^{2*} = \frac{-1 + \sqrt{1 + 4h^2\lambda(1 - h^2)}}{2\lambda(1 - h^2)}, \quad (9)$$

where  $\sigma_A^2$  and  $h^2$  denote the reference additive variance and heritability, respectively, prior to the first selection cycle. The asymptotic intraclass correlation of full sibs then can be defined as (Santiago and Caballero 1995):

$$\rho_{FS}^* = \frac{\sigma_b^{2*}}{\sigma_A^{2*} + \sigma_m^2}, \quad (10)$$

where  $\sigma_b^{2*}$  is the asymptotic additive variance between families and  $\sigma_m^2$  refers to the variance of masking effects ( $\sigma_m^2 = \sigma_{iy}^2 + \sigma_{il}^2/L + \sigma_{iy/l}^2/L + \sigma_e^2/LRT$ ). According to Santiago and Caballero (1995), the asymptotic additive variance between families is approximately

$$\sigma_b^{2*} = \varphi_{FS}\sigma_A^{2*}(1 - \lambda h^{2*}), \quad (11)$$

where  $\varphi_{FS}$  is the coefficient of coancestry of full sibs within a cross. If in Eq. 10 the variance due to masking effects is written as

$$\sigma_m^2 = \frac{\sigma_A^2(1 - h^2)}{h^2} \quad (12)$$

and  $\sigma_b^{2*}$  is substituted by the right-hand expression of (11), then

$$\rho_{FS}^* = \frac{\varphi_{FS}\sigma_A^{2*}(1 - \lambda h^{2*})}{\sigma_A^{2*} + \sigma_A^2(1 - h^2)/h^2}. \quad (13)$$

In the present study, we refer to the variance of additive effects between testcross progenies, i.e. the GCA variance ( $\sigma_{GCA}^2$ ) of the DH candidate lines for an index composed of grain yield and grain dry matter content. Thus, the additive variance component in Eqs. 8 and 10 to 13 was replaced by the covariance between the index value and GCA for grain yield:

$$\text{cov}_{I,GCA_{GY}} = b_{GY}\sigma_{GCA_{GY}}^2 + b_{DMC}\text{cov}_{GCA_{GY},DMC}.$$

Likewise, we use the parameter  $\rho_{I,GCA}$  instead of  $h^2$  to denote the accuracy of index selection. The corresponding parameters for dry matter content are calculated analogously.

This leads to the following extension of Eqs. 8, 9, and 13:

$$\begin{aligned} \text{cov}_{I,GCA_T}^* &= \frac{2\text{cov}_{I,GCA_T}(1 - \rho_{I,GCA_T}^2)}{1 - 2\rho_{I,GCA_T}^2 + \sqrt{1 + 4\rho_{I,GCA_T}^2\lambda(1 - \rho_{I,GCA_T}^2)}}, \\ \rho_{I,GCA_T}^{*2} &= \frac{-1 + \sqrt{1 + 4\rho_{I,GCA_T}^2\lambda(1 - \rho_{I,GCA_T}^2)}}{2\lambda(1 - \rho_{I,GCA_T}^2)}, \end{aligned}$$

and

$$\rho_{FS_T}^* = \frac{\varphi_{FS}\text{cov}_{I,GCA_T}^*(1 - \lambda\rho_{I,GCA_T}^{*2})}{\text{cov}_{I,GCA_T}^* + \text{cov}_{I,GCA_T}(1 - \rho_{I,GCA_T}^2)/\rho_{I,GCA_T}^2},$$

respectively, where  $\rho_{I,GCA_T}^{*2}$  denotes the asymptotic values of the squared correlation between index value and GCA for a given trait T, which corresponds to the squared accuracy of selection, and  $\text{cov}_{I,GCA_T}^*$  refers to the corresponding asymptotic covariance.

The accuracy of selection of  $m$  stages of selection is calculated as,

$$\rho_{I,GCA_m} = \frac{G_m}{i\sigma_{GCA}},$$

where  $G_m$  is the expected genetic gain after  $m$  stages of testcross selection. The selection intensity for  $m$  stages ( $i_m$ ) is obtained from corresponding multi-variate integrals calculated by numerical methods.

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