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Genetic drift and selection effects of modified recurrent full-sib selection programs in two F_2 populations of European flint maize

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Abstract Selection response of a modified recurrent full-sib (FS) selection scheme conducted in two European flint F_2 maize (*Zea mays* L.) populations was re-evaluated. Our objectives were to (1) determine the selection response for per se and testcross performance in both populations and (2) separate genetic effects due to selection from those due to random genetic drift. Modified recurrent FS selection was conducted at three locations using an effective population size $N_e = 32$ and a selection rate of 25% for a selection index, based on grain yield and grain moisture. Recombination was performed according to a pseudo-factorial mating scheme. Selection response was assessed using a population diallel including the source population and advanced selection cycles, as well as testcrosses with unrelatesd inbred line testers and the parental F_1 generation. Selection response per cycle was significant for grain yield and grain moisture in both populations. Effects of random genetic drift caused only a small reduction in the selection response. No significant selection response was observed for testcrosses, suggesting that for heterotic traits, such as grain yield, a high frequency of favorable alleles in the elite tester masked the effects of genes segregating in the populations. We conclude that our modified recurrent FS selection is an alternative to other commonly applied intrapopulation recurrent selection schemes, and some

of its features may also be useful for increasing the efficiency of interpopulation recurrent selection programs.

Introduction

Selection and genetic drift are the two main forces affecting selection response in recurrent selection programs. Selection increases the frequencies of favorable alleles and, hence, changes additive and/or dominance effects in the statistical model. In theory, maximum selection response from intrapopulation selection is expected at intermediate frequencies of favorable alleles, because additive variance is at a maximum (Falconer and Mackay 1996). Genetic drift is a random change in allele frequencies due to sampling effects associated with small population size, and may result in fixation of unfavorable alleles. Loss of favorable alleles due to sampling effects would reduce the per se performance of the population and, thus, hampers the selection response.

Gardner and Eberhart (1966) proposed a general quantitative-genetic model for the analysis of variety diallels and related populations. Hammond and Gardner (1974) adapted this model to the diallel cross of a parent variety and selection cycles. It includes different kinds of gene effects reflecting changes in allele frequencies due to selection, and separates linear from nonlinear effects contributing to the selection response under the asumption of an infinite population size. Smith (1979) extended this model to account for inbreeding depression in the selection cycles caused by a finite effective population

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size, but assumed that nonlinear effects in the Hammond–Gardner (1974) model were unimportant over a small number of cycles. Recently, Melchinger and Flachenecker (2006) provided an extended theory on the population diallel of selection cycles, which accounts for both the effects of directed selection and random genetic drift.

In 1990, a modified recurrent full-sib (FS) selection program was initiated at the University of Hohenheim (Germany) for evaluating the selection response in two European F_2 maize populations, previously employed in several QTL studies (Schön et al. 1994, Mihaljevic et al. 2004, 2005). As a new feature, we produced selfed progenies in all FS families simultaneously with the performance trials. The S_1 progenies were recombined according to a pseudo-factorial mating scheme (Cockerham and Burrows 1980) to establish the FS families of the next cycle. In two companion studies (Flachenecker et al. 2006a, 2006b), we investigated the selection response relative to check entries, estimated genetic variance components, and predicted the genetic value of single FS families in the recurrent FS selection program by using best linear unbiased prediction.

The objective of this study was to re-analyse the selection response in both populations by using a population diallel that included the source population and advanced selection cycles, as well as testcrosses with unrelated inbred line testers and the parental F_1 generation. Our objectives were to (1) determine the selection response for per se and testcross performance in a modified recurrent FS selection program and (2) separate genetic effects due to selection from those due to random genetic drift based on the model proposed by Melchinger and Flachenecker (2006).

Materials and methods

Plant materials

Four early maturing homozygous European flint lines KW1265, D146, D145 and KW1292, subsequently referred to as A, B, C, and D, respectively, were used as parents for the two F_2 populations $A \times B$ and $C \times D$. After completion of three generations of intermating in each population, four cycles of recurrent FS selection were conducted for population $A \times B$ and seven cycles for population $C \times D$. Details of the selection procedure were presented by Flachenecker et al. (2006a, 2006b) and are briefly described here.

Selection experiments

In 1994, pairs of plants of the F_2Syn3 generation (=cycle C0) were crossed to produce 120 FS families in populations $A \times B$ and $C \times D$. They were tested in field trials during the following season and, in parallel, six plants from each FS family were selfed in the breeding nursery. Thirty-six families with the highest selection index (see below) were selected for further breeding. The S_1 progenies of the selected FS families were divided into an upper-ranking group of parents mated to the lower-ranking group, according to the suggestion of Cockerham and Burrows (1980). The resulting 144 FS families were tested in an experiment similar to the trial in the previous cycle and again 36 families were selected based on the selection index. The production of six S_1 progenies per FS family and recombination of the selected 36 best families by a pseudo-factorial mating scheme were performed as described above for the first cycle.

The field trials for each cycle were conducted at three environments, each with three replications. The experimental design in each environment was an alpha lattice (10×15) complemented with six check entries from the F_2 generation. For calculating the selection index, (1) grain yield and dry matter content were expressed in percent of the mean of the F_2 check entries, and (2) relative values received a weight of 1 for grain yield and 2 for dry matter content.

Evaluation trials

For the population diallel, S_1 bulks of each cycle (Cn-self), crossings among the cycles ($Cn \times Cm$), and crosses with the F_1 generation ($Cn \times F_1$) were evaluated in each population, where $n < m$ are integers running from 0 to 4 for population $A \times B$ and from 0 to 7 for population $C \times D$. In addition, we tested the two parental lines (P1, P2), as well as the F_1, $F_2 = F_2Syn0$, F_2Syn1, F_2Syn2, F_2Syn3, and F_3 generations of both populations. Moreover, all cycles (Cn) were crossed to the unrelated dent inbred line testers KW4115 (T1) and KW5162 (T2) in population $A \times B$ and to tester T2 in population $C \times D$.

To minimize unequal competition effects among entries in the field trials, entries of each population were assigned to three experiments. Experiment 1 consisted of crosses among cycles and crosses with the F_1 generation as well as generations F_2Synt ($t = 0, 1, 2, 3$). Experiment 2 comprised the testcrosses to unrelated dent testers. Experiment 3 included the parental lines, P1 and P2, as well as the F_1, F_2, and F_3 generations, and S_1 bulks of each cycle (Cn-self). The

experiments were planted in three adjacent randomized complete-block designs with four replications at three locations in 2002 and 2003 for population C × D and in 2003 and 2004 for population A × B. The test locations (Hohenheim, Eckartsweier, and Bad Krozingen) were all located in Southwest Germany and identical to those previously used for testing the entries in each selection cycle. Each plot consisted of two rows in Experiment 1 and 2, and four rows in Experiment 3. Rows were 4.75 m long with 0.75 m between rows. Plots were overplanted and later thinned to 85,000 plants ha^{-1}. All experiments were machine planted and harvested as grain trials with a combine. In Experiment 3, only the two center rows were harvested to minimize unequal competition effects owing to entries with different levels of inbreeding. In six environments, data were collected for grain yield in Mg ha^{-1} adjusted to 15.5% grain moisture, grain moisture in g kg^{-1}, 1,000 kernel weight in g, and plant height in cm. Days to silking in d (=days from planting to 50% silk emergence) were recorded only in four environments.

Statistical analyses

Analyses of variance were performed for each experiment and environment (year by location combination) using software PLABSTAT (Utz 2001). Adjusted entry means were employed as observations in a model allowing for the separation of linear and nonlinear effects contributing to the selection response (Hammond and Gardner 1974, Smith 1979) including effects of random genetic drift (Melchinger and Flachenecker 2006). The model assumes populations in Hardy–Weinberg equilibrium, diploid inheritance, and absence of epistasis. Based on definitions by Smith (1979) and extensions by Melchinger and Flachenecker (2006), the genetic expectations of the entries included in this study are listed in Table 1. Inbreeding coefficients (F_n) of selection cycles were calculated as $1 - (1 - \frac{1}{2N_e})^n$, with $N_e = 32$ (Flachenecker et al. 2006a, 2006b) and assuming $F_0 = 0$ in the source populations F$_2$Syn3 - cycle C0. Using Falconer and Mackay's (1996) notation, let a, d, and $-a$ represent the genotypic values of the favorable homozygote, the heterozygote, and the unfavorable homozygote, respectively, and p and r the frequencies of the favorable allele in the population and the tester, respectively. Genetic parameters of the population diallel are defined as follows:

A0 $= \mu + \sum(2p - 1)a$ = mean plus contribution of additive effects in the initial population (cycle C0);
D0 $= \sum p(1 - p)d$ = contribution of dominance effects in cycle C0;

Table 1 Genetic expectation of population means and testcross population means expressed as linear combination of genetic parameters (A0, D0, AL, DQ, T0, TL) based on Smith's (1983) model with extensions by Melchinger and Flachenecker (2006)

Population[a]	Genetic expectation[b]
(P1 + P2)/2	A0
F$_1$	A0 + 4D0
F$_2$	A0 + 2D0
F$_3$	A0 + D0
F$_2$Syn$t$	A0 + 2D0
$Cn \times$ F$_1$	A0 + 2D0 + nAL
Cn-self	A0 + D0$(1 - F_n)$ + 2nAL $+ \frac{1}{2}(2n^2 - n^2 F_n)$DQ
$Cn \times Cm$	A0 + 2D0$(1 - F_n)$ + $(n + m)$AL $+ (2nm - -n2Fn)$DQ
$Cn \times$ T	T0 + nAL + nTL

[a] $t = 0,1,2,3; n < m = 0, 1, ..., 4$ and $0, 1, ..., 7$ for population A × B and C × D, respectively

[b] F_n refers to the inbreeding coefficient in cycleCn based on the assumption that $F_0 = 0$ for cycle C0 = F$_2$Syn3

AL $= \sum \Delta p \, a$ = linear changes in the population mean per selection cycle due to additive effects and changes in gene frequencies resulting from selection;
DL $= \sum \Delta p (1 - 2p)d$ = linear changes in the population mean per selection cycle due to dominance effects and linear changes in gene frequencies resulting from selection;
DQ $= -\sum(\Delta p)^2 d$ = quadratic changes in the population mean per selection cycle due to dominance effects and quadratic changes in genotype frequencies of heterozygotes resulting from selection;
T0 $= \mu + \sum(p + r - 1)a + \sum[r + p(1 - 2r)]d$ = mean plus contribution of additive and dominance effects in testcrosses between cycle C0 and the tester;
TL $= \sum \Delta p(1 - 2r)d$ = linear changes in the testcross population mean per selection cycle due to dominance effects and linear changes in gene frequencies resulting from selection.

The parameter DL is expected to be zero with $p = 0.5$, as applies to F$_2$ and F$_2$Syn$t$ populations and therefore was excluded in our model. Estimates of A0, D0, AL, DQ, T0, and TL were obtained by weighted least squares analysis ($\beta = (\mathbf{X'W^{-1}X})^{-1}\mathbf{X'W^{-1}y}$) using SAS PROC GLM (SAS Institute 2004). The **X** matrix was a function of the cycle number and genetic parameter coefficients. The **y** vector and the **W** matrix were composed of entry means across environments and their variances, respectively. Correlations between genetic parameter estimates were determined by using the elements of the variance–covariance matrix ($(\mathbf{X'W^{-1}X})^{-1}$). Estimates of relative selection response ($\Delta G\%$) were calculated as (2AL)/(A0 + 2D0) × 100 and estimates of

relative testcross response ($\Delta G_T\%$) as (AL + TL)/T0 × 100. Relative mid-parent heterosis (MPH%) was calculated as (F_1 – MP)/MP × 100, where MP is (P1 + P2)/2. Significance of absolute mid-parent heterosis (MPH) was tested by an appropriate t test using SAS PROC TTEST (SAS Institute 2004).

Results

Estimates of MPH% ranged from –7 and –6% for days to silking to 182 and 166% for grain yield in populations A × B and C × D, respectively (Table 2). In both populations, estimates of MPH were significant ($P < 0.05$) for all traits except grain moisture and days to silking.

Differences between the parameters calculated with the extended model of Melchinger and Flachenecker (2006) and the original model of Smith (1983) were small, as reflected by minor differences in the coefficient of determination R^2 (data not shown). For both models, R^2 values exceeded 0.98 in all traits. Although R^2 values were not consistently higher for the extended model of Melchinger and Flachenecker (2006), only estimates of the latter are presented.

Estimates of A0 were significant ($P < 0.01$) for all traits in both populations (Table 3). Estimates of D0 were significantly ($P < 0.01$) positive for selection index, grain yield, 1,000 kernel weight, and plant height and significantly ($P < 0.01$) negative for days to silking in both populations. Both source populations showed similar performance (A0 + 2D0) for selection index, grain yield, and plant height, but population A × B displayed higher 1,000 kernel weight, more days to silking, and lower grain moisture than population C × D.

Estimates of AL were significant ($P < 0.01$) for selection index, grain yield, grain moisture, and days to silking in population A × B and for all traits in population C × D (Table 3). Estimates of DQ were signifi-

cant ($P < 0.05$) for selection index, grain yield, and days to silking in population A × B, and for all traits except grain moisture and plant height in population C × D. Estimates of DQ had consistently opposite signs than those of AL.

Selection response per cycle ($\Delta G\%$) for grain yield was 14.07% for population A × B and 8.28% for population C × D (Table 3). Larger $\Delta G\%$ values in population A × B were also observed for selection index and days to silking, whereas $\Delta G\%$ for grain moisture, 1,000 kernel weight, and plant height was larger in population C × D. Interestingly, the original model of Smith (1983) yielded consistently smaller $\Delta G\%$ values for all traits except grain moisture in both populations.

Estimates of T0 were significant ($P < 0.01$) for all testers and populations (Table 3). In population A × B, crosses with T1 showed higher T0 values compared to crosses with T2 for grain moisture and days to silking and lower values for the other traits. Parameter TL was significant ($P < 0.01$) for selection index and grain yield in the crosses with both inbred testers in population A × B. In population C × D we observed highly significant ($P < 0.01$) estimates of TL for selection index, grain yield, 1,000 kernel weight, and plant height. For all traits and both populations, significant estimates of TL were of opposite sign as those of AL. Estimates of ΔG_T were not significant except for grain moisture in population C × D.

Discussion

In two previous studies, we evaluated the recurrent selection scheme applied to populations A × B and C × D (Flachenecker et al. 2006a, 2006b). The selection response for grain yield, calculated relative to the F_2Syn$t$ generations, was 0.1% per cycle for population A × B and 9.1% per cycle for population C × D. We detected no reduction in additive variance with ad-

Table 2 Means of the parental inbred lines P1 and P2 and their F_1, F_2 and F_3 generations and estimates of relative mid-parent heterosis (MPH%) in two populations (A × B, C × D) for selection index and five agronomic traits

Trait	Population A × B						Population C × D					
	P1	P2	F_1	F_2	F_3	MPH%	P1	P2	F_1	F_2	F_3	MPH%
Selection index (%)	236	249	331	294	259	37**	257	256	357	293	278	39**
Grain yield (Mg ha^{-1})	2.33	2.89	7.38	5.23	3.36	182**	3.61	2.94	8.70	5.18	4.52	166**
Grain moisture (g kg^{-1})	282	276	274	267	268	– 2	327	280	302	300	303	– 1
1,000 kernel weight (g)	234	208	274	253	236	24*	165	159	198	185	174	22**
Plant height (cm)	164	148	197	181	167	26**	162	112	200	174	171	46**
Days to silking (d)	84.2	84.3	78.7	80.8	82.7	– 7	81.1	78.7	75.4	77.0	80.5	– 6

*, **Significant at the 0.05 and 0.01 probability level, respectively

Table 3 Weighted least squares estimates of genetic parameters defined by Smith (1983), based on the extended model of Melchinger and Flachenecker (2006), for selection index (SI), grain yield (GY), grain moisture (GM), 1,000 kernel weight (TKW), plant height (PHT), and days to silking (DTS) in populations A × B and C × D

Parameter	SI (%)	GY (Mg ha^{-1})	GM (g kg^{-1})	TKW (g)	PHT (cm)	DTS (d)
Population A × B						
Per se performance						
A0	255.08**	3.14**	267.05**	228.74**	163.67**	83.27**
D0	21.75**	1.16**	2.71	11.54**	7.08**	− 1.49**
AL	7.84**	0.38**	− 2.34**	0.93	1.42*	− 0.53**
DQ	− 0.84*	− 0.04*	0.17	− 0.20	− 0.04	0.08*
ΔG%	5.25**	14.07**	− 1.72**	0.74	1.60	− 1.32**
ΔG%-Smith[a]	4.79**	12.59**	− 1.76**	0.41	1.35	− 1.21**
Testcross performance with tester T1						
T0	345.93**	7.97**	276.97**	264.86**	209.45**	79.74**
TL	− 7.60**	− 0.46**	0.04	− 3.06*	− 3.55**	0.31
ΔG_T%	0.07	− 0.96	− 0.83	− 0.80	− 1.02	− 0.28
Testcross performance with tester T2						
T0	373.42**	9.23**	253.03**	273.70**	223.23**	78.95**
TL	− 7.15**	− 0.35**	1.72	− 2.56*	− 2.61*	0.59**
ΔG_T%	0.19	0.34	− 0.25	− 0.59	− 0.53	0.07
Population C × D						
Per se performance						
A0	261.50**	3.21**	296.60**	169.92**	147.46**	79.24**
D0	20.80**	1.29**	2.64*	5.81**	15.49**	− 1.26**
AL	5.52**	0.24**	− 2.67**	2.02**	1.98**	− 0.35**
DQ	− 0.23**	− 0.01**	0.02	− 0.13**	− 0.09	0.02*
ΔG%	3.64**	8.28**	− 1.77**	2.23**	2.22**	− 0.91**
ΔG%-Smith[a]	3.43**	7.53**	− 1.79**	2.12**	1.97**	− 0.87**
Testcross performance with tester T2						
T0	395.56**	10.35**	269.92**	240.15**	235.25**	74.65**
TL	− 4.42**	− 0.24**	− 0.39	− 1.31**	− 2.27**	0.21*
ΔG_T%	− 0.84	− 2.38	− 1.28**	− 0.24	− 1.09	0.10

*, **Significant at the 0.05 and 0.01 probability level, respectively

[a] ΔG%-Smith refers to the relative selection response estimated from the original model of Smith (1983)

vanced selection cycles for grain yield and grain moisture in both populations, suggesting the larger effective population size ($N_e = 32$) used in our recurrent selection program was effective. In the present study, we re-evaluated the selection response in both populations including all materials in the same field trials and estimated parameters using an extension (Melchinger and Flachenecker 2006) of the genetic model of Smith (1979, 1983). The re-evaluation allows the separation of effects due to selection from those due to genetic drift and a better comparison of our modified recurrent FS selection scheme with other recurrent selection schemes.

Additive and dominance effects

Estimates of A0 explained more than 80% of the performance of the source populations (A0 + 2D0) for all traits except grain yield (Table 3). This agrees with other studies in maize, which reported relatively low A0 estimates for grain yield and higher estimates for grain moisture, plant height, and days to silking

(Tanner and Smith 1987; Eyherabide and Hallauer 1991; Stojsin and Kannenberg 1994a). In the source populations F$_2$Syn3 with $p = 0.5$, the parameter A0 is equal to μ. Therefore, no information about the importance of additive effects (a) could be obtained with our model.

In the absence of epistasis, estimates of D0 in F$_2$ populations correspond to one quarter of MPH. In our study, estimates of 4D0 agreed very well with the MPH estimates for all six traits (Tables 2 and 3). As expected, grain yield showed the highest D0 estimates, while D0 estimates for days to silking were negative. Other studies found similar estimates of D0 for days to silking and suggested that alleles with dominance effects were responsible for decreasing the number of days to silking (Keeratinijakal and Lamkey 1993; Stojsin and Kannenberg 1994b).

Mihaljevic et al. (2005) used the same source populations for generation means analyses with the F$_2$ metric. Their estimates of μ and d for grain yield and grain moisture agreed well with our results after conversion to the F$_\infty$ metric.

Selection response for per se performance

The parameter $\Delta G\%$ represents the response per selection cycle that could be expected after correcting for the effects of frequency changes in heterozygotes due to selection and random genetic drift. Estimates of $\Delta G\%$ for grain yield (Table 3) were for both populations larger than in other studies using a population diallel to evaluate progress from recurrent selection programs (Helms et al. 1989; Landi and Frascaroli 1993; Stojsin and Kannenberg 1994a). Additionally, the relatively high values of $\Delta G\%$ observed for grain moisture and days to silking corroborate the advantages of our modified recurrent FS selection scheme regarding the selection response.

For population C × D, the higher estimates of $\Delta G\%$ (Table 3) compare favorably with higher relative selection response for grain yield (9.1%) calculated in percent of the check entries ($F_2Syn t$) over the different years of selection (Flachenecker et al. 2006a). In population A × B, per se performance relative to check entries was 120% in cycle C1 and persisted at this level in later cycles (Flachenecker et al. 2006b). The linear increase for grain yield in this study supports the conjecture of Flachenecker et al. (2006b) that the relative selection response in their study was biased by the variable performance of the check entries over the years.

We ascribe the comparatively higher selection response mainly to the choice of two genetically broad F_2Syn3 source populations and the pseudo-factorial mating scheme. This mating scheme is expected to increase the selection response over the maximum achievable for the random mating schemes commonly applied in recurrent selection programs, while keeping the inbreeding coefficient at a moderate level (Cockerham and Burrows 1980). To determine the advantage of our modified recurrent FS selection scheme compared with commonly applied intrapopulation recurrent selection schemes, simulation studies or experiments with a common source population would be necessary.

Changes in heterozygote frequencies under selection

In earlier studies using a population diallel, the DQ parameter was used to determine the loss of heterozygotes from a population due to either selection and/ or random genetic drift (Smith 1983, Tanner and Smith 1987, Tragesser et al. 1989). DQ is a function of $(\Delta p)^2$, which suggests that a linear change in gene frequencies due to selection is accompanied by a quadratic change in genotype frequencies of heterozygotes. As demonstrated by Melchinger and Flachenecker (2006), random genetic drift enters the model through the quadratic term in the change of genotype frequencies of heterozygotes. Accounting to Melchinger and Flachenecker (2006), genetic drift, reflected by the inbreeding coefficient F_n, affects the coefficients of D0, DL and DQ in selection cycles Cn ($n \geq 1$) as well as their selfings and diallel crosses (Table 1). Smith (1979) ignored the parameter DQ and also disregarded the effects of drift except in the cycles Cn. Since Δp is assumed to be very small from one cycle to the next (Falconer and Mackay 1996), Smith (1979) argued that DQ could safely be ignored because it is a function of $(\Delta p)^2$. However, because the coefficient of DQ is a function of n^2, this argument is not entirely valid.

In our study, all significant DQ estimates were of opposite sign than those of AL. This is in accordance with previous studies, which observed negative DQ estimates for grain yield (Iglesias and Hallauer 1989, Frascaroli and Landi 1994) and plant height (Stojsin and Kannenberg 1994b), but positive estimates for days to silking (Keeratinijakal and Lamkey 1993). We estimated a correlation of –0.82 between the AL and the DQ term. Therefore, an increase in the favorable allele (AL) is very likely associated with a negative estimate of DQ.

Random genetic drift

To determine the effects of random genetic drift, we compared genetic parameters estimated by (1) ignoring and (2) including the inbreeding coefficient (F_n) in the model. The small average level of inbreeding in both populations resulted in similar genetic parameter estimates, irrespective of whether F_n was ignored or included in the model. Nevertheless, ignoring the effects of random genetic drift resulted in a reduction in $\Delta G\%$ in nearly all traits. The impact of random genetic drift to the selection response in the different traits is reflected by the difference between $\Delta G\%$ and $\Delta G\%$-Smith (Table 3). In studies with more selection cycles and/or higher rates of inbreeding, as applies to most recurrent selection studies reported in the literature (Hallauer and Miranda 1988, Weyhrich et al. 1998), the effect of random genetic drift is expected to be larger. Hence, ignoring it could result in a possible bias of genetic parameter estimates.

Testcross performance

Since selection in our study was based on per se performance of the FS families, changes in testcross performance reflect the correlated response and, thus,

depend on the genotypic correlation between per se and testcross performance. In maize, this correlation is medium to high for traits showing small heterotic effects such as grain moisture and days to silking, and generally lower for the highly heterotic trait grain yield (Hallauer and Miranda 1988, Seitz 1989). Especially for grain yield, non-additive genetic effects contributing to heterosis could result in a lower correlation between per se and testcross performance (Smith 1986, Hallauer 1990).

Another explanation for the non-significant $\Delta G_T\%$ estimates for grain yield is provided by the parameter TL, which was for all traits in the same range as the parameter AL but with negative sign. The parameter TL is defined as $\sum \Delta p(1\text{-}2r)d$, and its estimate is expected to be negative when one of its components is negative. As to the dominance effect, its sign is expected to be positive at the majority of loci for grain yield, in accordance with the significance of parameter D0 in both populations. The contribution of Δp should also be mostly positive due to the large estimates of AL. Therefore, the negative estimates of TL could be ascribed to the term $(1\text{-}2r)$. This term will become negative when the favorable allele is fixed in the tester, as applies presumably to the majority of loci controlling grain yield. This is in accordance with theoretical results of Smith (1986), who showed with simulation studies that the correlation between per se and testcross performance depends on the frequency of the favorable alleles in the tester, and approaches lower values if testcrosses were made to an unrelated elite tester.

In summary, the high selection response in per se performance was not accompanied by a substantial increase in testcross performance. Therefore, interpopulation recurrent selection schemes are more promising to increase testcross performance, especially for highly heterotic traits such as grain yield. Nevertheless, our modified recurrent FS selection is a serious alternative to other commonly applied intrapopulation recurrent selection schemes, which were already used to develop superior inbred lines (e.g., B73). Moreover, some aspects like the pseudo-factorial mating scheme could also be used to increase the efficiency of interpopulation recurrent selection programs usually employed in commercial hybrid breeding.

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