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Response to modified recurrent full-sib selection in two European F_2 maize populations analyzed with quantitative genetic methods

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Abbreviations

A	KW1265
ANOVA	analysis of variance
B	D146
BLUP	best linear unbiased prediction
C	D145
D	KW1292
FS	full-sib
MPH	mid-parent heterosis
QTL	quantitative trait loci
REML	restricted maximum likelihood
RS	recurrent selection

Mathematical notation

a, $(-a)$	genotypic value of favorable and unfavorable homozygote, respectively
d	genotypic value of heterozygote
$\bar{d}$	degree of dominance
ΔG	selection response
ΔG_T	testcross response
N_e	effective population size
f	coancestry coefficient
F	inbreeding coefficient
h^2	heritability
p	frequency of the favorable allele in the population
r	frequency of the favorable allele in the tester
σ^2_A	additive variance
σ^2_{AL}	additive×location interaction variance
σ^2_D	dominance variance
σ^2_{DL}	dominance×location interaction variance

1. General Introduction

Most procedures in plant breeding lead to a severe reduction in the genetic variance of the utilized breeding material. In contrast, the aim of recurrent selection (RS) is to gradually increase the frequency of favorable alleles while maintaining the genetic variance in a population (Hallauer, 1985). RS is a cyclical process, which includes three phases: (i) development of progenies, (ii) progeny evaluation, and (iii) recombination of selected progenies (Figure 1). Although most RS methods include these three phases, they vary in the types of progenies evaluated (*i.e.*, inbreds, full-sibs (FS), half-sibs, etc.); number of progenies evaluated; number of selected families; parental control; and the type of progenies intermated (Hallauer and Miranda, 1988). Among them, recurrent FS selection is characterized by a short cycle length, complete parental control and an high selection response (Weyhrich et al., 1998).

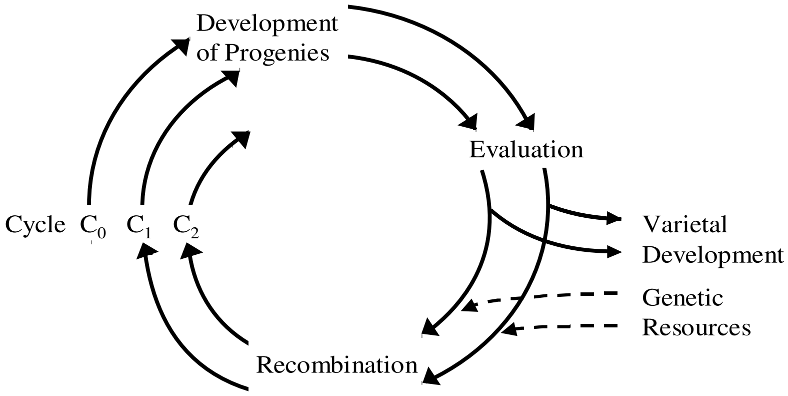

Figure 1. General recurrent selection scheme (Becker, 1993).

Modified recurrent full-sib selection

New genetic variation for the next cycle of an RS program is generated by recombination of selected genotypes. This is mostly performed by random mating, without recording pedigrees. Cockerham and Burrows (1980) proposed an alternative, where sexual roles are assigned after selection, using from s selected genotypes the s_1 best genotypes as male parents and the remaining $s - s_1$ genotypes as female parents. This mating scheme is expected to yield a greater long-term selection response with the same selection intesity, but has so far not been used in practice.

Maize (*Zea mays* L.) has been intensely subjected to recurrent selection and the populations most frequently utilized as sources have been open-pollinated and synthetic varieties (Hallauer and Miranda, 1988). In contrast, F_2 populations from biparental crosses have been employed only in a few instances (*cf.* Genter, 1982; Moll, 1991) because their use has been mainly devoted to recycling breeding programs (Bernardo, 2002). The breeding potential of F_2 populations could be enhanced by a few cycles of RS because the intermating of selected genotypes favors the recombination among linked loci, thereby increasing the chance of attaining superior recombinants. F_2 populations also are useful for investigating selection effects in that allelic frequencies at all segregating loci are known before starting selection ($p = 0.5$ for segregating alleles).

Inbreeding depression

Inbreeding depression in maize is a ubiquitous phenomenon found in all populations and for most traits associated with plant vigor. In RS programs inbreeding occurs in each selection cycle, because a finite number of genotypes are selected and recombined. The effects of inbreeding increase with continued selection. Inbreeding can be reduced by decreasing selection intensity (Sprague and Eberhart, 1977), which is the ratio of the number of lines selected for intermating to the number of lines evaluated. Estimation of inbreeding generated during selection can be useful for determining the optimum number of genotypes that will minimize the negative effects of inbreeding on genetic gain, and thereby maximize response to selection.

In RS programs, the number of individuals intermated approximates the effective population size N_e (Labate et al., 1997). Theoretical studies (Crow and Kimura, 1970) and empirical studies with *Drosophila* (Buri, 1956) have shown that small population size results in increased genetic uniformity as a consequence of random genetic drift. The use of inadequate N_e in artificial selection programs may result in the loss of genetic variability because of the fixation of alleles caused by random genetic drift (Vencovsky, 1978). Fixation may be for either favorable or unfavorable alleles, and unless mutation occurs or germplasm is introduced into the population, genetic variability will not generated at fixed loci (Hallauer, 1992). Up to now there are no studies availible, which calculated the realized N_e in each selection cycle of an RS program, and compared it with the predicted N_e.

Random genetic drift

Genetic drift is expected to occur in RS irrespective of the method because of the small number of selected progenies recombined to give rise to the improved populations. Furthermore, to increase the genetic gain and to lower the genetic load of populations, inbred progenies have been used for recombination. These factors lead to a decrease in N_e of the population under selection in which genetic drift is likely to take place, as has been reported for maize populations (Smith, 1979; Eyerhabide and Hallauer, 1991; Landi and Frascaroli, 1993).

For comparing the efficiency of different RS schemes, it is important to separate the effects due to selection from those due to random genetic drift. Based on the quantitative-genetic model of Gardner and Eberhart (1966), Hammond and Gardner (1974) devised a model for the analysis of the diallel cross of a parent variety and selection cycles derived from it. The model includes different kinds of gene effects reflecting canges in allele frequencies due to selection under the asumption of an infinite N_e. Smith (1979) extended this model to acount for inbreeding depression in the selection cycles caused by a finite N_e, but assumed that nonlinear effects in the Hammond-Gardner (1974) model were unimportant over a small number of cycles. Up to now no complete model under full consideration of inbreeding depression due to random genetic drift is availible.

Genetic variance components

The use of variance component analysis to study quantitative traits began early in the 20th century (Weinberg, 1909; Fisher, 1918). Fisher (1918) described a partition of the total variance of a quantitative trait in an outbred population into variance due to environment, additive effects, dominance, and epistasis. In populations undergoing RS the estimation of genetic variance components is important for examining the amount of remaining additive variance for future selection cycles, determining the narrow-sense heritability and predicting the response to selection. In particular, for diagnozing trends in variance components over selection cycles, optimal estimation of variance components is necessary in view of the large standard errors associated with them.

In maize populations, variance components are commonly estimated from classical mating schemes such as the diallel or factorial design with analysis of variance (ANOVA) methods (*cf.* Crossa and Gardner 1989; Moll 1991; Wolf et al. 2000). ANOVA has the advantage of providing unbiased estimators even when the data are not normally distributed, but the method requires genotypes to be classified into different groups and homogenous relationships within each group. Only balanced experiments fulfil these requirements. More complex mating designs (*c.f.* Cockerham, 1956; Kempthorne, 1957) are difficult to handle with the ANOVA method.

For estimation of genetic variance components from complex pedigrees, mixed linear models and restricted maximum likelihood estimation (REML) can be employed. REML estimation is meanwhile state-of-the-art in animal breeding (Hudson and Van Vleck 1982; Dong and Van Vleck 1989; Meyer and Smith 1996). Bernardo (1994) proposed its application in plant breeding, but the method has hitherto rarely been used in this context.

Best linear unbiased prediction of progeny performance

Methods for predicting the selection response are important to optimize RS programs. Predicted and realized responses to intrapopulation selection often show large discrepancies (Penny and Eberhart 1971; Crossa and Gardner 1989). A possible reason may be that the expressions of the predicted response to selection have been derived under simplifying assumptions, such as random mating, which are often not fulfilled in practice. An alternative is best linear unbiased prediction (BLUP).

BLUP is a general procedure that allows comparisons among genotypes developed from different breeding populations and evaluated in different environments. The BLUP procedure allows the analysis of unbalanced data and exploits information from relatives, thereby maximizing the use of all availible data when comparing genotypes. The BLUP procedure was developed by Henderson (1975; 1985) and has been used extensively in dairy cattle evaluation (Henderson, 1988; Freeman, 1991; Schaeffer, 1991). However, the application of BLUP in crop plants has been very limited (White and Hodge, 1989; Bernardo 1994).

Objectives

In 1990, a long-term recurrent FS selection program with two European F_2 maize population was initiated. As a novel feature, adopting the idea of Cockerham and Burrows (1980), a pseudo-factorial mating scheme was used for recombination of selected candidates and pedigrees among all FS families across all selection cycles were recorded. In particular, the objectives of my thesis research were to

1. monitor trends across selection cycles in the estimates of population mean, inbreeding coefficients and variance components;
2. determine selection response for *per se* and testcross performance;
3. compare predicted with realized selection response;
4. extend the population diallel analysis under full consideration of inbreeding depression due to random genetic drift;
5. separate genetic effects due to selection from those due to random genetic drift; and
6. investigate the usefulness of mean additive genetic BLUP of parents for predicting progeny performance under the recurrent FS selection scheme applied.

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ORIGINAL PAPER

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Trends in population parameters and best linear unbiased prediction of progeny performance in a European F2 maize population under modified recurrent full-sib selection

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Abstract Recurrent selection is a cyclic breeding procedure designed to improve the mean of a population for the trait(s) under selection. Starting from an F_2 population of European flint maize (*Zea mays* L.) intermated for three generations, we conducted seven cycles of a modified recurrent full-sib (FS) selection scheme. The objectives of our study were to (1) monitor trends across selection cycles in the estimates of the population mean, additive and dominance variances, (2) compare predicted and realized selection responses, and (3) investigate the usefulness of best linear unbiased prediction (BLUP) of progeny performance under the recurrent FS selection scheme applied. Recurrent FS selection was conducted at three locations using 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, where the selected FS families were divided into an upper-ranking group of parents mated to the lower-ranking group. Variance components were estimated with restricted maximum likelihood. Average grain yield increased 9.1% per cycle, average grain moisture decreased 1.1% per cycle, and the selection index increased 11.2% per cycle. For the three traits we observed, no significant changes in additive and dominance variances occurred, suggesting future selection response at or near current rates of progress. Predictions of FS family performance in $Cn+1$ based on mean performance of parental FS families in Cn were of equal or higher precision as those based on the mean additive genetic BLUP of their parents, and corresponding correlations were of moderate size only for grain moisture. The significant increase in grain yield combined with the decrease in grain moisture suggest that the F_2 source population with use of a pseudo-factorial mating scheme is an appealing alternative to other types of source materials and random mating schemes commonly used in recurrent selection.

Introduction

Recurrent selection is a cyclical breeding strategy aiming at a continuous increase in the frequencies of favorable alleles while maintaining the genetic variance in a population (Hallauer 1985). The improved population can either be used as an open-pollinated variety or as a source for developing superior inbreds. Several intra-population recurrent selection methods have been proposed for population improvement in maize (*Zea mays* L.) (for review see, Sprague and Eberhart 1977; Hallauer 1985). Among them, recurrent full-sib (FS) selection is characterized by a short cycle length, complete parental control and a relatively high selection response (Hallauer and Miranda 1988; Weyhrich et al. 1998).

Recombination of the selected genotypes to generate new genetic variation for the next cycle is a key element in recurrent selection. Recombination is generally achieved by random mating, without recording pedigrees. Cockerham and Burrows (1980) proposed an alternative, where sexual roles are assigned after selection, using from s selected genotypes the s_1 best genotypes as male parents and the remaining $s–s_1$ genotypes as female parents. This mating scheme is expected to yield a greater long-term selection response with the same selection intensity, but has so far not been used in practice.

In recurrent selection programs of maize, either open-pollinated varieties or synthetics have mostly been used as source populations (Hallauer and Miranda 1988). In contrast, F_2 populations from biparental crosses are the major type of base populations used in recycling breeding programs (Bernardo 2002). Nevertheless, F_2 populations have been employed in a few recurrent selection programs with the U.S. dent germplasm (cf.

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Genter 1982; Moll 1991). Advantages for use of F_2 populations in recurrent selection include that allele frequencies are known ($p=0.5$ at all segregating loci) and the additive variance is maximum at the beginning of the selection program, irrespective of the degree of dominance (Falconer and Mackay 1996).

Estimation of genetic variance components in populations undergoing recurrent selection is important for examining the amount of remaining genetic variance for future selection cycles, determining the narrow-sense heritability and predicting the response to selection. To determine trends in variance components over selection cycles, optimal estimation of variance components is necessary because of the large standard errors associated with them. Variance components are commonly estimated from classical mating schemes, such as the diallel or factorial designs with analysis of variance methods (cf. Crossa and Gardner 1989; Moll 1991; Wolf et al. 2000). For estimation of genetic variance components from complex pedigrees, mixed linear models and restricted maximum likelihood (REML) can be employed. REML estimation is the state-of-the-art method in animal breeding (Hudson and Van Vleck 1982; Dong and Van Vleck 1989; Meyer and Smith 1996). Bernardo (1994) proposed its application in plant breeding, but the method has hitherto rarely been used in this context.

Methods for predicting the selection response are important to optimize recurrent selection programs. Predicted and realized responses to intrapopulation selection often show large discrepancies (Penny and Eberhart 1971; Crossa and Gardner 1989). A possible reason may be that the expressions of the predicted response to selection have been derived under simplifying assumptions, such as random mating, which are not always fulfilled in practice. An alternative method would be best linear unbiased prediction (BLUP), which has been found useful in previous studies on predicting the performance of single-cross hybrids of maize (Bernardo 1994, 1996), but has not been applied in recurrent selection programs.

In 1990, we initiated a long-term recurrent FS selection program within an F_2 population (D145 × KW1292) also employed in mapping of quantitative trait loci (QTL) for per se and testcross performance (Mihaljevic et al. 2004, 2005). Adopting the suggestion of Cockerham and Burrows (1980), we used a pseudo-factorial mating scheme for recombination of selected FS families and recorded pedigrees among all FS families across all selection cycles. Our goal was to investigate the changes in the population structure over seven cycles at the level of the phenotype and individual marker loci.

The objectives of the present study were to (1) monitor trends across selection cycles in the estimates of the population mean, and additive and dominance variances, (2) compare predicted and realized selection responses, and (3) investigate the usefulness of mean additive genetic BLUP of parents for predicting progeny performance under the recurrent FS selection scheme applied.

Materials and methods

Plant materials

Two early maturing homozygous European flint lines D145 and KW1292, referred to as C and D consistent with the terminology of Mihaljevic et al. (2004), were used as parents to produce the F_2 generation. The F_2Syn3 generation was derived from the F_2 generation by three generations of chain crossing using 240 F_2 plants, i.e., crossings 1×2, 2×3, ..., and 240×1.

Selection procedure

In 1994, the F_2Syn3 generation was grown and pairs of S_0 plants were crossed to produce 120 FS families. In the following year, they were tested in field trials at three locations. In parallel, six S_0 plants from each FS family were selfed in the breeding nursery. The 36 FS families with the highest selection index (see below) were chosen and divided into two sets, consisting of even and odd numbered families. The six S_1 progenies of the 18 FS families in each set were recombined according to a pseudo-factorial mating scheme (Fig. 1). The selected FS families were divided into an upper-ranking group of parents mated to the lower-ranking group with unequal gametic contributions to the next generation, according to the suggestion by Cockerham and Burrows (1980). Consequently, the six S_1 progenies of the FS families with the highest selection index scores in each set were mated to S_1 progenies of the remaining 12 FS families in an off-season nursery, using bulked pollen of 15 S_1 plants from each progeny. The resulting 144 FS families were tested in an experiment similar to the trial in the previous cycle and 36 families were again selected based on the selection index. Likewise, the production of six S_1 progenies per FS family and recombination of the selected 36 top FS families by two sets of pseudo-factorial mating schemes were performed as described for the first cycle. Following this scheme, seven cycles of recurrent FS selection were conducted between 1994 and 2001. The field trials for each cycle were conducted at three locations in South Germany (Eckartsweier, Bad Krozingen, Ladenburg). In 2000 (Cycle 6 (C6)), only two locations could be harvested because of severe hail damage at Ladenburg. The experimental design at each location was an alpha lattice (10×15) with three replications. Thirty reciprocal crosses in C0 and six F_2 check entries from the source population in C1 to C7 were used to complement the lattice design. Each plot consisted of one row, 4.75 m long and spaced 0.75 m between rows. Plots were thinned to 85,000 plants ha^{-1}. All experiments were machine planted and harvested as

M	F 13	15	17	19	· · ·	33	35
1	1.1 × 13.1	1.1 × 15.1	1.2 × 17.1	1.2 × 19.1	· · ·	1.6 × 33.1	1.6 × 35.1
3	3.1 × 13.2	3.1 × 15.2	3.2 × 17.2	3.2 × 19.2	· · ·	3.6 × 33.2	3.6 × 35.2
5	5.1 × 13.3	5.1 × 15.3	5.2 × 17.3	5.2 × 19.3	· · ·	5.6 × 33.3	5.6 × 35.3
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
11	11.1 × 13.6	11.1 × 15.6	11.2 × 17.6	11.2 × 19.6	· · ·	11.6 × 33.6	11.6 × 35.6

Fig. 1 Pseudo-factorial mating scheme for intermating the odd-numbered FS families ranked according to the selection index. *M* male parent, *F* female parent, and *i.r* × *j.q* cross between the *r*th S_1 progeny of the *i*th ranking FS family with the *q*th S_1 progeny of the *j*th ranking FS family. The same scheme was also applied to the set with even numbers

grain trials with a combine. Data were recorded for grain moisture (g kg^{-1}) and grain yield (Mg ha^{-1}) adjusted to 155 g kg^{-1} grain moisture. For calculating the selection index, (1) grain yield and dry matter content were expressed in percent of 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 ($\mathbf{b}' = (1,2)$).

Statistical analyses

Ordinary lattice analyses of variance for grain yield and grain moisture were performed for each experiment and location using software PLABSTAT (Utz 2001). Adjusted entry means were then used to compute combined analyses of variance across locations (Cochran and Cox 1957). Population means across locations, relative to the F_2 check entries, were calculated for each cycle to determine the realized response to selection in percent. Phenotypic and genotypic correlations between grain yield and grain moisture were calculated according to established methods (Mode and Robinson 1959).

Based on the known pedigree records, the inbreeding coefficient *F* of each FS family and the coancestry coefficient *f* among FS families were calculated according to the rules described by Falconer and Mackay (1996), using procedure PROC INBREED in SAS (SAS Institute 2004) and setting $F = 0$ and $f = 0$ in the F_2Syn3 generation.

For each selection cycle from C1 to C7, additive and dominance variances were estimated based on adjusted entry means and effective error mean squares from the individual lattice analyses by REML, using PROC MIXED in SAS (SAS Institute 2004). The linear model was

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\alpha + \mathbf{Z}_2\delta + \mathbf{Z}_3\alpha l + \mathbf{Z}_4\delta l + \varepsilon,$$

where **y** is the $n\times 1$ vector of observed phenotypic values; $\boldsymbol{\beta}$ is the $b\times 1$ vector of fixed effects (location); $\boldsymbol{\alpha}$ is the $a\times 1$ vector of additive effects; $\boldsymbol{\delta}$ is the $d\times 1$ vector of dominance effects; $\boldsymbol{\alpha l}$ is the $al\times 1$ vector of additive × location interaction effects; $\boldsymbol{\delta l}$ is the $dl\times 1$ vector of dominance × location interaction effects; ε is the $n\times 1$ vector of errors and $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, $\mathbf{Z}_3$, and $\mathbf{Z}_4$ are design matrices of 1s and 0s relating **y** to $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$, $\boldsymbol{\delta}$, $\boldsymbol{\alpha l}$, and $\boldsymbol{\delta l}$, respectively. The random factors have the following variance–covariance matrix:

$$\mathrm{Var}\begin{bmatrix}\alpha\\ \delta\\ \alpha l\\ \delta l\\ \varepsilon\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma^2_{\mathrm{A}} & 0 & 0 & 0 & 0\\ 0 & \mathbf{D}\sigma^2_{\mathrm{D}} & 0 & 0 & 0\\ 0 & 0 & (\mathbf{I}\otimes\mathbf{A})\sigma^2_{\mathrm{AL}} & 0 & 0\\ 0 & 0 & 0 & (\mathbf{I}\otimes\mathbf{D})\sigma^2_{\mathrm{DL}} & 0\\ 0 & 0 & 0 & 0 & \mathbf{I}\sigma^2_{\mathrm{e}}\end{bmatrix},$$

where **A** is an $n\times n$ matrix with elements equal to *t*; **D** an $n\times n$ matrix with elements equal to *u*; **I** identity matrices of appropriate dimensions; $\otimes$ is the Kronecker product; σ^2_{A} is the additive, σ^2_{D} is the dominance, σ^2_{AL} is the additive × location, σ^2_{DL} is the dominance × location, and σ^2_{e} is the error variance. We assumed no correlations between genotype × location interaction effects across locations. Values for *t* and *u* between FS family *x* with parents *a* and *b* and FS family *y* with parents *c* and *d* were obtained as $t = 2f_{xy}$ and $u = f_{ac}f_{bd} + f_{ad}f_{bc}$, respectively (Falconer and Mackay 1996). Variance components of advanced cycles were calculated with the coancestry coefficients expected from the pseudo-factorial mating scheme (Fig. 1) by (1) ignoring or (2) considering additional coancestries from previous generations. In our model, REML only warrants that the total genetic variance is positive and, therefore, negative values are possible for individual variance components. In the latter case, we set these variance components equal to 0 and re-estimated the other variance components from the reduced model (Searle 1971). BLUP values of random effects were obtained with the SOLUTION option of SAS procedure PROC MIXED

(SAS Institute 2004), which employs the mixed model equations of Henderson (1975).

Heritability was calculated as

$$h^2 = \frac{\sigma^2_A/2}{\left(\sigma^2_A + \sigma^2_{AL}/l\right)/2 + \left(\sigma^2_D + \sigma^2_{DL}/l\right)/4 + \sigma^2_e/rl},$$

where l and r correspond to the number of locations and replicates, respectively. Estimates of σ^2_A and σ^2_D were used to estimate the degree of dominance as $\bar{d} = \left(2\sigma^2_D/\sigma^2_A\right)^{1/2}$. The prediction of the selection response per cycle for the selection index was calculated as (Wricke and Weber 1986)

$$R = i \cdot \frac{\mathbf{b}'\mathbf{G_a}\mathbf{b}}{\sqrt{\mathbf{b}'\mathbf{P}\mathbf{b}}},$$

where $\mathbf{P}$ and $\mathbf{G_a}$ denote the phenotypic and additive-genetic covariance matrix, respectively; $\mathbf{b}$ is the vector of weights; and i the selection intensity, calculated as $i = N \cdot z / N_e$ (Cockerham and Burrows 1980), where N is the number of FS families tested in the respective cycle; the effective population size N_e is $1/2\Delta F$; ΔF is the increase in F from one cycle to the next; and z is the ordinate of the standardized normal distribution at the truncation point. Prediction of grain yield and grain moisture relative to the mean of F_2 checks was calculated as

$$\Delta\mu = i \cdot \frac{\mathbf{G_a}\mathbf{b}}{\sqrt{\mathbf{b}'\mathbf{P}\mathbf{b}}}.$$

Furthermore, the performance of individual FS families in C$n+1$ was correlated with the mean BLUP of their parents in Cn. Likewise the performance of individual FS families in C$n+1$ was correlated with the mean performance of the respective parental FS families in Cn.

Multiple regression analyses weighted by inverse standard errors were used to investigate changes in population means and variance components over selection cycles. All regression and correlation analyses were performed with the statistical software R (R Development Core Team 2004).

Results

The average inbreeding coefficients across all 144 FS families increased from 0.003 in C1 to 0.120 in C7 (Table 1). Likewise, the average coancestry coefficients increased from 0.018 in C1 to 0.118 in C7. We found no significant difference in the mean of F values between the 36 selected FS families and the remaining 108 FS families for each cycle. The effective population size (N_e) ranged between 20 in C5 and 47 in C6.

Mean grain yield relative to the F_2 checks increased from 98% in C1 to 158% in C7, corresponding to an average rate of 9.1% cycle^{-1} (Fig. 2). Mean grain moisture relative to the F_2 checks ranged from 101% in C2 to 94% in C7 and decreased 1.1% cycle^{-1}. The selection index increased from 298 to 369, with an average rate of 11.2% cycle^{-1}. The weighted linear regression of observed performance on selection cycles was significant ($P < 0.01$) for all three traits, and neither quadratic nor cubic regressions gave a significantly better fit to the data. The correlations between the realized and different predicted selection responses exceeded 0.88 and were significant ($P < 0.05$) for all traits.

Estimates of σ^2_A under consideration of exact pedigree relationships were significant ($P < 0.05$) for grain yield in C2, C3, and C5, for grain moisture in all cycles, and for the selection index in C2 and C3 (Table 2). Estimates of σ^2_D were positive in most selection cycles but significant ($P < 0.05$) only in C1 and C4 for grain yield and the selection index, and in C1 for grain moisture. Estimates of σ^2_{AL} were significant ($P < 0.01$) in all cycles, except in C6 for grain yield, in C1 and C2 for grain moisture, and from C1 to C5 for the selection index. Significant ($P < 0.05$) estimates of σ^2_{DL} were observed only in C5 for grain moisture and in C6 for the selection index. Linear regression of variance component estimates on selection cycles was not significant, except for an increase of σ^2_A in grain moisture and σ^2_{DL} in selection index. Estimates of h^2 ranged from 0.00 in C4 to 0.85 in C3 for grain yield, from 0.49 in C1 to 0.92 in C3 for grain moisture, and from 0.11 in C4 to 0.83 in C3 for selection index. Estimates of $\bar{d}$ calculated from the mean variance compo-

Table 1 Average inbreeding coefficient and coancestry coefficient of all 144 full-sib families (F_{all} and f_{all}) and the 36 selected full-sib families (F_{sel} and f_{sel}), effective population size (N_e), as well as phenotypic (r_p) and genotypic correlations (r_g) between grain yield and grain moisture in each selection cycle

Cycle	F_{all}	F_{sel}	f_{all}	f_{sel}	N_e	r_p	r_g
C1	0.003	0.007	0.018	0.020	25	0.01	−0.01
C2	0.023	0.031	0.035	0.041	23	$0.67^{a,b}$	$0.62^{a,b}$
C3	0.044	0.040	0.055	0.060	26	$0.22^{a,b}$	0.20^{a}
C4	0.064	0.057	0.073	0.083	25	$0.39^{a,b}$	$0.32^{a,b}$
C5	0.084	0.087	0.095	0.098	20	$-0.45^{a,b}$	$-0.38^{a,b}$
C6	0.109	0.099	0.109	0.108	47	$-0.41^{a,b}$	$-0.37^{a,b}$
C7	0.120	0.113	0.118	0.122	24	0.12^{a}	0.10

[a,b] Phenotypic correlation was significant at the 0.05 and 0.01 probability level, respectively, and the genotypic correlation exceeded once and twice its standard error, respectively

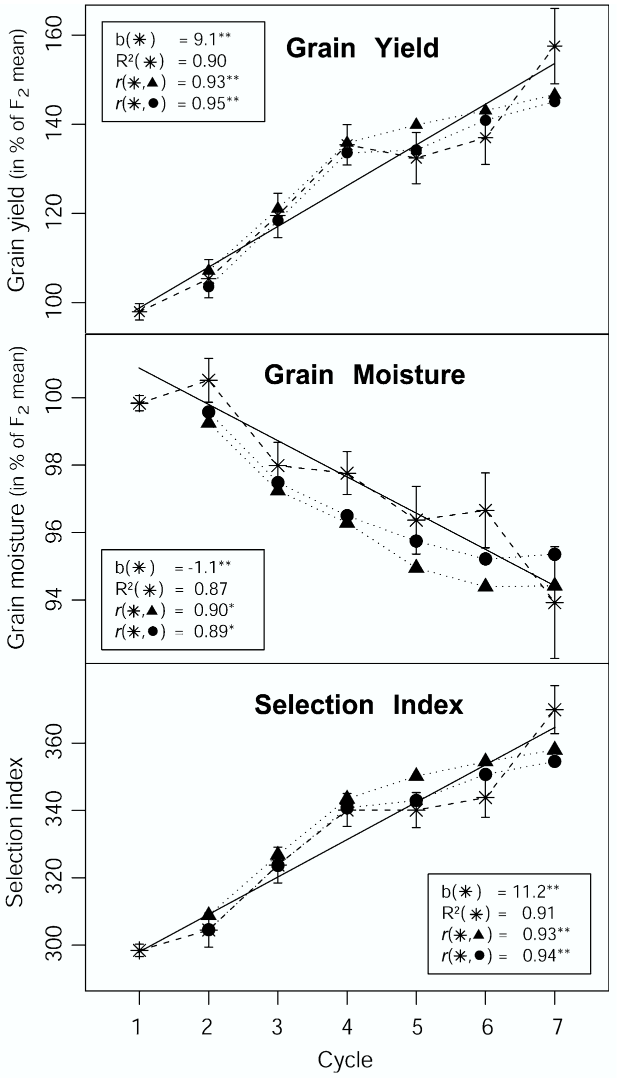

Fig. 2 Grain yield, grain moisture and selection index relative to the mean performance of the six F_2 checks: realized (*asterisks*) and predicted selection response, ignoring (*filled triangle*) and including (*filled circle*) exact pedigree relationships in REML estimates of variance components; the *bars* indicate standard errors, *b* is the slope of realized selection response (*solid line*), R^2 is the coefficient of determination of these values in the linear regression, *r* is the correlation between realized and predicted selection response, and * and ** denote the 0.05 and 0.01 probability level, respectively

nents amounted to 1.04 for grain yield, 0.47 for grain moisture and 1.17 for the selection index.

Phenotypic correlations between grain yield and grain moisture varied widely among cycles and ranged from –0.45 in C5 to 0.67 in C2 (Table 1). Genotypic correlations were similar to phenotypic correlations and ranged from –0.38 in C5 to 0.62 in C2.

Correlations between the performance of all 144 FS families in C$n+1$ and the mean additive genetic BLUP of their parents in Cn for grain yield ranged from 0.14 in C4 to 0.35 in C6, and were significant ($P<0.01$) in C2, C3, and C6 (Table 2). The respective correlations for grain moisture were much higher ($0.46 \le r \le 0.66$) and significant ($P<0.01$) in all cycles. For the selection index, the correlations ranged between –0.02 in C5 and 0.40 in C2, and were significant ($P<0.01$) only in C2, C3 and C4. For all traits, these correlations were equal to or smaller than the correlations between the performance of the FS families in C$n+1$ and the mean performance of their parental FS families in Cn.

Discussion

Ordinary recurrent FS selection involves two steps: (1) testing and selection of the FS families, and (2) recombination of the selected FS families to generate the test candidates of the next cycle. We modified this scheme by producing selfed progenies in all FS families simultaneously with the performance trials. During the next season, the S_1 progeny of Cn were used for recombination in the winter nursery to establish the FS families of C$n+1$. Compared with the conventional procedure, this modification requires additional pollinations in the nursery, but it offers the following advantages necessary for application of the pseudo-factorial mating scheme: (1) large quantities of seeds can be produced for evaluating the performance of the FS families in C$n+1$ in multi-location trials with an arbitrary degree of precision, and (2) S_1 progeny of the best FS families in Cn can be used twice as parents to generate closer pedigree relationships (half-sibs) between some FS families in C$n+1$. With BLUP, the information of relatives can be weighted in a manner optimal for the estimation of the additive genetic value of each FS family in C$n+1$. However, it was unknown whether this approach would result in an improved prediction power compared with the mean performance of the parental FS families.

Selection response

Grain yield has historically been the most important trait in maize improvement. Although we used a selection rate of 30% (C0) and 25% (C1–C7), elite breeding material, and a selection index considering also grain moisture, we observed a very high average selection response (9.1%) for grain yield. Previous studies on recurrent FS selection in F_2 populations achieved average responses between 4.5 and 7.3% across 4–16 selection cycles (Genter 1982; Moll 1991; Landi and Frascaroli 1993). Other studies using open-pollinated and synthetic base populations reported an average response of 3–4% for recurrent FS selection (Pandey et al. 1987; Hallauer and Miranda 1988; Stromberg and Compton 1989).

Several factors may have contributed to the comparatively high selection response per cycle in our study: (1) use of a pseudo-factorial mating scheme. In this

Table 2 REML estimates of variance components (± SE), their mean across cycles and slope coefficient (*b*) of the linear regression across selection cycles, heritability (h^2), degree of dominance $\bar{d}$ correlation (r_1) between full-sib (FS) family performance in C*n* + 1 and mean BLUP of their parents in C*n*, and correlation (r_2) between FS family performance in C*n* + 1 and mean performance of their parental FS families in C*n* for grain yield, grain moisture and selection index

Cycle	σ^2_A	σ^2_D	σ^2_{AL}	σ^2_{DL}	σ^2_e	h^2	$\bar{d}$	r_1	r_2
				Grain yield (Mg ha^{-1})					
C1	0.21 ± 0.11	0.36 ± 0.14*	0.11 ± 0.04**	0.03 ± 0.05	0.40 ± 0.04**	0.42	1.85	-[a]	0.24**
C2	0.54 ± 0.22*	0.21 ± 0.23	0.24 ± 0.05**	0.00	0.80 ± 0.07**	0.63	0.88	0.28**	0.37**
C3	0.69 ± 0.10**	0.00	0.11 ± 0.03**	0.00	0.51 ± 0.04**	0.85	0.00	0.24**	0.28**
C4	0.00	0.39 ± 0.08**	0.30 ± 0.09**	0.04 ± 0.11	0.57 ± 0.05**	0.00	-[b]	0.14	0.14
C5	0.49 ± 0.25*	0.15 ± 0.27	0.44 ± 0.07**	0.00	0.72 ± 0.06**	0.59	0.79	-[b]	−0.05
C6	0.50 ± 0.28	0.16 ± 0.31	0.21 ± 0.14	0.12 ± 0.18	0.53 ± 0.05**	0.59	0.80	0.35**	0.36**
C7	0.17 ± 0.11	0.13 ± 0.14	0.18 ± 0.04**	0.00	0.54 ± 0.05**	0.44	1.26	0.16	0.17*
Mean	0.37 ± 0.15	0.20 ± 0.17	0.23 ± 0.07	0.03 ± 0.05	0.58 ± 0.05	0.57 [c]	1.04 [c]	0.23	0.22
b	−0.02	−0.03	0.02	0.01					
				Grain moisture (g kg^{-1})					
C1	32.8 ± 15.4*	49.5 ± 19.1**	13.4 ± 2.2**	0.00	30.5 ± 2.7**	0.49	1.74	-[a]	0.45**
C2	162.1 ± 23.5**	0.00	31.4 ± 11.3**	11.6 ± 15.3	105.1 ± 9.3**	0.84	0.00	0.56**	0.61**
C3	188.7 ± 24.7**	0.00	15.1 ± 6.4*	16.9 ± 8.9	46.8 ± 4.1**	0.92	0.00	0.46**	0.47**
C4	104.7 ± 15.7**	0.00	7.6 ± 7.1	15.7 ± 12.2	96.5 ± 8.5**	0.83	0.00	0.66**	0.66**
C5	226.7 ± 30.9**	0.00	16.2 ± 12.0	39.8 ± 17.6*	74.6 ± 6.6**	0.90	0.00	0.55**	0.56**
C6	229.4 ± 31.9**	0.00	17.8 ± 12.1	6.9 ± 15.7	53.0 ± 4.7**	0.91	0.00	0.59**	0.59**
C7	475.6 ± 197.9	108.6 ± 202.9	40.2 ± 30.2	67.9 ± 42.0	187.8 ± 16.6**	0.81	0.68	0.46**	0.46**
Mean	202.9 ± 48.6	22.6 ± 31.7	20.2 ± 11.6	22.7 ± 16.0	84.9 ± 7.5	0.85 [c]	0.47 [c]	0.55	0.54
b	37.2*	6.3	0.9	4.8					
				Selection index (%)					
C1	49.4 ± 23.9	72.0 ± 30.5*	18.3 ± 5.0**	0.00	114.4 ± 10.1**	0.45	1.71	-[a]	0.21*
C2	274.1 ± 96.6**	55.0 ± 99.7	65.1 ± 17.1**	0.00	368.2 ± 32.7**	0.71	0.63	0.40**	0.47**
C3	226.2 ± 32.9	0.00	31.4 ± 9.0	0.00	205.4 ± 18.1**	0.83	0.00	0.31**	0.34**
C4	25.3 ± 54.0	189.6 ± 76.8*	106.7 ± 23.5**	0.00	405.4 ± 35.8**	0.11	3.87	0.22**	0.21*
C5	62.6 ± 45.7	59.7 ± 55.4	62.1 ± 15.9**	0.00	311.4 ± 27.5**	0.38	1.38	−0.02	−0.07
C6	70.0 ± 45.6	0.00	44.1 ± 52.7	24.6 ± 11.4*	177.6 ± 15.6**	0.49	0.00	0.12	0.16
C7	123.4 ± 111.1	190.1 ± 142.5	27.1 ± 54.7	58.2 ± 94.7	768.0 ± 68.3**	0.34	1.76	0.03	0.03
Mean	118.7 ± 58.5	80.9 ± 57.9	50.7 ± 25.4	11.8 ± 15.2	335.8 ± 29.7	0.50[c]	1.17[c]	0.18	0.19
b	−3.6	13.4	7.8	8.0*					

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

[a] Not calculated, because BLUP values were not available from C0

[b] Denominator was zero

[c] Calculated from the variance components averaged across cycles

mating scheme the gametic contribution of the best selected FS families is doubled compared to the gametic contribution of the remaining selected FS families. Therefore, the pseudo-factorial mating scheme will increase the ultimate response over the maximum achievable for the random mating scheme commonly applied in recurrent selection (Cockerham and Burrows 1980). (2) Completion of only seven selection cycles. Long-term recurrent selection programs are expected to show the largest response during the initial cycles with a reduction in more advanced cycles (Gardner 1977). (3) Moderate genotype × location interactions. All three test locations used in our study are located in South Germany and have similar agro-ecological conditions. Crossa and Gardner (1989) emphasized that response per cycle is expected to be maximum when selection is made for adaptation to well-defined, homogeneous target environments. (4) Use of an F_2 population. In F_2 populations with allele frequencies $p = 0.5$ at all segregating loci, epistatic gene action could condition a greater and longer-term selection response than additive gene action alone (Jannink 2003).

In the experiments reported herein, the expected N_e was 32 (estimated after Cockerham and Burrows 1980) and the observed N_e was on average 27. The differences between the expected and observed N_e reflect the effects of selection, which reduce N_e below the value expected from drift. Only with small population sizes (< 25), effects of genetic drift are expected to be large relative to the effects of selection (Smith 1983; Helms et al. 1989). Drift would then affect not only the genetic variance components, but also the population mean, as a result of inbreeding depression. In our study, the average level of inbreeding after seven cycles of recurrent selection was too small to cause a significant inbreeding depression for grain yield.

Variance components

The estimates of σ^2_A for grain yield and grain moisture were nearly as large as the values reported for the U.S. Corn Belt dent maize F_2 populations (Hallauer and Miranda 1988; Wolf et al. 2000). Estimates agreed well with the large estimates of σ_{A}^2 of both traits when population C×D was compared with other European flint F_2 populations (Mihaljevic et al. 2004). Previous estimates of σ_{D}^2 and $\bar{d}$ for grain yield in dent maize (Robinson et al. 1949; Han and Hallauer 1989; Edwards and Lamkey 2002) suggest that $\bar{d}$ is generally in the partial to complete dominance range, which is in accordance with our results for flint maize. Estimates of σ_{D}^2 for grain moisture were smaller than those reported in the literature and five negative values occurred, which were interpreted as zero. Negative values for σ_{D}^2 are not unexpected and in reality are either zero or very small. By interpreting them as zero, the average of σ_{D}^2 and for grain moisture was slightly inflated in our study. Ratios of variance components and $\bar{d}$ for the selection index were similar to those for grain yield, because of the larger genetic variance of relative grain yield compared with relative grain moisture.

Estimates of $\bar{d}$ tend to be upwardly biased by linkage disequilibrium, i.e., pseudo-overdominance (Comstock and Robinson 1948). Coupling phase linkages cause an upward bias in the estimates of both σ_{A}^2 and σ_{D}^2, whereas repulsion phase linkages cause an upward bias of σ_{D}^2 estimates but a downward bias of σ_{A}^2 estimates. In F_2 populations, where linkage disequilibrium will be maximum, estimates of $\bar{d}$ decrease with random mating within F_2 generations (Hallauer and Miranda 1988). The relatively low estimates of σ_{D}^2 for grain yield and grain moisture observed in our study suggest that the three generations of chain crossing before initiation of selection reduced linkage disequilibrium in the F_2Syn3 population. In theory, selection is expected to generate new coupling phase linkage disequilibrium (Falconer and Mackay 1996) and, therefore, will reduce σ_{A}^2 by the Bulmer effect (Bulmer 1971). However, we observed no significant decrease in σ_{A}^2 in later cycles as expected from the low selection intensity and high N_{e} applied in our study (Table 2). In contrast, we even found a significant increase of σ_{A}^2 in grain moisture indicating a further reduction of repulsion phase linkages due to intermating during the selection procedure.

The estimates of σ_{A}^2 were generally lower than the estimates of σ_{A}^2 for each trait. The ratios of σ_{AL}^2: σ_{A}^2 and σ_{DL}^2: σ_{D}^2 were intermediate compared with the corresponding ratios in other studies (Han and Hallauer 1989; Wolf et al. 2000). The genotype × location interaction variance was smaller for grain moisture than for grain yield, which corresponds to the estimates in literature (Hallauer and Miranda 1988).

Trait correlations

In contrast to other studies (Walters et al. 1991; Schnicker and Lamkey 1993), we observed no stable correlations between grain yield and grain moisture across selection cycles. This was mainly attributable to the different climatic conditions in the various years of testing. Under the marginal growing conditions for maize in Germany, the sign and magnitude of the correlation between these traits depend heavily on the general maturity level of the germplasm at harvest (Utz et al. 1978). Hence, under favorable climatic conditions, e.g., from 1996 to 1998, both early- and late-maturing genotypes reached full maturity and the correlations were positive. However, under unfavorable conditions, which prevailed in 1999 and 2000, the late-maturing genotypes did not realize their full yield potential and, therefore, the correlations were negative.

Correlations between predicted and realized selection response

For all three traits, we observed a tighter correlation between predicted and realized response per cycle than other authors (Moll and Stuber 1971; Moll and Smith 1981; Crossa and Gardner 1989). This close agreement indicates that the number of test candidates ($N = 144$) and expected $N_{\mathrm{e}} = 32$ employed in our selection experiment were large enough so that the effects of drift and inbreeding did not override the effects of selection. Discrepancies between expected and realized selection response were small, and slightly higher when more remote coancestries were ignored in estimates of variance components. This may be attributable to a generally moderate precision of variance component estimates. Furthermore, ignoring genotype × location × year interactions, which are in maize generally larger than genotype × location interactions (Rojas and Sprague 1952), could lead to a minor overestimation of the selection response, due to upwardly biased estimates of σ_{A}^2 and h^2.

Use of BLUP in recurrent selection

It has been demonstrated that BLUP is useful for evaluating inbreds from different breeding populations (Bernardo 2002) and for predicting the performance of untested single-cross hybrids in maize (Bernardo 1994, 1996). We predicted the performance of individual FS families in C$n+1$ using the mean additive genetic BLUP of their parents in Cn. In our study, the additive genetic BLUP of each parent is a linear function of the phenotypic values from each environment of (1) its FS relatives (one family), (2) its paternal half-sib relatives (one family), (3) its paternal (ten families) and maternal simple cousin relatives (five families), and in advanced cycles (4) more distant relatives.

The low correlations between the performance of individual FS families and the mean additive genetic BLUP of their parents can be attributable to segregation for additive effects in the parental FS families and ignoring of dominance effects in the progeny FS families. With $h^2 = 1$ and no dominance effects, the correlation between the criteria reaches its maximum with an expectation of $1/\sqrt{2} = 0.71$, reflecting the effects of segregation of additive effects for the prediction. In our study, the correlations for grain moisture nearly reached this maximum, whereas dominance and other types of masking effects (e.g., genotype × location interactions, experimental error) reduced the prediction power of additive genetic BLUP for grain yield and selection index. Using additive genetic BLUP of the FS families in C*n*+1 instead of their phenotypic mean did not improve the correlations with the mean additive genetic BLUP of their parents in C*n* (data not shown), suggesting that dominance effects were not the major cause of the low correlations. Hence, we conclude that the precision of additive genetic BLUP in our study was fairly low due to the small number of related families with high coancestry coefficient f to a given FS family under the pseudo-factorial mating scheme employed. Increasing the number of closely related families should increase the precision of BLUP, but at the expense of a reduced N_e and all negative side effects related to it in recurrent selection.

Conclusions

The relatively high increase in grain yield combined with a decrease in grain moisture suggest that the F_2 source population and the modified recurrent FS selection using a pseudo-factorial mating scheme for recombination is an alternative recurrent selection scheme to other types of source material and intermating schemes normally used in recurrent selection. There was no evidence of a reduction in additive variance for grain yield and grain moisture, suggesting future response at or near current rates of progress. For a direct comparison with other recurrent selection methods, further research with a common base population would be necessary.

In our study, the REML procedure proved to be a robust method for estimating genetic variance components. In contrast to traditional methods, it has no special requirements on the mating scheme and accounts for the relationships among families in a breeding population. However, the variance component estimates are still associated with a high standard error, which are an obstacle in determining trends across the cycles. For reducing the estimation error, a larger number of test locations and larger population size N is recommended for future studies.

We found no advantage for using mean additive genetic BLUP of the parents instead of mean performance of parental FS families to predict progeny performance in our recurrent selection program. Nevertheless, further research (e.g., computer simulations) is necessary to investigate under which circumstances prediction based on BLUP is more powerful than prediction based on parental means. Additionally, considering the performance of the parents and more remote ancestors in C*n* for calculating the BLUP in C*n*+1, and not only the f values among the test candidates, could improve the prediction of FS family performance.

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Modified full-sib selection and best linear unbiased prediction of progeny performance in a European F_2 maize population

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Abstract

Four cycles of modified recurrent full-sib (FS) selection were conducted in an intermated F_2 population of European flint maize. The objectives of our study were to monitor trends across selection cycles in the estimates of population mean, inbreeding coefficients and variance components, and to investigate the usefulness of best linear unbiased prediction (BLUP) of progeny performance under the recurrent FS selection scheme applied. We used a selection rate of 25% for a selection index, based on grain yield and dry matter content. A pseudo-factorial mating scheme was used for recombination. In this scheme, the selected FS families were divided into an upper-ranking group of parents mated to the lower-ranking group. Variance components were estimated with restricted maximum likelihood (REML). Average grain yield increased 1.2 t/ha per cycle, average grain moisture decreased 20.1 g/kg per cycle, and the selection index relative to the F_2 check entries decreased 0.3% per cycle. For a more precise calculation of selection response, the four cycles should be tested together in multi-environmental trials. We observed a significant decrease in additive variance in the selection index, suggesting smaller future selection response. Predictions of FS family performance in Cn + 1 based on mean performance of parental FS families in Cn were of equal precision as those based on the mean additive genetic BLUP of their parents, and corresponding correlations were of moderate size for grain moisture and selection index.

Key words: *Zea mays* — additive genetic best linear unbiased prediction — pseudo-factorial mating scheme — recurrent selection — selection response — variance components

Improvement of breeding populations by applying recurrent selection (RS) provides a continuous increase in the frequency of favourable alleles while maintaining the genetic variance in the population (Hallauer 1985). Numerous intrapopulation RS schemes have been proposed to improve maize populations (for review, see Sprague and Eberhart 1977). Recurrent full-sib (FS) selection enables complete parental control, permits greater selection response, and has shorter cycle length (Weyhrich et al. 1998). Using an F_2 population as source population has the advantages that allele frequencies are known ($p = 0.5$ at all segregating loci) and the additive genetic variance is maximum at the beginning of the selection programme, irrespective of the level of dominance (Falconer and Mackay 1996).

New genetic variation for the next cycle of an RS programme is generated by recombination of selected genotypes. This is performed mostly by random mating, without recording pedigrees. An alternative approach by Cockerham and Burrows (1980) suggest to use from s selected genotypes the s_1 best genotypes as male parents and the remaining (s–s_1) genotypes as female parents. Although a higher long-term selection response is anticipated with this pseudo-factorial mating scheme, it has not been applied in practice.

Optimal estimation of variance components is essential to diagnose their trends over selection cycles of an RS program. The usual way of estimating variance components is by ANOVA methods (cf. Crossa and Gardner 1989, Moll 1991, Wolf et al. 2000) from classical diallel and factorial mating schemes. For complex pedigrees, however, mixed linear models and restricted maximum likelihood (REML) can be employed (Bernardo 1994). The REML-based analysis could also be used to estimate the best linear unbiased prediction (BLUP) of single FS families. Application of BLUP in RS programs has not yet been studied.

As a part of a maize-breeding project, we started a long-term recurrent FS selection programme within an F_2 population also employed in mapping of quantitative trait loci (QTL) for *per se* and testcross performance (Mihaljevic et al. 2004, 2005). Following the suggestion of Cockerham and Burrows (1980), we applied a pseudo-factorial mating scheme for recombination of selected candidates and recorded pedigrees among all FS families across all selection cycles. Four cycles of FS selection were completed to determine the changes in the population structure at the phenotype and individual marker loci levels.

The study was designed to monitor trends across selection cycles in the estimates of the population mean, inbreeding coefficients and variance components, and to investigate the usefulness of mean additive genetic BLUP of parents for predicting progeny performance under the recurrent FS selection scheme applied.

Materials and Methods

Plant materials: Two early maturing homozygous European flint lines KW1265 and D146 of maize, *Zea mays* L., referred to as A and B consistent with the terminology of Mihaljevic et al. (2004), were used as parents to produce the F_2 generation. Line A is a private line developed by KWS (Kleinwanzlebener Saatzucht AG, Einbeck, Germany). Line B is a public line bred by Dr W. G. Pollmer at the University of Hohenheim (Stuttgart, Germany). Both lines have excellent combining ability for grain yield, good standability and are similar in maturity (Schön et al. 1994). The F_2Syn3 generation was derived from the F_2 generation by three generations of chain crossing using 240 F_2 plants, i.e. crossings 1 × 2, 2 × 3, … and 240 × 1.

Selection procedure: In 1994, the F_2Syn3 generation was grown and pairs of S_0 plants were crossed to produce 120 FS families. In the following year, the 120 FS families were tested in field trials at three locations, and six S_0 plants from each FS family were selfed in the breeding nursery. The 36 FS families with the highest selection index (see below) were chosen and divided into two sets, consisting of even and odd numbered families. The six S_1 progeny of the 18 FS families in each set were intermated according to a pseudo-factorial mating scheme (Fig. 1). The selected FS families were divided into an upper-ranking group of parents mated to the lower-ranking group with unequal gametic contributions to the next generation, according to the suggestion by Cockerham and Burrows (1980). Consequently, the six S_1 progeny of the FS families with the highest selection index scores in each set were mated to S_1 progeny of the remaining 12 FS families in the following year, using bulked pollen of 15 S_1 plants from each progeny. The resulting 144 FS families were tested in an experiment similar to the trial in the previous cycle and 36 families were again selected based on the selection index. Likewise, the production of six S_1 progeny per FS family and recombination of the selected 36 top FS families by two sets of pseudo-factorial mating schemes were performed as described above for the first cycle. Following this scheme, four cycles of recurrent FS selection were conducted between 1994 and 2002. The field trials for each cycle were conducted at three locations in south Germany (Eckartsweier, Bad Krozingen, Ladenburg). In 2000 [cycle 3 (C3)], only two locations could be harvested because of severe hail damage at Ladenburg. The experimental design at each location was an α-lattice (10×15) with three replications. Thirty reciprocal crosses in C0 and six F_2 check entries in C1 to C4 were used to complement the lattice design. Each plot consisted of one row, 4.75 m long and spaced 0.75 m between rows. Plots were thinned to 85 000 plants/ha. All experiments were machine-planted and harvested as grain trials with a combine. Data were recorded for grain yield in t/ha adjusted to 84.5% dry matter content, and grain moisture in g/kg. For calculating the selection index, (i) grain yield and dry matter content were expressed in percentage of mean of the F_2 check entries and (ii) relative values received a weight of 1 for grain yield and 2 for dry matter content [$b' = (1, 2)$].

Statistical analyses

Ordinary lattice analyses of variance for grain yield and grain moisture were performed for each experiment and location using software PLABSTAT (Utz 2001). Adjusted entry mean values were then used to compute combined ANOVA across locations (Cochran and Cox 1957). Population mean values across locations, relative to the F_2 check entries, were calculated for each cycle to determine the realized response to selection in percentage. Phenotypic and genotypic correlations between grain yield and grain moisture were calculated according to established methods (Mode and Robinson 1959).

Based on the known pedigree records, the inbreeding coefficient F of each FS family and the coancestry coefficient f among FS families were calculated according to the rules described by Falconer and Mackay (1996), using procedure PROC INBREED in SAS (SAS Institute 2004) and setting $F = 0$ and $f = 0$ in the F_2Syn3 generation.

M	F 13	15	17	19	· · ·	33	35
1	1.1 × 13.1	1.1 × 15.1	1.2 × 17.1	1.2 × 19.1	· · ·	1.6 × 33.1	1.6 × 35.1
3	3.1 × 13.2	3.1 × 15.2	3.2 × 17.2	3.2 × 19.2	· · ·	3.6 × 33.2	3.6 × 35.2
5	5.1 × 13.3	5.1 × 15.3	5.2 × 17.3	5.2 × 19.3	· · ·	5.6 × 33.3	5.6 × 35.3
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
11	11.1 × 13.6	11.1 × 15.6	11.2 × 17.6	11.2 × 19.6	· · ·	11.6 × 33.6	11.6 × 35.6

Fig. 1: Pseudo-factorial mating scheme for intermating the odd-numbered full-sib (FS) families ranked according to the selection index. M refers to the male parent, F to the female parent, and is the cross between the rth S_1 progeny of the ith ranking full-sib family with the qth S_1 progeny of the jth ranking full-sib family. The same scheme was also applied to the set with even numbers $i{\cdot}r \times j{\cdot}q$

For each selection cycle from C1 to C4, additive and dominance variances were estimated based on adjusted entry mean values and effective error mean squares from the individual lattice analyses by REML, using PROC MIXED in SAS (SAS Institute 2004). The linear model was

$$y = \mathbf{X}\beta + \mathbf{Z}_1\alpha + \mathbf{Z}_2\delta + \mathbf{Z}_3\alpha l + \mathbf{Z}_4\delta l + \varepsilon,$$

where y is the $n \times 1$ vector of observed phenotypic values; β is the $b \times 1$ vector of fixed effects (location); α is the $a \times 1$ vector of additive effects; δ is the $d \times 1$ vector of dominance effects; αl is the $al \times 1$ vector of additive × location interaction effects; δl is the $dl \times 1$ vector of dominance × location interaction effects; ε is the $n \times 1$ vector of errors and $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, $\mathbf{Z}_3$ and $\mathbf{Z}_4$ are design matrices of 1s and 0s relating y to β, α, δ, αl and δl respectively. The random factors have the following variance–covariance matrix:

$$\mathrm{Var}\begin{bmatrix} \alpha \\ \delta \\ \alpha l \\ \delta l \\ \varepsilon \end{bmatrix} = \begin{bmatrix} A\sigma_A^2 & 0 & 0 & 0 & 0 \\ 0 & D\sigma_D^2 & 0 & 0 & 0 \\ 0 & 0 & (I \otimes A)\sigma_{AL}^2 & 0 & 0 \\ 0 & 0 & 0 & (I \otimes D)\sigma_{DL}^2 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix},$$

where $\mathbf{A}$ is a $n \times n$ matrix with elements equal to t; $\mathbf{D}$ is a $n \times n$ matrix with elements equal to u; $\mathbf{I}$ are identity matrices of appropriate dimensions; $\otimes$ is the Kronecker product; σ_A^2 is the additive, σ_D^2 is the dominance, σ_{AL}^2 is the additive × location, σ_{DL}^2 is the dominance × location and σ_e^2 is the error variance. Values for t and u between FS family x with parents a and b and FS family y with parents c and d were obtained as $t = 2f_{xy}$ and $u = f_{ac}f_{bd} + f_{ad}f_{bc}$ respectively (Falconer and Mackay 1996). Variance components of advanced cycles were calculated with the coancestry coefficients expected from the pseudo-factorial mating scheme (Fig. 1) by (i) ignoring or (ii) considering additional coancestries from previous generations. In our model, REML only warrants that the total genetic variance is positive and, therefore, negative values are possible for individual variance components. For negative values, we set these variance components equal to zero and re-estimated the other variance components from the reduced model (Searle 1971). BLUP values of random effects were obtained with the SOLUTION option of SAS procedure PROC MIXED (SAS Institute 2004), which employs the mixed model equations of Henderson (1975).

Heritability was calculated as:

$$h^2 = \frac{\sigma_A^2/2}{(\sigma_A^2 + \sigma_{AL}^2/l)/2 + (\sigma_D^2 + \sigma_{DL}^2/l)/4 + \sigma_e^2/rl},$$

where l and r correspond to the number of locations and replicates respectively. Estimates of σ_A^2 and σ_D^2 were used to estimate the degree of dominance as $\bar{d} = (2\sigma_D^2/\sigma_A^2)^{1/2}$.

The performance of individual FS families in Cn + 1 was correlated well with the mean BLUP of their parents in Cn. Likewise, the performance of individual FS families in Cn + 1 was correlated with the mean performance of the respective parental FS families in Cn.

Multiple regression analyses weighted by inverse standard errors were used to investigate changes in population mean values and variance components over selection cycles. All regression and correlation analyses were performed with the statistical software R (R Development Core Team 2004).

Results

The average inbreeding coefficients across all 144 FS families increased from 0.003 in C1 to 0.060 in C4 (Table 1). Likewise, the average coancestry coefficients increased from 0.019 in C1 to 0.063 in C4. We found no significant difference in the mean of F values between the 36 selected FS families and the remaining 108 FS families for each cycle. The effective population size (N_e) ranged between 17 in C1 and 271 in C2.

Table 1: Average inbreeding coefficient and coancestry coefficient of all 144 full-sib families (F_{all} and f_{all}) and the 36 selected full-sib families (F_{sel} and f_{sel}), effective population size (N_e), and phenotypic (r_{p}) and genotypic correlations (r_{g}) between grain yield and grain moisture in each selection cycle

Cycle	F_{all}	F_{sel}	f_{all}	f_{sel}	N_e	r_{p}	r_{g}
C1	0.003	0.003	0.019	0.026	17	0.02	0.07
C2	0.033	0.024	0.039	0.038	271	−0.20*	−0.22**
C3	0.035	0.036	0.049	0.053	20	0.09	0.06
C4	0.060	0.068	0.063	0.062	50	0.18*	0.25**

*, **Phenotypic correlation was significant at P = 0.05 and P = 0.01, respectively, and the genotypic correlation exceeded once and twice its standard error, respectively.

Phenotypic correlations among grain yield and grain moisture varied widely among cycles, and ranged from –0.20 in C2 to 0.18 in C4 (Table 1). Genotypic correlations were similar to phenotypic correlations, and ranged from –0.22 in C2 to 0.25 in C4.

Grain yield varied between 5.91 t/ha in C1 and 9.07 t/ha in C3, corresponding to an average increase of 1.15 t/ha per cycle (Table 2). Grain moisture ranged from 350.4 g/kg in C1 to 267.6 g/kg in C3, and decreased 20.1 g/kg per cycle. Mean grain yield relative to the F_2 checks varied from 120.2% in C1 to 129.1% in C2, and mean grain moisture relative to the F_2 checks ranged from 103.0% in C2 to 101.4% in C3. Selection index varied between 315.3 in C1 and 323.2 in C2. The weighted linear and quadratic regression of observed and relative performance on selection cycles was not significant for all three traits.

Estimates of σ^2_A were significant ($P < 0.05$) for grain yield in C1, C2 and C3, and for grain moisture and selection index in all cycles (Table 3). Estimates of σ^2_D were negative in most selection cycles and not significant for each trait. Estimates of σ^2_{AL} were significant ($P < 0.05$) in C1, C3 and C4 for grain moisture, and in C1 and C2 for selection index. Significant ($P < 0.05$) estimates of σ^2_{DL} were observed in C1, C2 and C4 for grain moisture, and in all cycles for the selection index. Linear regression of variance component estimates on selection cycles was not significant, except for an increase in σ^2_A in grain moisture and a decrease in σ^2_A and σ^2_{DL} in selection index. Estimates of h^2 ranged from 0.32 in C4 to 0.57 in C2 for grain yield, from 0.84 in C1 to 0.93 in C4 for grain moisture, and from 0.62 in C1 to 0.85 in C4 for selection index. Estimates of $\bar{d}$ calculated from the mean variance components were 1.03 for grain yield, 0.00 for grain moisture and 0.68 for the selection index.

Correlations between the performance of all 144 FS families in Cn + 1 and the mean additive genetic BLUP of their parents in Cn were significant in C2 for grain yield, and in C2, C3 and C4 for grain moisture and selection index (Table 4). For all traits, these correlations were equal to the correlations between the performance of the FS families in Cn + 1 and the mean performance of their parental FS families in Cn, and smaller than the correlations between the additive genetic BLUP in Cn + 1 and the mean additive genetic BLUP of their parents in Cn.

Discussion

Previous studies have shown that recurrent FS selection can be successfully utilized for the improvement of maize populations. Relatively high selection response for grain yield, the most important trait in maize breeding, was reported in recurrent FS selection programmes (Zorilla and Crane 1982, Singh et al. 1986, Pandey et al. 1987, Moll 1991). In our study, the selection response relative to the F_2 check entries was only 0.1% and was maintained at 120% from C1 to C4. The increase from C0 to C1 and the same response in later cycles is because of experimental errors in the check entries and calculation errors of the relative performance, particularly in early cycles.

Absolute response over the years for grain yield (1.15 t/ha/cycle) and grain moisture (−20.10 g/kg/cycle) was greater than in other studies on recurrent FS selection (Stromberg and Compton 1989, Landi and Frascaroli 1993, Weyhrich et al. 1998). The completion of only four selection cycles and the climatic conditions in testing years may have contributed to the comparatively greater selection response per cycle in our study. Long-term RS programmes are expected to show the largest response during the initial cycles with a reduction in more advanced cycles (Gardner 1977). However, comparison among selection cycles was not possible because of erroneous estimates of relative performance. When using the absolute performance, variable climatic conditions in the testing years could have caused a considerable bias of the selection response. For a precise calculation of selection response, the four cycles should be re-evaluated together in multi-environmental trials. More detailed information about the relative increase in performance would be possible, when an F_2 source population with a pseudo-factorial mating scheme for

Table 2: Mean performance (±SE) of grain yield, grain moisture and selection index, b is the coefficient of linear and quadratic regression, and R^2 is the coefficient of determination in the linear regression

	Grain yield		Grain moisture		
Cycle	t/ha	% of F_2	g/kg	% of F_2	Selection index (%)
C1	5.91 ± 0.15	120.2 ± 2.4	350.4 ± 23.8	102.4 ± 0.6	315.3 ± 2.3
C2	6.02 ± 0.16	129.1 ± 4.3	311.3 ± 3.2	103.0 ± 1.0	323.2 ± 4.7
C3	9.07 ± 0.18	124.2 ± 2.6	267.6 ± 4.6	101.4 ± 1.7	321.5 ± 4.9
C4	8.61 ± 0.14	123.1 ± 2.2	311.8 ± 5.3	102.8 ± 1.7	317.6 ± 4.9
Regression on cycle					
b (linear)	1.15	0.10	−20.10	0.00	−0.31
b (quadratic)	−0.17	−2.84	21.40	0.40	−2.82
R^2	0.73	0.00	0.63	0.00	0.01

Table 3: Restricted maximum likelihood (REML) estimates of variance components (± SE), their mean across selection cycles, the coefficient (b) of the linear regression across selection cycles, heritability (h^2) and degree of dominance ($\bar{d}$)

Cycle	σ^2_A ± SE	σ^2_D ± SE	σ^2_{AL} ± SE	σ^2_{DL} ± SE	σ^2_e ± SE	h^2	$\bar{d}$
Grain yield (t/ha)							
C1	0.38 ± 0.16*	0.35 ± 0.20	0.02 ± 0.03	0.00	1.21 ± 0.11**	0.50	1.36
C2	0.25 ± 0.05**	0.00	0.01 ± 0.02	0.00	1.12 ± 0.10**	0.57	0.00
C3	0.27 ± 0.13*	0.11 ± 0.16	0.00	0.00	1.14 ± 0.07**	0.44	0.89
C4	0.12 ± 0.07	0.08 ± 0.10	0.00	0.00	1.29 ± 0.11**	0.32	1.18
Mean	0.26 ± 0.10	0.14 ± 0.12	0.01 ± 0.01	0.00	1.19 ± 0.10	0.47[1]	1.03[1]
b	−0.08	−0.07	−0.01	0.00			
Grain moisture (g/kg)							
C1	92.5 ± 13.6**	0.0	35.9 ± 9.0**	23.5 ± 10.0*	11.4 ± 1.0**	0.84	0.00
C2	111.8 ± 16.7**	0.0	11.9 ± 7.6	70.0 ± 12.4**	15.8 ± 1.4**	0.86	0.00
C3	167.2 ± 24.0**	0.0	30.6 ± 13.1*	29.1 ± 15.4	13.7 ± 0.8**	0.87	0.00
C4	183.9 ± 24.4**	0.0	23.1 ± 8.4**	29.0 ± 10.3**	13.3 ± 1.2**	0.93	0.00
Mean	138.8 ± 19.7	0.0	25.4 ± 9.5	37.9 ± 12.1	13.5 ± 1.1	0.88[1]	0.00[1]
b	32.9*	0.0	−2.0	−2.4			
Selection index (%)							
C1	207.5 ± 82.5*	152.1 ± 95.3	46.3 ± 20.8*	184.1 ± 32.9**	30.9 ± 2.7**	0.62	1.21
C2	198.9 ± 31.9**	0.0	70.2 ± 24.1**	119.0 ± 31.3**	34.8 ± 3.1**	0.80	0.00
C3	174.5 ± 64.3**	13.7 ± 65.2	45.7 ± 23.7	76.5 ± 30.4*	25.7 ± 1.5**	0.76	0.40
C4	140.3 ± 21.9**	0.0	31.1 ± 13.5	59.5 ± 17.6**	26.7 ± 2.4**	0.85	0.00
Mean	180.3 ± 49.9	41.5 ± 40.1	48.3 ± 20.5	109.8 ± 28.1	29.5 ± 2.4	0.74[1]	0.68[1]
b	−22.6*	−44.3	−7.0	−41.7*			

*, **Significant at $P = 0.05$ and $P = 0.01$, respectively.

[1] Calculated from the variance components averaged across selection cycles.

Table 4: Correlation (r_1) between FS family performance in Cn + 1 and mean BLUP of their parents in Cn, correlation (r_2) between FS family performance in Cn + 1 and mean performance of their parental FS families in Cn, and correlation (r_3) between BLUP in Cn + 1 and mean BLUP of parents in Cn for grain yield, grain moisture and selection index for each cycle of recurrent FS selection

Cycle	r_1	r_2	r_3
Grain yield (t/ha)			
C1	–[1]	0.05	–[1]
C2	0.48**	0.56**	0.59**
C3	0.13	0.10	0.18*
C4	0.11	0.13	0.17*
Mean[2]	0.24	0.26	0.32
Grain moisture (g/kg)			
C1	–[1]	0.54**	–[1]
C2	0.59**	0.59**	0.63**
C3	0.41**	0.41**	0.42**
C4	0.51**	0.51**	0.52**
Mean[2]	0.50	0.50	0.52
Selection index (%)			
C1	–[1]	−0.03	–[1]
C2	0.65**	0.66**	0.69**
C3	0.38**	0.38**	0.42**
C4	0.41**	0.42**	0.43**
Mean[2]	0.48	0.48	0.51

*, **Significant at $P = 0.05$ and $P = 0.01$, respectively.

[1] Not calculated, because BLUP values were not available from C0.

[2] Mean values from C2, C3 and C4.

BLUP, best linear unbiased prediction; FS, full-sib.

recombination is applied. For a direct comparison with other RS methods, further research with a common base population would be necessary.

In our study, the expected N_e was 32 (estimated after Cockerham and Burrows 1980). In C2, the observed N_e was nearly 10 times as large. The huge difference between the expected and observed N_e is because we tried to avoid closely related entries in early selection cycles. Therefore, N_e increased beyond the expected value. In contrast to C2, the avoidance of closely related parents was not successful in C1 and C3. The small N_e in the two cycles suggest that the effects of genetic drift are expected to be large relative to the effects of selection. Drift would then affect not only the genetic variance components, but also the population mean, as a result of inbreeding depression. The average level of inbreeding, however, was even after four cycles of RS too small ($F = 0.06$) to result in a noticeable inbreeding depression.

We observed no stable correlations between grain yield and grain moisture across selection cycles, which could be mainly attributed to the different climatic conditions in testing years. Under the marginal growing conditions for maize in Germany, the sign and magnitude of the correlation between both traits depend on the general maturity level of the germplasm at harvest (Utz et al. 1978). The increase in the correlations from C2 to C4 suggests amelioration in growing conditions and supports the assumption of a positive bias in the absolute selection response.

The estimates of σ^2_A for grain yield and grain moisture were smaller than that found for U.S. Corn Belt dent maize F_2 populations (Hallauer and Miranda 1988, Wolf et al. 2000). The estimates are similar to those reported by Mihaljevic et al. (2004), who observed relatively small estimates of σ^2_A for population A × B compared with other European flint F_2 populations. Over 50% of the estimates of σ^2_D were negative and interpreted as zero. By definition, a variance component is always positive. Nevertheless, negative values for σ^2_D are not unexpected and in reality are either zero or very small. In F_2 populations, estimates of the degree of dominance of genes affecting quantitative traits have nearly always been > 1, corresponding to overdominance (Comstock and Robinson 1948, Edwards and Lamkey 2002). Random mating of F_2 populations to reduce linkage disequilibrium, however, has reduced the estimate of the degree of dominance to approximately 1 or less, corresponding to partial or complete dominance (Moll et al. 1964, Han and Hallauer 1989). The comparatively low degree of dominance for all traits in our study suggests that the three generations of intermating reduced linkage disequilibrium in the F_2Syn3 generation.

Linkage disequilibrium is increased by finite population size and selection (Hill and Robertson 1968) and, therefore, σ_A^2 will be reduced by the Bulmer effect (Bulmer 1971). Although a low selection intensity and high N_e were applied in our study, we observed a decrease in σ_A^2 for grain yield and selection index. Our study cannot provide any proof of existence of the Bulmer effect, because the variance component estimates are associated with large standard errors, which are an obstacle in uncovering trends across the cycles. For reducing the standard errors, larger number of test locations, larger population size (N), and more selection cycles are recommended for future studies.

The BLUP approach has been established in the evaluation of inbreds from different breeding populations (Bernardo 2002) and in the prediction of the performance of untested single-cross hybrids in maize (Bernardo 1994, 1996). We used the mean additive genetic BLUP of parents in Cn to predict the performance (r_1) and the additive genetic BLUP (r_3) of individual FS families in Cn + 1. Furthermore, the performance of individual FS families in Cn + 1 was predicted with the mean performance of parents in Cn (r_2). We calculated the additive genetic BLUP of each FS family as a linear function of the phenotypic values from each environment of: (i) its FS relatives (one family), (ii) its paternal half-sib relatives (one family), (iii) its paternal (10 families) and maternal simple cousin relatives (five families), and in advanced cycles (iv) more distant relatives.

The magnitude of the three correlations is restricted by the effects of segregation, and has a maximum of $1/\sqrt{2} = 0.71$ with $h^2 = 1$ and no dominance effects. We observed correlations close to this maximum for grain moisture and selection index, whereas significant dominance variances and low heritabilities reduced the prediction power of additive genetic BLUP for grain yield. The small differences between r_1 and r_3 suggest that excluding dominance effects results only in a small increase in the prediction power of additive genetic BLUP. We conclude that the population size N and the number of closely related families in our study was too small for an exact estimation of dominance effects. Therefore, there was no advantage for using mean additive genetic BLUP of the parents instead of mean performance of parental FS families to predict progeny performance in our RS programme. Nevertheless, slightly higher values of r_3 compared with r_2 show that prediction based on BLUP could be more powerful than prediction based on parental mean values. Further research is necessary to determine if selection based on additive genetic BLUP would result in a higher selection response than selection based on mean performance.

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ORIGINAL PAPER

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 reevaluated. 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, $F_2 = F_2$Syn0, 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_2Syn$t$ (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_2Syn3 = -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_2Syn$t$	A0 + 2D0
$Cn \times F_1$	A0 + 2D0 + nAL
Cn-self	$\mathrm{A0} + \mathrm{D0}(1-F_n) + 2n\mathrm{AL}$ $+\frac{1}{2}(2n^2 - n^2F_n)\mathrm{DQ}$
$Cn \times Cm$	$\mathrm{A0} + 2\mathrm{D0}(1-F_n) + (n+m)\mathrm{AL}$ $+(2nm - -n2Fn)DQ$
$Cn \times$ T	T0 + nAL + nTL

[a] $t = 0,1,2,3$; $n < m = 0, 1, \ldots, 4$ and $0, 1, \ldots, 7$ 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_2Syn3

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_2Syn$t$ populations and therefore was excluded in our model. Estimates of A0, D0, AL, DQ, T0, and TL were obtained by weighted least squares analysis ($\beta = (\mathbf{X}'\mathbf{W}^{-1}\mathbf{X})^{-1}\mathbf{X}'\mathbf{W}^{-1}\mathbf{y}$) 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 ($(\mathbf{X}'\mathbf{W}^{-1}\mathbf{X})^{-1}$). Estimates of relative selection response ($\Delta G\%$) were calculated as (2AL)/(A0 + 2D0) × 100 and estimates of relative testcross response (ΔG_{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 significant ($P < 0.05$) 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 (ΔG%) for grain yield was 14.07% for population A × B and 8.28% for population C × D (Table 3). Larger ΔG% values in population A × B were also observed for selection index and days to silking, whereas ΔG% 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 ΔG% 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_2Syn3 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_∞ 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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Short Communication

An extension of the Smith model for quantitative genetic analysis of selection response under recurrent selection

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With 2 tables

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Abstract

Selection and random genetic drift are the main forces affecting selection response in recurrent selection (RS) programmes. The correct assessment of both forces allows a better comparison of the efficiency of different RS schemes. The objective of this study was to extend the population diallel analysis proposed by Hammond and Gardner in 1974 and the model proposed by Smith in 1979 with full consideration of inbreeding depression due to random genetic drift. The effect of random genetic drift is expected to be large, particularly in studies with many selection cycles and/or high rates of inbreeding. Therefore, the extension of the population diallel allows a better assessment of the selection response in RS programmes.

Key words: diallel analysis — random genetic drift — recurrent selection — selection response

Numerous studies have evaluated the progress from recurrent selection (RS) programmes and compared the efficiency of different RS schemes. However, it is important to separate effects due to selection from those due to random genetic drift. Based on the quantitative genetic model of Gardner and Eberhart (1966), Hammond and Gardner (1974) devised a model for the analysis of the diallel cross of a parent variety and selection cycles generated from it. The model includes different kinds of gene effects reflecting changes in allele frequencies due to selection, and it separates linear from nonlinear effects contributing to the selection response under the assumption 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 size, but assuming that nonlinear effects in the model proposed by Hammond and Gardner (1974) were unimportant.

The objectives of this study were to extend the population diallel analysis (Hammond and Gardner 1974, Smith 1979) with full consideration of inbreeding depression due to random genetic drift.

Genotype frequencies under RS: Consider a locus k, where A_k represents the favourable allele and a_k the unfavourable allele. Let ${}_np_k$ and ${}_nq_k$ be the corresponding gene frequencies of these alleles in cycle Cn, and r_k be the frequency of A_k in the tester T. The standard quantitative genetic model (Falconer and Mackay 1996) was employed, where μ denotes the mean of the two homozygotes, a_k is half the difference in homozygotes, and d_k is the departure of the heterozygote from μ due to dominance. For a diploid base population with two alleles per locus and no epistasis, the genotype frequencies of the population and population crosses are presented in Table 1.

Taking into consideration selection and random genetic drift, the gene frequencies of the favourable allele in cycle Cn can be expressed as ${}_np_k = {}_0p_k + {}_n\Delta p_k + {}_n\delta p_k$, where ${}_0p_k$ is the frequency of A_k in the source population, ${}_n\Delta p_k$ is the total change in allele frequency from cycle C0 to Cn due to selection, and ${}_n\delta p_k$ is the total change in allele frequency due to random genetic drift over these selection cycles. Following Hammond and Gardner (1974) and Smith (1979), ${}_n\Delta p_k$ is equal to $n\Delta p_k$, assuming a constant change in gene frequencies Δp_k over all n selection cycles.

Gene frequency changes because of random genetic drift are undirectional. Therefore, $E({}_n\delta p_k) = 0$ (Crow and Kimura 1970). In the absence of selection, $E(({}_n\delta p_k)^2) = {}_0p_k\,{}_0q_k\,F_n$, where F_n is the inbreeding coefficient due to random genetic drift (Crow and Kimura 1970). In the presence of selection, the gene frequency changes over selection cycles and therefore the following approximation is suggested:

$$E(({}_n\delta p_k)^2) \approx \Big(\frac{{}_0p_k\,{}_0q_k + {}_np_k\,{}_nq_k}{2}\Big)F_n.$$

To separate the influence of additive (a_k) and dominance (d_k) effects during recurrent selection the differences between the frequency of homozygous genotypes (${}_nP_k - {}_nQ_k$) and the frequency of heterozygous genotypes (${}_nH_k$) in the different cycles and crosses have to be determined. Thus, the genotype frequencies of the different populations and their expected values, denoted by E, can be expressed for any $n = 0,1,\ldots$ and $m \geq n$ as follows:

Cn

$$\begin{aligned}
{}_nP_k - {}_nQ_k &= {}_np_k - {}_nq_k = 2\,{}_np_k - 1 = (2\,{}_0p_k - 1) + 2\,{}_n\Delta p_k + 2\,{}_n\delta p_k,\\
E({}_nP_k - {}_nQ_k) &= (2\,{}_0p_k - 1) + 2n\Delta p_k.\\
{}_nH_k &= 2({}_0p_k + {}_n\Delta p_k + {}_n\delta p_k)({}_0q_k - {}_n\Delta p_k - {}_n\delta p_k)\\
E({}_nH_k) &\approx 2\,{}_0p_k\,{}_0q_k + 2n\Delta p_k(1 - 2\,{}_0p_k) - 2n^2(\Delta p_k)\\
&\quad - ({}_0p_k\,{}_0q_k + {}_np_k\,{}_nq_k)F_n.
\end{aligned}$$

Cn × Cm

$$\begin{aligned}
{}_{n\times m}P_k - {}_{n\times m}Q_k &= {}_np_k\,{}_mp_k - {}_nq_k\,{}_mq_k\\
&= {}_np_k({}_np_k + {}_{m-n}\Delta p_k + {}_{m-n}\delta p_k)\\
&\quad - {}_nq_k({}_nq_k - {}_{m-n}\Delta p_k - {}_{m-n}\delta p_k)\\
&= {}_np_k - {}_nq_k + {}_{m-n}\Delta p_k + {}_{m-n}\delta p_k,
\end{aligned}$$

$$
\begin{aligned}
E({}_{n\times m}P_k - {}_{n\times m}Q_k) &= {}_0p_k - {}_0q_k + (n+m)\Delta p_k.\\
{}_{n\times m}H_k &= {}_np_k\,{}_mq_k + {}_mp_k\,{}_nq_k\\
&= 2{}_np_k{}_nq_k + ({}_{m-n}\Delta p_k + {}_{m-n}\delta p_k)({}_nq_k - {}_np_k)\\
&= {}_nH_k + ({}_{m-n}\Delta p_k + {}_{m-n}\delta p_k)(1 - 2{}_n\Delta p_k)\\
&= {}_nH_k + ({}_{m-n}\Delta p_k + {}_{m-n}\delta p_k)\\
&\quad (1 - 2{}_0p_k - 2{}_n\Delta p_k - 2{}_n\delta p_k),\\
E({}_{n\times m}H_k) &= E({}_nH_k) + (m-n)\Delta p_k(1 - 2{}_0p_k - 2n\Delta p_k)
\end{aligned}
$$

C$n \times T$

$$
\begin{aligned}
{}_{n\times \mathrm{T}}P_k - {}_{n\times T}Q_k &= {}_0p_k + r_k - 1 + {}_n\Delta p_k + {}_n\delta p_k,\\
E({}_{n\times T}P_k - {}_{n\times T}Q_k) &= {}_0p_k + r_k - 1 + n\Delta p_k.\\
{}_{n\times \mathrm{T}}H_k &= r_k + (1-2r_k){}_np_k,\\
E({}_{n\times \mathrm{T}}H_k) &= r_k + (1-2r_k){}_0p_k + (1-2r_k)n\Delta p_k.
\end{aligned}
$$

After one generation of selfing, the expectation of heterozygotes (E(H_k)) in the different populations has to be divided by two.

Quantitative genetic parameters: The following parameters need to be defined (Hammond and Gardner 1974, Smith 1979):

$$\mathrm{A0} = \mu + \sum_k ({}_0p_k - {}_0q_k)a_k$$

= mean and contribution of additive effects in the initial population (cycle C0);

$$\mathrm{D0} = \sum_k {}_0p_k\,{}_0q_k\,d_k$$

= contribution of dominance effects in cycle C0;

$$\mathrm{AL} = \sum_k \Delta p_k\,a_k$$

= linear changes in the population mean per selection cycle due to additive effects and changes in gene frequencies resulting from selection;

$$\mathrm{DL} = \sum_k \Delta p_k(1 - 2\,{}_0p_k)d_k$$

= linear changes in the population mean per selection cycle due to dominance effects and linear changes in gene frequencies resulting from selection;

$$\mathrm{DQ} = \sum_k (\Delta p_k)^2 d_k$$

= quadratic changes in the population mean per selection cycle due to dominance effects and quadratic changes in genotype frequencies of heterozygotes resulting from selection;

$$\mathrm{T0} = \mu + \sum_k ({}_0p_k + r_k - 1)a_k + \sum_k (r_k\,{}_0p_k(1 - 2r_k))d_k$$

= mean and contribution of additive and dominance effects in a test cross between cycle C0 and the tester;

$$\mathrm{TL} = \sum_k \Delta p_k(1 - 2r_k)d_k$$

= linear changes in the testcross population mean per selection cycle due to dominance effects.

These parameters are used in several studies to compare the efficiency of different recurrent selection schemes.

Population means expressed with quantitative genetic parameters: For any population $\prod$,

$$E(\Pi)\mu + \sum_k E(P_k - Q_k)a_k + \sum_k E(H_k)d_k.$$

Inserting the above values for the different populations yields genetic expectations which can be expressed by the quantitative genetic parameters given in Table 2.

Application example: The extension of the model was used to assess the impact of selection and random genetic drift to the selection response in two European flint maize populations under modified recurrent full-sib selection (Flachenecker et al. 2006). In this study only small differences between the original model of Smith and the modified model were found. This was ascribed to the small number of selection cycles and the high effective population size, which minimize the effects of random genetic drift.

Conclusions

In the case of an infinite effective population size ($N_e = \infty$), the genetic expectation of different populations reduce to formulae given by Hammond and Gardner (1974). In his paper, Smith (1979) ignored the parameter DQ and disregarded the effects

Table 1: Genotype frequencies for biallelic loci in cycles C0 and Cn, and crosses Cn × Cm[1] and Cn × *Tester* (*T*)

			Genotype frequencies			
Genotype	Genotypic value	General	C0	Cn	Cn × Cm	Cn × T
A_kA_k	$\mu + a_k$	P_k	${}_0P_k = ({}_0p_k)^2$	${}_nP_k = ({}_np_k)^2$	${}_{n\times m}P_k = {}_np_k\,{}_mp_k$	${}_{n\times \mathrm{T}}P_k = {}_np_k\,r_k$
A_ka_k	$\mu + d_k$	H_k	${}_0H_k = 2\,{}_0p_k\,{}_0q_k$	${}_nH_k = 2\,{}_np_k\,{}_nq_k$	${}_{n\times m}H_k = {}_np_k\,{}_mq_k + {}_mp_k\,{}_nq_k$	${}_{n\times \mathrm{T}}H_k = {}_np_k(1 - r_k) + r_k\,{}_nq_k$
a_ka_k	$\mu - a_k$	Q_k	${}_0Q_k = ({}_0q_k)^2$	${}_nQ_k = ({}_nq_k)^2$	${}_{n\times m}Q_k = {}_nq_k\,{}_mq_k$	${}_{n\times \mathrm{T}}Q_k = {}_nq_k(1 - r_k)$

[1] Cn and Cm refer to any cycle $n = 0,1,\ldots$ and $m \geq n$.

Table 2: Genetic expectation of population means and testcross population means expressed as linear combinations of genetic parameters (A0, D0, AL, DL, DQ, T0, TL)

Population	Genetic expectation[1]
Cn	A0 + 2D0 $(1{-}F_n)$ + 2nAL + $(2n - nF_n)$ DL + $(2n^2 - n^2F_n)$ DQ
Cn-self	A0 + D0 $(1 - F_n)$ + 2nAL + $(2n - nF_n)$ DL + $(2n^2 - n^2F_n)$ DQ
Cn × Cm	A0 + 2D0 $(1{-}F_n)$ + $(n + m)$ AL + $(n + m - nF_n)$ DL + $(2nm - n^2F_n)$ DQ
Cn × T	T0 + nAL + nTL

[1] F_n refers to the inbreeding coefficient in cycle Cn.

of random genetic drift, except in the cycle C*n*. 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. Furthermore, inbreeding depression accumulated in cycle C*n* is not resolved by crossing it to an advanced cycle C*m*. Therefore, the inbreeding coefficient of cycle C*n* not only affects the performance of C*n* itself but also the performance of C*n* × C*m*.

In studies with many selection cycles and/or high rates of inbreeding, as applies to most RS studies reported in the literature (Hallauer and Miranda 1988), the effect of random genetic drift is expected to become large. Ignoring these effects could result in a considerable bias of genetic parameter estimates. The formulae here extend the models of Hammond and Gardner (1974) and Smith (1979) by full consideration of random genetic drift, and thus allow a better assessment of selection response in RS programmes.

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6. General Discussion

Ordinary recurrent FS selection comprises testing and selection of the FS families, and recombination of the selected FS families to generate the test candidates of the next cycle. We modified this scheme by producing selfed progenies in all FS families in parallel to the performance trials (Figure 2). The S_1 progeny were then recombined according to a pseudo-factorial mating scheme to establish the FS families of cycle C$n+1$. Compared with the conventional procedure, this modification requires additional pollinations in the nursery, but it offers the following advantages: (i) large quantity of seed can be produced for evaluating the performance of the FS families in C$n+1$ in multi-location trials, and (ii) S_1 progeny of the best FS families in Cn can be used twice as parents to generate closer pedigree relationships (half-sibs) between some FS families in C$n+1$.

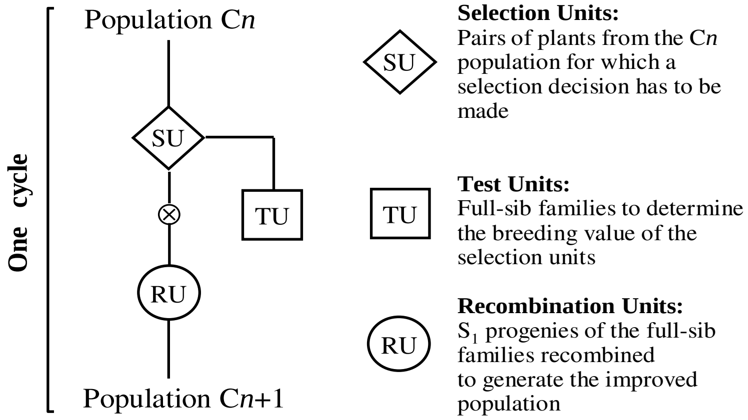

Figure 2. Scheme of the modified recurrent full-sib selection procedure

Relative selection response

Grain yield has been the trait most frequently used for RS in maize. In all selection cycles of both populations, the mean performance of six check entries from the respective F_2Syn$t$ population was recorded. Therefore, selection response could be calculated relative to these check entries. We observed a very high relative selection response (9.1% per cycle) for grain yield in population C×D (Flachenecker et al., 2006a, Figure 2), although we used a moderate selection rate, elite breeding material, and a selection index taking into account also grain moisture. In population A×B, the relative performance was kept at 120% from cycle C1 to C4 (Flachenecker et al., 2006b, Table 2). The high increase from C0 to C1 and the following stagnation can be mainly assigned to experimental errors in the check entries and consequential miscalculation of the relative performance, particularly in the early selection cycles. In previous studies on recurrent FS selection in F_2 populations, Moll (1991) observed a selection response of 4.5% across 16 selection cycles, and Landi and Frascaroli (1993) reported an average yield increase of 7.3% over four selection cycles. However, the calculation of selection response relative to check entries could be erroneous and comparisons with the literature are difficult to interpret. For a more precise calculation of selection response, all cycles of both populations should be re-evaluated together in multi-environmental trials.

Population diallel

We used a population diallel analysis on six environments to re-evaluate the selection response and to estimate parameters (Table 1) obtained with an extension (Melchinger and Flachenecker, 2006) of the genetic model of Smith (1979, 1983). The re-evaluation allows a more accurate estimation of selection response and a better assessment of our modified recurrent FS selection scheme in comparison with other RS schemes.

Table 1. Parameters based on Smith's (1983) model and their genetic interpretation.

Parameter	Genetic interpretation
A0	$\mu + \sum (2p-1)a$
D0	$\sum p(1-p)d$
AL	$\sum \Delta pa$
DL	$\sum \Delta p(1-2p)d$
DQ	$-\sum (\Delta p)^2 d$
T0	$\mu + \sum (p+r-1)a + \sum [r + p(1-2r)]d$
TL	$\sum \Delta p(1-2r)d$

In our F_2Syn3 source population with $p = 0.5$, parameter A0 is equal to μ and parameter D0 to $1/4d$. In general, the estimates of A0 and D0 are in close agreement with those in other studies on maize (Tanner and Smith, 1987; Eyherabide and Hallauer, 1991; Stojsin and Kannenberg, 1994a). As expected, A0 estimates were predominant in both source populations (C0 = A0 + 2D0) for all six traits (Flachenecker et al., 2006c, Table 3). However, the proportion of A0 and D0 estimates differed among traits. Grain yield showed the highest proportion of parameter D0, while D0 estimates for days to silking were even negative, indicating the opposite mode of gene action compared with that of A0 estimates. Other authors found similar relationships of A0 and D0 estimates 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).

Response to selection is achieved by changes in the frequencies of alleles with additive effects (AL) and/or frequencies of alleles with dominance effects (DL and DQ). The type of change depends predominantly on the selection method and the population undergoing selection. In F_2Syn3 populations, the heterozygote frequency is at a maximum (0.5), and no further increase in the frequencies of alleles with dominance effects is possible. In this case, DL is zero by definition and can be excluded from the model. The relative response per selection cycle, which could be expected after correcting for the effects of frequency changes in heterozygotes due to selection and random genetic drift, could be calculated as $\Delta G\% = (2\text{AL})/(\text{A0}+2\text{D0})\times 100$.

For grain yield, estimates of $\Delta G\%$ (Flachenecker et al., 2006c, Table 3) for populations A×B (14.1%) and C×D (8.3%) were larger than in other studies using a population diallel to evaluate the selection response in RS programs (Helms et al., 1989; Landi and Frascaroli, 1993; Stojsin and Kannenberg, 1994a). For population C×D, the high estimates of $\Delta G\%$ for grain yield agree favorably with the high relative selection response (9.1%) calculated in percent of the check entries (Flachenecker et al., 2006a, Figure 2). In population A×B, the relative selection response for grain yield was only 0.1% (Flachenecker et al., 2006b, Table 2). The high estimate of $\Delta G\%$ for population A×B supports the hypothesis that the selection response relative to check entries was biased by experimental errors in the check entries.

We ascribed the comparatively high selection response per cycle in our study to several factors: (i) Application of a pseudo-factorial mating scheme. This mating scheme is expected to increase the selection response over the maximum achievable for commonly applied random mating schemes, while keeping the inbreeding coefficient at a moderate level (Cockerham and Burrows, 1980). (ii) Completion of a relatively small number of selection cycles. Long-term RS programs are expected to show larger responses in the first cycles and smaller responses in the more advanced ones due to a reduced genetic variance (Gardner, 1977). (iii) Genotype×location interactions were kept at a modest level, because all three test locations have similar agro-ecological conditions. Crossa and Gardner (1989) emphasized that response per cycle is expected to be maximum when selection is made for adaptation to well-defined, homogeneous target environments. Nevertheless, 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 are necessary.

In RS programs, the linear change in allele frequencies due to selection (AL and DL) is accompanied by a quadratic change in genotype frequencies of heterozygotes (DQ). 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). The sign of the DQ parameter is mainly attributable to the high negative correlation (-0.82) between the AL and the DQ term, given by the model. Therefore, a high increase in the favorable allele (AL) is very likely associated with a negative estimate of DQ.

Effective population size and random genetic drift

In our experiments, the expected N_e was 32 (estimated after Cockerham and Burrows, 1980). The observed N_e, calculated as $1/2\Delta F$, was in most cycles of both populations smaller than the expected value. The differences between expected and observed N_e reflect the effects of selection, which reduce N_e below the value expected from drift. Only with small population sizes (< 25), effects of genetic drift are expected to be large relative to the effects of selection (Smith, 1983; Helms et al., 1989). Drift would then affect not only the genetic variance components, but also the population mean as a result of inbreeding depression.

To determine the effects of random genetic drift, we compared genetic parameters (Table 1) estimated by (i) ignoring (Smith, 1983) and (ii) including the inbreeding coefficient (F_n) in the model (Flachenecker et al., 2006c, Table 1). 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 the estimate of $\Delta G\%$ in nearly all traits. In studies with more selection cycles and/or higher rates of inbreeding, as applies to most of the 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, as is often done in these studies, could result in a considerable bias of the genetic parameter estimates.

Testcross performance

In our modified recurrent FS selection program, selection was based on *per se* performance of the FS families. Therefore, an increase in testcross performance depends directly on the genotypic correlation between *per se* and testcross performance. In maize, the magnitude of this correlation is based on the degree of heterosis of the trait under selection (Hallauer and Miranda, 1988; Seitz, 1989). Especially for the highly heterotic trait grain yield, a low correlation between *per se* and testcross performance is expected due to non-additive genetic effects contributing to heterosis (Smith, 1986; Hallauer, 1990).

We observed no significant selection response for testcross performance in most of the traits (Flachenecker et al., 2006c, Table 3). Particularly for grain yield, the large heterosis in our populations could be a reason for the low testcross response. A more detailed explanation for the lacking increase in testcross performance is given by the parameter TL ($\sum \Delta p(1-2r)d$), which was of the same amount as the parameter AL ($\sum \Delta pa$) for all traits but with opposite sign. For all traits except days to silking, additive effects (a) had the same sign as dominance effects (d), in accordance with the A0 and D0 estimates. Therefore, the different signs between the paramters AL and DL could at least in part be ascribed to the term $(1-2r)$. This term will become negative when the tester has the favorable allele (r) fixed at more than 50% of all loci. The results of a simulation study support our conjecture that the correlation between *per se* and testcross performance depends on the frequency of the favorable alleles in the tester (Smith, 1986).

In both populations, the high selection response in *per se* performance was not accompanied by an increase in testcross performance. Therefore, interpopulation recurrent selection schemes are better suited to increase testcross performance, particularly for highly heterotic traits like grain yield. Nevertheless, our modified recurrent FS selection is a serious alternative to other commonly applied intrapopulation recurrent selection schemes, because of the very high selection response for *per se* performance without a significant decrease in additive variance. In addition, the pseudo-factorial mating scheme and the detailed investigation of the effects of random genetic drift can also be used to increase the efficiency of interpopulation recurrent selection programs usually employed in commercial hybrid breeding.

Variance components

In both populations, the REML procedure was employed to estimate genetic variance components (Flachenecker et al., 2006a, Table 2; Flachenecker et al., 2006b, Table 3). To account for different relationships between the 144 full-sib families in each cycle, we used the model described by Lynch and Walsh (1998) and the variance-covariance matrix V (Figure 3). In our model, REML warrants that the total genetic variance is positive. However, negative values are possible for individual variance components. In the latter case, we set these variance components equal to zero and re-estimated the other variance components from the reduced model (Searle, 1971).

The magnitude of σ_A^2 for grain yield and grain moisture in both populations was similar to that reported for U.S. Corn Belt dent maize F_2 populations (Hallauer and Miranda, 1988; Wolf et al., 2000). Furthermore, they agreed well with the estimates of σ_A^2 of both traits when population A×B and C×D were compared with other European flint F_2 populations (Michaljevic et al., 2004). Estimates of σ_D^2 were in both populations smaller than reported in the literature (Robinson et al., 1949; Han and Hallauer, 1989; Edwards and Lamkey, 2002) and, especially in population A×B, many negative values were found that were interpreted as zero (Flachenecker et al., 2006b, Table 3). By definition, a variance component is always positive or zero. Nevertheless, negative values for σ_D^2 can occur and in reality are either zero or very small.

In F_2 populations, estimates of $\bar{d}$ have nearly always been greater than one, corresponding to overdominance (Comstock and Robinson, 1948; Edwards and Lamkey, 2002). In several studies, random mating of F_2 popu-

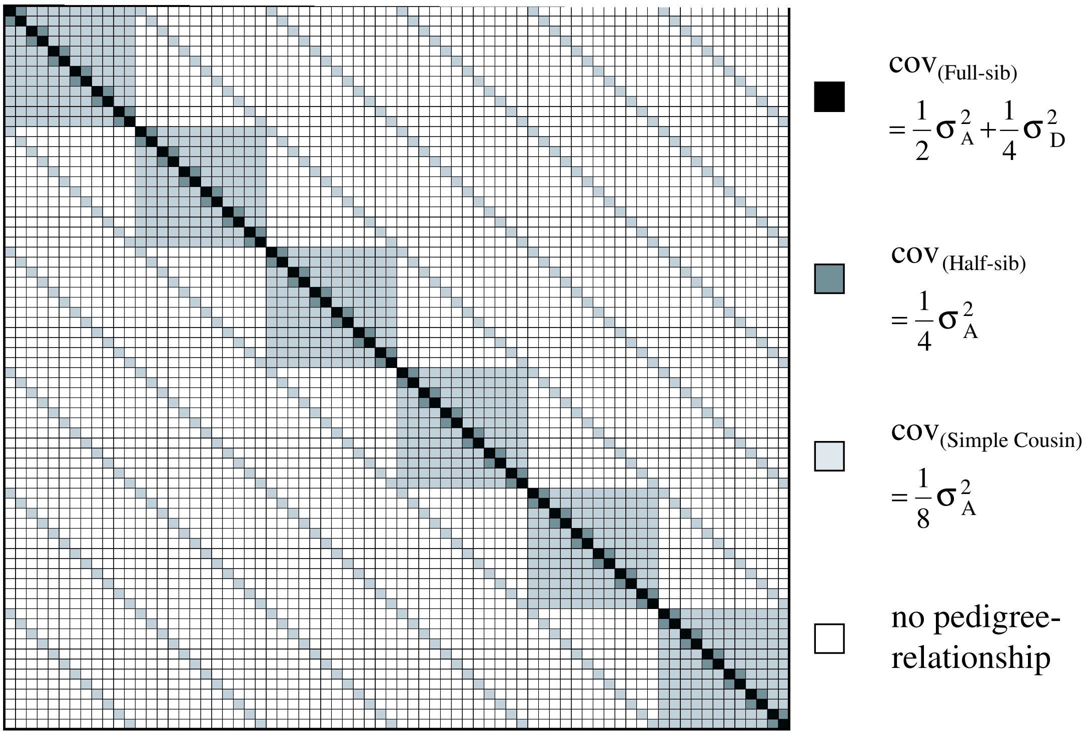

Figure 3. Illustration of the structure of the variance-covariance matrix for one set consisting of 72 entries and corresponding covariances between relatives in terms of additive (σ_A^2) and dominance variance (σ_D^2).

lations to reduce linkage disequilibrium has reduced the estimates of $\bar{d}$ to approximately one or less (Moll et al., 1964; Han and Hallauer, 1989). The relatively low estimates of σ_D^2 for grain yield and grain moisture observed in our study suggest that the three generations of chain crossing before initation of selection have considerably reduced linkage disequilibrium in the F_2Syn3 population. In theory, selection is expected to generate new coupling phase linkage disequilibrium (Falconer and Mackay, 1996) and therefore will reduce σ_A^2 by the Bulmer effect (Bulmer, 1985). Although a low selection intensity and high N_e were applied in our study, we observed a decrease in σ_A^2 for grain yield and selection index in population A×B. Nevertheless, we cannot prove the existence of the Bullmer effect, because the variance component estimates are still associated with large standard errors, which are an obstacle in uncovering trends across the cycles.

Use of BLUP in recurrent selection

The BLUP approach was suggested for evaluation of inbreds from different breeding populations (Bernardo 2002) and the prediction of the performance of untested single-cross hybrids in maize (Bernardo 1994, 1996). We predicted the performance of individual FS families in C$n + 1$ using the mean additive genetic BLUP of their parents in Cn and, alternatively, the mean performance of their parents in Cn. In our study, the additive genetic BLUP of each parent is a linear function of the phenotypic values from each environment of (i) its FS relatives (one family), (ii) its paternal half-sib relatives (one family), (iii) its paternal (ten families) and maternal simple cousin relatives (five families), and in advanced cycles (iv) more distant relatives (Figure 3).

The correlation between predicted and realized performance is restricted by the effects of segregation and has a maximum of $1/\sqrt{2} = 0.71$, if the heritability is one and no dominance effects occur. In our study, the correlations for grain moisture nearly reached this maximum, whereas dominance and other types of masking effects (*e.g.*, genotype×location interactions, experimental error) reduced the prediction power of additive genetic BLUP for grain yield and selection index (Flachenecker et al., 2006a, Table 2; Flachenecker et al., 2006b, Table 4). Using additive genetic BLUP of the FS families in $\mathrm{C}n+1$ instead of their phenotypic mean did not improve the correlations with the mean additive genetic BLUP of their parents in $\mathrm{C}n$, suggesting that dominance effects were not the major cause of the low correlations. These results agree well with the findings of several simulation studies, where the advantage of BLUP selection compared with phenotypic mean selection increases with lower heritability and higher relationships in the population under selection (Bauer and Léon, 2006a, 2006b).

Hence, we conclude that the precision of additive genetic BLUP in our study was fairly low due to the (i) small number of related families with high coancestry coefficient f to a given FS family under the pseudo-factorial mating scheme employed and (ii) high heritability estimates in almost all cycles and traits. Increasing the number of closely related families should increase the precision of BLUP, but at the expense of a reduced N_e and all negative side effects related to it in RS.

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7. Summary

Many plant breeding strategies lead to a reduction in the genetic variance of the source population. However, a sufficient genetic variance is essential for the long-term selection response. Hence, the aim of recurrent selection (RS) is a continuous increase in the frequencies of favorable alleles while maintaining genetic variability in the population. Several intrapopulation RS methods have been proposed in maize: *e.g.*, mass selection, half-sib selection, full-sib (FS) selection, S_1 selection. Among them, recurrent FS selection is characterized by a short cycle length, complete parental control, and a high selection response.

The goal of this thesis was to investigate the changes in the population structure over several cycles of a modified recurrent FS selection program in two European F_2 maize populations. In detail, the objectives were to (i) monitor trends across selection cycles in the estimates of population mean, inbreeding coefficients, and variance components, (ii) determine selection response for *per se* and testcross performance, (iii) compare predicted with realized selection response, (iv) extend the population diallel analysis under full consideration of inbreeding depression due to random genetic drift, (v) separate genetic effects due to selection from those due to random genetic drift, and (vi) investigate the usefulness of best linear unbiased prediction (BLUP) estimates of parents for predicting progeny performance under the recurrent FS selection scheme applied.

Four early maturing European flint inbreds were used as parents to produce two F_2 populations (A×B and C×D). Both populations were three

times intermated by chain crossing to reduce the gametic phase disequilibrium. Starting from the F_2Syn3 population obtained in this manner, a modified recurrent FS selection program was conducted over four cycles in population A×B and over seven cycles in population C×D. In each cycle, 144 FS families were tested in field trials and, in parallel, six plants from each FS family were selfed. The selfed ears of the 36 families with the highest selection index (SI = 2 × dry matter content + grain yield) were selected and intermated according to a pseudo-factorial mating scheme. In this mating scheme, the gametic contribution of the best selected FS families is doubled compared with the gametic contribution of the remaining selected FS families. Afterwards, all cycles of both populations were tested in two population diallel analyses in six environments. Based on the known pedigree records, the inbreeding coefficient of each FS family and the coancestry coefficients among them were calculated. Variance components and best linear unbiased prediction (BLUP) values were obtained using phenotypic means and coancestry coefficients.

For grain yield, the selection response per cycle, which could be expected after correcting for the effects of random genetic drift, was higher than reported in the literature (14.1% and 8.3% in populations A×B and C×D, respectively). We ascribe the comparatively high selection response mainly to the pseudo-factorial mating scheme. This mating scheme is expected to increase the selection response compared with commonly applied random mating schemes, without a major reduction in the effective population size (N_e). In this study, the expected N_e was 32, suggesting a minor influence of random genetic drift compared with that of selection. This assumption was verified by an extended population diallel analysis, showing that random genetic drift reduced the selection response only by about 1-2% in both populations.

In contrast to an estimation of variance components with moment estimators, the REML procedure has no special requirements on the mating scheme and accounts for any relationship among families in a breeding population. As expected from the high N_e applied in our study, we observed only a moderate decrease in additive variance for grain yield and grain moisture in both populations. Nevertheless, the variance components were still associated with high standard errors, which prevented the revealing of trends across cycles. A larger number of test locations and larger population size would reduce the standard errors of variance components at the cost of oversized and expensive field trials.

Methods for predicting the performance of progenies are important to optimize RS programs. Due to simplifying assumptions, a prediction with phenotypic means is often inaccurate. An alternative method is BLUP, which was suggested for predicting the performance of untested single-cross hybrids but has not been applied in RS programs. In our study, the prediction of progeny performance based on BLUP was only marginally better than prediction based on the phenotypic mean. However, higher degree of relationship between the entries and lower heritabilities would increase the advantage of BLUP compared with phenotypic means.

The high selection response for grain yield combined with a reduction in grain moisture suggests that our modified recurrent FS selection scheme is an alternative to commonly used mating schemes. In both populations, we observed only moderate reductions in additive variances for grain yield and grain moisture, indicating selection response at or near current rates of progress in future selection cycles. Finally, we have shown that under certain circumstances a selection on BLUP estimates compared with a selection on phenotypic means would further increase the selection response.

8. Zusammenfassung

Viele Zuchtverfahren in der Pflanzenzüchtung führen zu einer Einengung der genetischen Variation im verwendeten Zuchtmaterial. Deswegen ist es das erklärte Ziel der rekurrenten Selektion (RS), durch kontinuierliche Erhöhung der Frequenz günstiger Allele zu einer stetigen Leistungsverbesserung von Zuchtpopulationen unter Beibehaltung der genetischen Varianz beizutragen. Für RS innerhalb einer Population hat man unter anderem die Wahl zwischen Massen-, Halbgeschwisterfamilien-, Vollgeschwisterfamilien- (VGF), und S_1-Familien-Selektion. Entscheidende Kriterien bei der Wahl der VGF-Selektion für das vorliegende Experiment waren die Nutzung der Hälfte der Additivvarianz, die vollständige elterliche Kontrolle und die kurze Zykluslänge.

Im Rahmen dieser Dissertation wurde ein langjährig durchgeführtes rekurrentes VGF-Selektionsprogramm in zwei europäischen Maispopulationen untersucht. Die Ziele der Arbeit waren (i) die Ermittlung der Trends des Populationsmittels, der Inzuchtkoeffizienten und der Varianzkomponenten über die Selektionszyklen hinweg, (ii) die Quantifizierung des Selektionserfolgs für *per se*- und Testkreuzungsleistung, (iii) der Vergleich von vorhergesagtem und realisiertem Selektionserfolg, (iv) die Erweiterung der Populationsdiallelanalyse unter Berücksichtigung von Inzuchtdepression auf Grund von genetischer Zufallsdrift, (v) die Trennung der genetischen Effekte von Selektion und Zufallsdrift und (vi) die Untersuchung des Nutzens der Zuchtwertschätzung zur Leistungsvorhersage der Nachkommen.

Für die Untersuchungen wurden vier Flintlinien (A, B, C, und D) verwendet, die zu Beginn der 90er Jahre zum leistungsstärksten Elitezuchtmaterial im europäischen Flint-Formenkreis zählten. In jeder der beiden Kreuzungen A×B und C×D wurde die F_2-Generation in drei aufeinanderfolgenden Generationen mittels eines „chain-crossing“-Verfahrens durchkreuzt, um das Gametenphasenungleichgewicht abzubauen. Ausgehend von den dadurch erzeugten F_2Syn3-Generationen wurden in Population A×B vier und in Population C×D sieben Zyklen eines modifizierten rekurrenten VGF-Selektionsprogramms durchgeführt. In jedem Zyklus wurde nach einem pseudo-faktoriellen Schema durchkreuzt, bei dem die besten der selektierten VGF doppelt zur nächsten Generation beitragen. Anschließend wurden alle VGF einer Leistungsprüfung in drei Umwelten mit drei Wiederholungen unterzogen sowie parallel sechs Selbstungskolben pro VGF hergestellt. Zur Selektion wurden die Prüfglieder nach dem üblichen Selektionsindex ($2 \times$ Trockenmasse + Kornertrag, jeweils prozentual zur F_2) rangiert. Die Selbstungskolben der 25% besten VGF wurden in den nächsten Zyklus weitergeführt und erneut durchkreuzt. Für die Berechnung des Selektionserfolgs wurden sämtliche Zyklen beider Populationen zusammen an sechs Umwelten mit vier Wiederholungen angebaut. Basierend auf den bekannten Pedigrees wurden die Inzuchtkoeffizienten aller VGF und die Abstammungskoeffizienten zwischen den VGF berechnet. Mit den phänotypischen Mittelwerten und den Abstammungskoeffizienten konnten die Varianzkomponenten und Zuchtwerte in jedem Zyklus geschätzt werden.

In beiden Populationen übertraf der um Zufallsdrift korrigierte Selektionserfolg für Kornertrag von durchschnittlich 14,1% (A×B) und 8,3% (C×D) die Erwartungen, da vergleichbare Versuche aus der Literatur lediglich einen Selektionserfolg von 2% bis 7% pro Zyklus aufwiesen. Ein Grund für den dauerhaft hohen Selektionserfolg über mehrere Zyklen und Umwelten könnte das hier verwendete pseudo-faktorielle Kreuzungsschema sein. Im Vergleich zu allgemein verwendeten Kreuzungsschemata kann damit ein höherer Selektionserfolg erzielt werden, ohne die effektive Populationsgröße stark einzuschränken. In der vorliegenden Studie lag die effektive Populationsgröße bei 32, so dass der Einfluss von Zufallsdrift im Verhältnis zur Selektion relativ klein sein dürfte und daher nur eine sehr geringe Inzuchtdepression zu erwarten war. Diese Vermutung konnte durch eine erweiterte Populationsdiallelanalyse bestätigt werden, denn die genetische Zufallsdrift reduzierte den Selektionserfolg in beiden Populationen nur um 1-2%.

Im Gegensatz zu traditionellen Methoden können bei der Schätzung der Varianzkomponenten mit dem REML-Verfahren beliebige Abstammungskoeffizienten zwischen den Prüfgliedern verwendet werden. In beiden Populationen wurde sowohl für Kornertrag als auch für Kornfeuchte keine gravierende Reduktion der Additivvarianz festgestellt. Dennoch können die fehlenden Trends auch mit dem relativ großen Standardfehler der Varianzkomponenten zusammenhängen. Um diesen zu reduzieren, müssten mehr Testumwelten und/oder größere Populationsumfänge verwendet werden.

Die Vorhersage der Leistung von VGF anhand des phänotypischen Mittelwerts ihrer Eltern ist sehr ungenau. Eine Alternative dazu stellt die Zuchtwertschätzung mittels BLUP dar. In unserer Studie war die Vorhersage des Zuchtwertes einzelner VGF mit Hilfe des Zuchtwertes ihrer Eltern jedoch nur marginal besser als die Vorhersage mit dem phänotypischen Mittelwert der Eltern. Allerdings zeigten Versuche mit Selbstbefruchtern, dass sich bei niedrigeren Heritabilitäten und höheren Verwandtschaftsgraden zwischen den Prüfgliedern der Vorteil des Zuchtwertes gegenüber dem phänotypischen Mittelwert deutlicher bemerkbar machen würde.

Der hohe Selektionserfolg für Kornertrag kombiniert mit einer Reduktion der Kornfeuchte zeigt, dass unser modifiziertes rekurrentes VGF-Selektionsschema eine vielversprechende Alternative zu den bisher angewandten RS Verfahren darstellt. Sowohl für Kornertrag als auch für Korntrockenmasse wurde keine Reduktion der Additivvarianz beobachtet, so dass auch in weiteren Zyklen ein ähnlich hoher Selektionserfolg zu erwarten ist. Zuletzt konnte gezeigt werden, dass in einer Population mit bekannten Abstammungsverhältnissen eine Selektion auf den Zuchtwert immer einen größeren Selektionserfolg verspricht als eine Selektion auf die mittlere Leistung der Eltern.

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Curriculum vitae

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