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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 F₂ 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 C_{n+1} based on mean performance of parental FS families in C_n 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 F₂ 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, F₂ populations from biparental crosses are the major type of base populations used in recycling breeding programs (Bernardo 2002). Nevertheless, F₂ 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 \times 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_2 Syn3 generation was derived from the F_2 generation by three generations of chain crossing using 240 F_2 plants, i.e., crossings 1 \times 2, 2 \times 3, ..., and 240 \times 1.

Selection procedure

In 1994, the F_2 Syn3 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 \times 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 $i.r \times j.q$ 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_2 Syn3 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

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

where \mathbf{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 \times location interaction effects; $\boldsymbol{\delta}l$ is the $dl \times 1$ vector of dominance \times location interaction effects; $\boldsymbol{\varepsilon}$ 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 \mathbf{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:

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

where \mathbf{A} is an $n \times n$ matrix with elements equal to t ; \mathbf{D} an $n \times n$ matrix with elements equal to u ; \mathbf{I} 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 \times location, σ_{DL}^2 is the dominance \times location, and σ_ε^2 is the error variance. We assumed no correlations between genotype \times 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

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

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 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 $i = Nz/N_e$ (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 C_n . Likewise the performance of individual FS families in C_{n+1} was correlated with the mean performance of the respective parental FS families in C_n .

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_A^2 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_D^2 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_{AL}^2 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_{DL}^2 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_A^2 in grain moisture and σ_{DL}^2 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

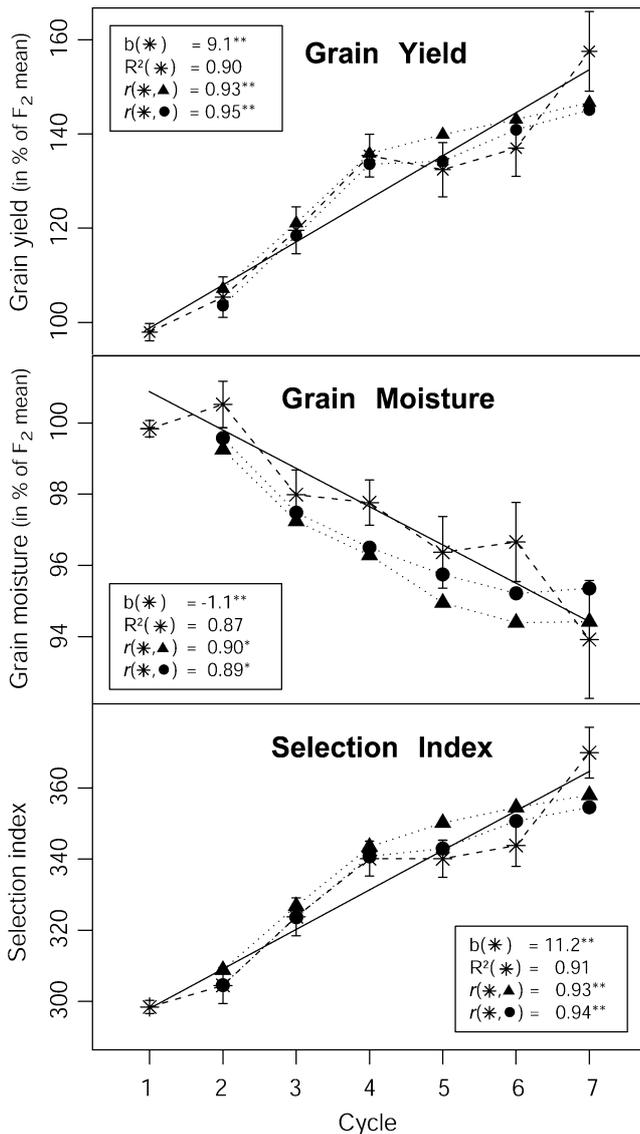


Fig. 2 Grain yield, grain moisture and selection index relative to the mean performance of the six F_2 checks: realized (asterisks) and predicted selection response, ignoring (filled triangle) and including (filled circle) exact pedigree relationships in REML estimates of variance components; the bars 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 C_n 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 ($0.46 \leq r \leq 0.66$) 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 C_n .

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 C_n 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 C_n 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 (\pm 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 $Cn+1$

and mean BLUP of their parents in Cn , and correlation (r_2) between FS family performance in $Cn+1$ and mean performance of their parental FS families in Cn for grain yield, grain moisture and selection index

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

^aNot calculated, because BLUP values were not available from C0

^bDenominator was zero

^cCalculated 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 \times 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 F₂ population. In F₂ 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_A^2 for grain yield and grain moisture were nearly as large as the values reported for the U.S. Corn Belt dent maize F₂ 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 F₂ 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 F₂ populations, where linkage disequilibrium will be maximum, estimates of \bar{d} decrease with random mating within F₂ 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 F₂Syn3 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 $N_e=32$ 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 C_n. 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 \times 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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References

- Bernardo R (1994) Prediction of maize single-cross performance 1 using RFLPs and information from related hybrids. *Crop Sci* 34:20–25
- Bernardo R (1996) Best linear unbiased prediction of maize single-cross performance. *Crop Sci* 36:50–56
- Bernardo R (2002) Breeding for quantitative traits in plants. Stemma, Woodbury
- Bulmer MG (1971) The effect of selection on genetic variability. *Am Nat* 105:201–211
- Cochran WG, Cox GM (1957) Experimental designs, 2nd edn. Wiley, New York
- Cockerham CC, Burrows PM (1980) Selection limits and strategies. *Proc Natl Acad Sci USA* 77:546–549
- Comstock RE, Robinson HF (1948) The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. *Biometrics* 4:254–266
- Crossa J, Gardner CO (1989) Predicted and realized grain yield responses to full-sib family selection in CIMMYT maize (*Zea mays* L.) populations. *Theor Appl Genet* 77:33–38
- Dong MC, Van Vleck LD (1989) Effect of relationship on estimation of variance components with an animal model and restricted maximum likelihood. *J Dairy Sci* 71:3047–3052
- Edwards JW, Lamkey KR (2002) Quantitative genetics of inbreeding in a synthetic maize population. *Crop Sci* 42:1094–1104
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th edn. Longman Group Ltd, London
- Gardner CO (1977) Quantitative genetics studies and population improvement in maize and sorghum. In: Pollak E, Kempthorne O, Bailey TB (eds) Proceedings of the international conference on quantitative genetics. Iowa State University Press, Ames, pp 475–479
- Genter CF (1982) Recurrent selection for high inbred yields from the F_2 of maize single cross. *Proc Ann Corn Sorghum Ind Res Conf* 37:67–76
- Hallauer AR (1985) Compendium of recurrent selection methods and their applications. *Crit Rev Plant Sci* 3:1–33
- Hallauer AR, Miranda JBF (1988) Quantitative genetics in maize breeding, 2nd edn. Iowa State University Press, Ames
- Han G-C, Hallauer AR (1989) Estimates of genetic variability in F_2 maize populations. *J Iowa Acad Sci* 96:14–19
- Henderson CR (1975) Best linear unbiased estimation and prediction under a selection model. *Biometrics* 31:423–447
- Helms TC, Hallauer AR, Smith OS (1989) Genetic drift and selection evaluated from recurrent selection programs in maize. *Crop Sci* 29:602–607
- Hudson GFS, Van Vleck LD (1982) Estimation of components of variance by method 3 and Henderson's new method. *J Dairy Sci* 65:435–441
- Jannink J-L (2003) Selection dynamics and limits under additive \times additive epistatic gene action. *Crop Sci* 43:489–497
- Landi P, Frascaroli E (1993) Responses to four cycles of full-sib family recurrent selection in an F_2 maize population. *Maydica* 38:31–37
- Meyer K, Smith SP (1996) Restricted maximum likelihood estimation for an animal model using derivatives of the likelihood. *Gen Sel Evo* 28:23–49
- Mihaljevic R, Utz HF, Melchinger AE (2004) Congruency of quantitative trait loci detected for agronomic traits in test-crosses of five populations of European maize. *Crop Sci* 44:114–124

- Mihaljevic R, Schön CC, Utz HF, Melchinger AE (2005) Correlations and QTL correspondence between line per se and test-cross performance for agronomic traits in four populations of European maize. *Crop Sci* 45:114–122
- Mode CJ, Robinson HF (1959) Pleiotropism and the genetic variance and covariance. *Biometrics* 15:518–537
- Moll RH (1991) Sixteen cycles of recurrent full-sib family selection for grain weight in two maize populations. *Crop Sci* 31:959–964
- Moll RH, Smith OS (1981) Genetic variances and selection responses in an advanced generation of a hybrid of widely divergent population of maize. *Crop Sci* 21:387–391
- Moll RH, Stuber CW (1971) Comparisons of response to alternative selection procedures initiated with two populations of maize (*Zea mays* L.). *Crop Sci* 22 11:706–710
- Pandey S, Diallo AO, Islam TMT, Deutsch J (1987) Response to full-sib selection in four medium maturity maize populations. *Crop Sci* 27:617–622
- Penny LH, Eberhart SA (1971) Twenty years of reciprocal recurrent selection with two synthetic varieties of maize (*Zea mays* L.). *Crop Sci* 11:900–903
- R Development Core Team (2004) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Robinson HF, Comstock RE, Harvey PH (1949) Estimates of heritability and the degree of dominance in corn. *Agron J* 41:353–359
- Rojas BA, Sprague GF (1952) A comparison of variance components in corn yield trials: III. General and specific combining ability and their interaction with locations and years. *Agron J* 4:462–466
- SAS Institute (2004) SAS Version 9.1. SAS Institute, Cary
- Schnicker BJ, Lamkey KR (1993) Interpopulation genetic variance after reciprocal recurrent selection in BSSS and BSCB1 maize populations. *Crop Sci* 33:90–95
- Searle SR (1971) Linear models. Wiley, New York
- Smith OS (1983) Evaluation of recurrent selection in BSSS, BSCB1, and BS13 maize populations. *Crop Sci* 23:35–40
- Sprague GF, Eberhart SA (1977) Corn breeding. In: Sprague GF (ed) Corn and corn improvement. American Society of Agronomy, Madison, pp 305–362
- Stromberg LD, Compton WA (1989) Ten cycles of full-sib selection in maize. *Crop Sci* 29:1170–1172
- Utz HF (2001) PLABSTAT: a computer program for the statistical analysis of plant breeding experiments. Institute of Plant Breeding, Seed Science, and Population Genetics. University of Hohenheim, Stuttgart
- Utz HF, Schnell FW, Singh IS (1978) Maturity corrected yield as a way to reduce genotype-environment interactions in maize trials. *Cereal Res Commun* 6:399–404
- Walters SP, Russell WA, Lamkey KR (1991) Performance and genetic variances among S1 lines and testcrosses of Iowa stiff stalk synthetic maize. *Crop Sci* 31:76–80
- Weyhrich RA, Lamkey KR, Hallauer AR (1998) Responses to seven methods of recurrent selection in the BS11 maize population. *Crop Sci* 38:308–321
- Wolf DP, Peternelli LA, Hallauer AR (2000) Estimates of genetic variance in an F₂ maize population. *J Hered* 91:384–391
- Wricke G, Weber WE (1986) Quantitative genetics and selection in plant breeding. Walter de Gruyter, Berlin