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ORIGINAL PAPER

Multiple-trait breeding values for parental selection in self-pollinating crops

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Abstract Using breeding values in parental selection of self-pollinating crops seems to be superior to conventional selection strategies, where selection is often based on several traits which are correlated among each other. However, analysing each trait separately can bias estimates of breeding values. This study examined responses to selection for total merit indices based on breeding values resulting from single- and multiple-trait best linear unbiased prediction (BLUP). We generated data for a multi-environment trial of a "virtual" parental population in which the phenotypic value of inbred lines was influenced by additive, additive-by-additive epistatic, year, location, block and genotype-by-environment interaction effects. Two traits with heritabilities of 0.7 and 0.3 and nine different correlation scenarios between traits (estimated phenotypic correlation ranging from –0.39 to +0.36) were simulated. Gain in selection response was greater for multiple-trait than for single-trait breeding values, especially if traits were negatively correlated. For all correlation scenarios, the overall standard errors of difference of multiple-trait predictors were lower than those of single-trait analysis.

Introduction

A previous study has shown that selection among parental inbred lines of self-pollinating crops can be improved by the estimation of breeding values using best linear unbiased prediction (BLUP) (Bauer et al. 2006). In contrast to the standard BLUP approach, the prediction of BLUP breeding values is characterized by including pedigree information in the mixed model equations (MME). BLUP is able to handle large, unbalanced data sets where all available information from cultivar registration, official recommendation, and private trials can be used in the prediction. Using data sets merged from different trials, BLUP-breeding values can be calculated even for newly-developed lines with only a few records of data. As Piepho and Möhring (2006) stated, BLUP is useful for analysis of multi-environment trials, provided that all data are considered in the analysis.

Usually, the selection of superior parental lines is based on several traits, which may be genetically and phenotypically correlated. Selection bias can result if such traits are analysed individually, especially if selection is based on independent culling levels. For example: after selection of lines based on one trait, the lines remaining to be considered for a second trait do not represent a random sample of the entire parental population (Pollak et al. 1984; Im et al. 1989). Considering all target traits simultaneously in the prediction of BLUP breeding values can greatly enhance the genetic merit of selected lines. Multiple-trait evaluations are commonly used in animal breeding (Henderson and Quaas 1976). Mrode (2000) considered the multiple-trait BLUP as the best methodology to simultaneously evaluate animals on two or more correlated traits, and proposed a selection index involving BLUP breeding values weighted by economic weights. Relative to the standard selection index introduced by Smith (1936) and Hazel (1943), such an index has the advantage that the genetic relatedness among the lines can be taken into account as a random factor.

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Multiple-trait breeding values have been used in forest tree breeding and in perennial crops. Persson and Andersson (2004) compared single-trait versus multiple-trait REML-based BLUP breeding values using a Monte Carlo simulation model which resembled the breeding design of Swedish Scots pine (*Pinus sylvestris* L.). The authors stated that multiple-trait predictors resulted in a lower average bias than single-trait analysis. Using single-trait analysis, genetic correlation between traits was underestimated (Persson and Andersson 2004). Costa e Silva et al. (2000) first carried out single-trait evaluations to identify favourable parents of Norway spruce [*Picea abies* (L.) KARST.]. Afterwards, the authors applied a multiple-trait model to construct indices for genetic improvement of multiple traits. A multiple-trait BLUP-model was also used in analysing data from Persian walnut (*Juglans regia* L.) (Aleta et al. 2004). In this study, BLUP-based estimates of parental performance were superior to the common family-mean. Da Costa et al. (2002) examined multiple-trait BLUP in rubber tree (*Hevea*) breeding, considering genotype-by-environment interaction. The authors stated that multiple-trait predictors were more accurate than a single-trait model. In peach [*Prunus persica* (L.) Batsch], de Souza et al. (1998a, b) used a bivariate BLUP model to estimate genetic and phenotypic correlations between traits. In general, for reproductive as well as fruit traits, genetic correlations among pairs of traits were higher than phenotypic correlations.

Piepho and Möhring (2006) and Piepho et al. (2007) recommended the use of multiple-trait BLUP breeding values in annual crops. In the study reported here, we compared the accuracy of single-trait versus multiple-trait REML-based BLUP breeding values using multi-environmental data of a “virtual” parental population of inbred lines generated by Monte Carlo simulation.

The objective of our research was to examine whether a total merit index based on single- or multiple-trait breeding values is superior for parent selection in self-pollinated crops in terms of different genetic and residual correlations among traits.

Theory and methods

Simulation

Using Monte Carlo simulation in the interactive matrix language (IML) in SAS 9.1 (SAS Institute 2004), a computer program to generate a “virtual” plant population was developed, assuming a finite number of 150 loci with two alleles each and a finite population size of 250 parental inbred lines.

To create the population, we first simulated a base population of 50 lines, which were assumed to be unrelated and homozygous with an inbreeding coefficient of $F = 0.99$. In the first crossing cycle, lines of the base population were randomly chosen and crossed among each other to produce 100 progeny lines. Starting from these progeny lines, in the second crossing cycle the progeny lines were randomly crossed among each other to generate 100 further progeny lines. The progeny lines were also assumed to be homozygous. Thus, pedigree information was available for the entire population.

The genotypic value of a line was influenced by normally-distributed additive and epistatic effects with a mean of zero and a standard deviation σ of 1 [N (0,1)]. As the lines are assumed to be inbred, dominance effects do not exist. On average, 25 random allele combinations were influenced by additive-by-additive epistatic effects. Genotypic value for a line resulted from the sum of the additive effects over all alleles and loci, plus an epistatic effect, if present.

The simulation of phenotypic information of the lines followed from the structure of a multi-environment trial with three years and with a total of 55 locations. In the first year, only the base population lines were tested at 25 locations. In the second year, the lines for the base population and the first crossing cycle were grown at 15 locations. In the third year, all 250 lines (of the base population, the first and the second crossing cycle) were grown at 15 locations. The resulting data set was systematically unbalanced, since there were many records available for established lines (of the base population) and little information about the newly developed progeny lines (of the crossing cycles). In all cases, we assumed a randomized complete block design with two blocks and two replications. The phenotypic value for each line was simulated by adding normally-distributed [N (0,1)] year, location, block, genotype-by-environment interaction, and residual effects to the genotypic value. In the simulation, related lines also had similar genotype-by-environment interaction effects.

Furthermore, we simulated two traits v and w with heritabilities of $h^2 = 0.7$ and 0.3, resulting from residual standard deviations of $\sigma = 50$ and 160, respectively. Between both traits, all simulated effects of genotypic value, year, location, block, genotype-by-environment interaction, and the residue were uncorrelated among each other. Then, in calculating the phenotypic value of the traits, a genetic and a residual correlation between the traits was simulated, with the simulation of the genetic correlation based on the genotypic value.

Four scenarios of identical genetic r_g and residual r_e correlation among both traits were generated with $r_g = r_e = -0.8, -0.4, +0.4$ or $+0.8$. In four further correlation scenarios, r_g and r_e were different: (1) $r_g = -0.2$ and $r_e = +0.4$, (2) $r_g = +0.4$ and $r_e = +0.8$, (3) $r_g = +0.8$ and $r_e = +0.4$, and (4) $r_g = -0.8$ and $r_e = -0.4$. In addition, for comparison, no correlation between traits was simulated

($r_g = r_e = 0$). Phenotypic value P_{vijkmn} of trait v ($h^2 = 0.7$) was calculated by:

$$P_{vijkmn} = g_{vi} + y_{vj} + l_{vk} + b_{vm} + ge_{vik} + \varepsilon_{vijkmn}$$

with genotypic effect g_{vi} of trait v ($i = 1, \ldots, 250$), year effect y_{vj} of trait v ($j = 1$–3), location effect l_{vk} of trait v ($k = 1, \ldots, 55$), block effect b_{vm} of trait v ($m = 1, 2$), genotype-by-environment interaction effect ge_{vik} of trait v, and residual effect ε_{vijkmn} of trait v ($n = 1, \ldots, 165{,}000$).

For trait w ($h^2 = 0.3$), phenotypic value P_{wijkmn} was calculated following Olausson and Rönningen (1975):

$$P_{wijkmn} = \left[(r_g \times g_{vi}) + \left(\sqrt{1 - r_g^2} \times g_{wi}\right)\right] + y_{wj} + l_{wk} + b_{wm} + ge_{wik} + \left[(r_e \times \varepsilon_{vijkmn})\right] + \left(\sqrt{1 - r_e^2} \times \varepsilon_{wijkmn}\right)\Big]$$

with genotypic effect g_{wi} of trait w, year effect y_{wj} of trait w, location effect l_{wk} of trait w, block effect b_{wm} of trait w, genotype-by-environment interaction effect ge_{wik} of trait w, residual effect ε_{wijkmn} of trait w, genetic correlation coefficient r_g, and residual correlation coefficient r_e.

Simulated phenotypic correlation among traits was calculated by Pearson's correlation coefficient. The observed phenotypic and genetic correlation was estimated using ASReml software (Gilmour et al. 2002).

The computer simulation procedure of the "virtual" parental population was repeated 100 times using different seeds. To avoid overlapping streams of random numbers, seeds were generated using the SEEDGEN Macro developed by Fan et al. (2002).

Data analysis

Single-trait and multiple-trait analysis were both performed using ASReml software (Gilmour et al. 2002).

In the analysis, each correlation scenario was evaluated separately. The statistical model was as follows:

$$Y_{ijkmn} = \mu + g_i + y_i + l_k + b_m + ge_{ik} + \varepsilon_{ijkmn}$$

where: Y_{ijkmn} = observation n of genotype i in year j, location k and block m; μ = overall mean; g_i = random genetic effect of the lines i; y_j = random year effect j; l_k = random location effect k; b_m = random block effect m; ge_{ik} = random genotype-by-environment interaction effect; ε_{ijkmn} = residual effect.

The mixed model equations (MME) used for single-trait analysis are presented in the appendix. In single-trait analysis, the residuals are identically and independently distributed, so that the covariance matrix of the residuals R will be $I \times \sigma_\varepsilon^2$ where I is an identical matrix and $\sigma^2{}_\varepsilon$ is the residual variance. In multiple-trait BLUP, several traits are considered in a single analysis so it is necessary to specify the covariance matrix R of the residuals. Following Gilmour et al. (2002), the error structure for the residuals was defined as two-dimensional with independent observations and an unstructured covariance matrix.

According to Henderson and Quaas (1976), in multiple-trait analysis the MME matrices become:

$$X = \begin{vmatrix} X_1 & 0 \\ 0 & X_2 \end{vmatrix}, \quad Z = \begin{vmatrix} Z_1 & 0 \\ 0 & Z_2 \end{vmatrix}, \quad S = \begin{vmatrix} S_1 & 0 \\ 0 & S_2 \end{vmatrix},$$

$$T = \begin{vmatrix} T_1 & 0 \\ 0 & T_2 \end{vmatrix}, \quad V = \begin{vmatrix} V_1 & 0 \\ 0 & V_2 \end{vmatrix},$$

$$W = \begin{vmatrix} W_1 & 0 \\ 0 & W_2 \end{vmatrix}, \quad \hat{b} = \begin{vmatrix} \hat{b}_1 \\ \hat{b}_2 \end{vmatrix}, \quad \hat{u} = \begin{vmatrix} \hat{u}_1 \\ \hat{u}_2 \end{vmatrix},$$

$$\hat{o} = \begin{vmatrix} \hat{o}_1 \\ \hat{o}_2 \end{vmatrix}, \quad \hat{p} = \begin{vmatrix} \hat{p}_1 \\ \hat{p}_2 \end{vmatrix}, \quad \hat{q} = \begin{vmatrix} \hat{q}_1 \\ \hat{q}_2 \end{vmatrix}, \quad \hat{r} = \begin{vmatrix} \hat{r}_1 \\ \hat{r}_2 \end{vmatrix}.$$

Relatedness among lines is accounted for in the genetic relationship matrix A. Following Henderson (1976), the additive genetic covariance c_{ij} between lines i and j is calculated as twice the coefficient of coancestry θ (Malécot 1948):

$$c = 2\theta = \begin{cases} 1 + F_i & \text{for } c_{ii}\ (F_i = \text{inbreeding coefficient}) \\ 0.5 \times (c_{ip} + c_{iq}) & \text{for } c_{ij} \text{ and parents } p \text{ and } q \text{ of the } j\text{th line} \end{cases}$$

Computing the genetic relationship matrix A, in contrast to Henderson (1976), the inbreeding of the ancestor lines in the base population was considered by calculating all diagonal elements c_{ii} by $1 + F_i$. Then the value of c_{ii} equals one if line i is not inbred and two if line i is fully homozygous.

Heritability was calculated based on variance components resulting from single-trait analysis following Hanson (1963).

Selection

In both single-trait and multiple-trait analysis, superior parental lines were selected by a total merit index. Following Smith (1936) and Hazel (1943), an optimum index resulting from the sum of breeding values of both traits predicted for each line multiplied by weighted factors was calculated by $y = b_1\ x_1 + b_2\ x_2$, where b_1 and b_2 are the weighted factors, and x_1 and x_2 are the breeding values of trait v and trait w, respectively. The b values were obtained from $b = P^{-1} \times G \times a$, where b is an $n \times 1$ vector of b_1 and b_2 values, P is an $n \times n$ matrix of phenotypic covariance among traits, G is an $n \times n$ matrix of genotypic covariance among traits, and a is an $n \times 1$ vector of economic weights for the traits. The matrices P and G were estimated using the ASReml software package (Gilmour et al. 2002).

Economic weights for the traits were assumed to be equal for both traits.

In each correlation scenario, 10% of the lines with the largest index value obtained from both single- and multiple-trait analysis were selected. For comparison of single- and multiple-trait analysis, mean genotypic value of selected superior lines averaged over both traits was computed.

Results

In this study, two traits with heritabilities of 0.7 and 0.3 were considered, with varying genetic and residual correlation relationships between traits. Simulated (real) and estimated (observed) correlations are displayed in Table 1. As expected, estimated phenotypic correlation among traits is similar to the simulated phenotypic correlation. But estimated genotypic correlation is also close to the simulated genotypic correlation.

The objective of this study was to determine whether a total merit index based on single- or multiple-trait breeding values is superior. In general, the gain in selection response is increased if multiple-trait breeding values are used in the selection (Figs. 1, 2), regardless of whether genetic (r_g) and residual (r_e) correlation among traits are identical. For three correlation scenarios with (1) $r_g = r_e = +0.8$, (2) $r_g = +0.4$ and $r_e = +0.8$, and (3) $r_g = -0.2$ and $r_e = +0.4$ there is little difference between mean genotypic value of lines selected by a total merit index of single- or by multiple-trait analysis, but in all other correlation scenarios, the mean genotypic value of lines selected by a total merit index of multiple-trait breeding values is higher than that of lines selected by index values of single-trait predictors. When traits are negatively correlated, the difference between multiple- and single-trait analysis is enhanced (Figs. 1, 2). The association of breeding values from single-trait analysis with those from multiple-trait analysis, is lowest for negatively-correlated traits and highest for positively-correlated traits (Figs. 3, 4).

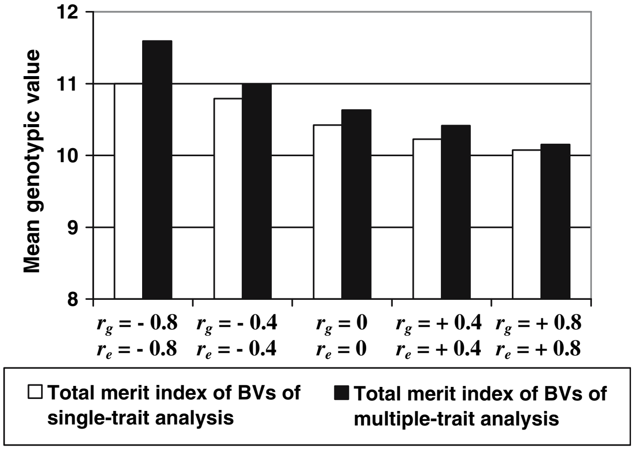

Fig. 1 Mean genotypic value of superior parental lines selected by total merit indices of single- and multiple-trait analysis and considering varying correlation coefficients among traits (with identical genetic r_g and residual r_e correlation). The mean genotypic value was averaged over both traits. *BV* breeding value

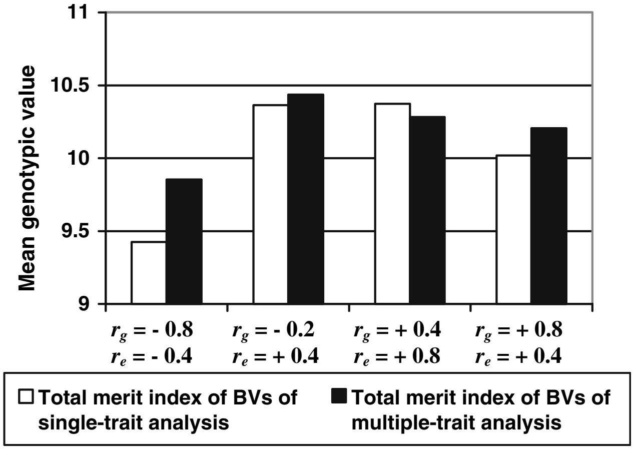

Fig. 2 Mean genotypic value of superior parental lines selected by total merit indices of single- and multiple-trait analysis and considering varying correlation coefficients among traits (where genetic correlation r_g is unequal to residual correlation r_e). The mean genotypic value was averaged over both traits. *BV* breeding value

Table 1 Simulated and estimated genotypic and phenotypic correlation between the traits considering varying genetic (r_g) and residual (r_e) correlation coefficients

Correlation scenario	Estimated genotypic correlation	Simulated phenotypic correlation	Estimated phenotypic correlation
$r_g = r_e = 0$	–0.02	0	–0.01
$r_g = r_e = -0.8$	–0.79	–0.38	–0.39
$r_g = r_e = -0.4$	–0.40	–0.13	–0.15
$r_g = r_e = +0.4$	0.36	0.13	0.12
$r_g = r_e = +0.8$	0.76	0.38	0.36
$r_g = -0.2$, $r_e = +0.4$	–0.22	0.12	0.12
$r_g = +0.4$, $r_e = +0.8$	0.36	0.37	0.36
$r_g = +0.8$, $r_e = +0.4$	0.76	0.14	0.12
$r_g = -0.8$, $r_e = -0.4$	–0.80	–0.14	–0.15

In general, the overall standard error of difference of multiple-trait predictors is lower than the overall standard error of difference of single-trait breeding values (Table 2). For multiple-trait breeding values, the overall standard error of difference is lower for negatively-correlated traits than for positively-correlated traits.

Discussion

In general, predictions were highly accurate, with simulated and estimated phenotypic and genotypic correlation close

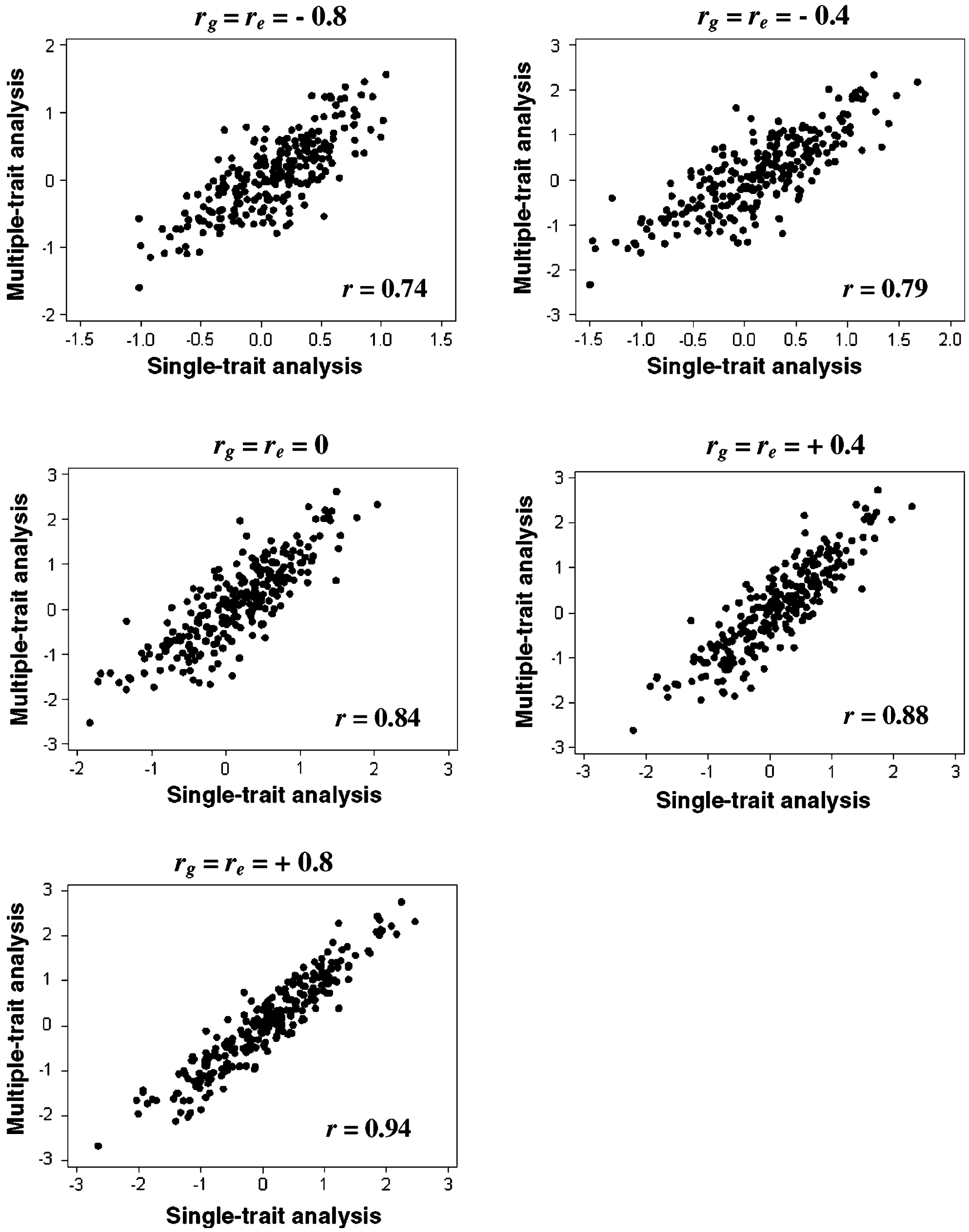

Fig. 3 Scatter plots of breeding values resulting from single- and multiple-trait analyses considering varying correlation coefficients among traits [with identical genetic (r_g) and residual (r_e) correlation]. Breeding values of each analysis were averaged over both traits. For each correlation scenario, Spearman's correlation coefficient *r* was computed (*right corner* of the graph)

together (Table 1). Using the REML estimation of genotypic and phenotypic correlations, Holland (2006) found that the power of detection was greater for phenotypic than for genotypic correlation. However, in our study the detection rates of genotypic and phenotypic correlation were similar.

The inclusion of information for correlated traits in one analysis results in a higher selection response than analysing these traits separately (Figs. 1, 2). In general, the mean genotypic value increased if lines were selected by a total merit index based on multiple-trait breeding values. This can be confirmed also by considering overall standard error of difference (Table 2). As the overall standard error of difference is lower in multiple-trait analysis than in a single-trait model, the gain in accuracy of multiple-trait breeding values is superior to single-trait analysis. Thompson and Meyer (1986) stated that the increase in selection response using multiple-trait breeding values is due to taking information for all correlated traits into consideration simultaneously in a single analysis and thus accounting for the residual covariance structure among traits. In addition, following Bernardo (1999), in the multiple-trait model the selection pressure for the traits is decreased. This decrease

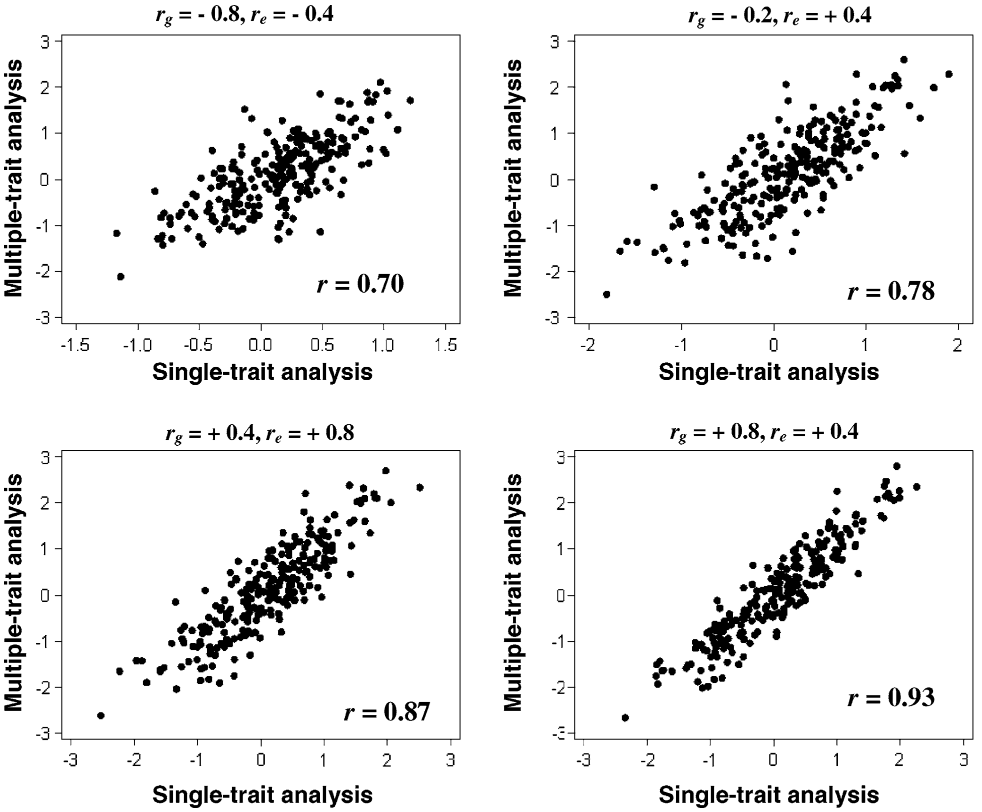

Fig. 4 Scatter plots of breeding values resulting from single- and multiple-trait analyses considering unequal genetic (r_g) and residual (r_e) correlation coefficients among traits. Breeding values of each analysis were averaged over both traits. For each correlation scenario, Spearman's correlation coefficient r was computed (*right corner* of the graph)

of selection pressure is the higher the more traits are considered (Bernardo 1991).

The advantages of multiple-trait analysis over a single-trait approach are greatest when traits are negatively correlated. For positively-correlated traits, the phenotypic values of the traits change in the same direction, whereas phenotypic values of negatively-correlated traits change in opposing directions. If two traits are negatively correlated, single-trait selection to increase one trait would result in a decrease in phenotypic performance for the second trait, whereas selection based on multiple-trait breeding values should provide opportunities for simultaneous gain in both traits. Consistent with this, we found that negative correlation between traits increases differences between mean genotypic values from multiple-trait analysis and those from single-trait analysis (Figs. 1, 2). Further, negative correlation between traits weakened the rank correlation between multiple-trait and single-trait breeding values (Figs. 3, 4), indicating that the breeding values estimated by the two methods differ more when traits are negatively correlated. Selection based on multiple-trait breeding values should therefore provide a greater gain in selection response if traits are negatively correlated. As noted by Verrier (2001), who examined marker-assisted selection using a multiple-trait BLUP model in an animal population, positively correlated traits can be simultaneously improved regardless of the selection strategy.

In our study, we used a total merit index resulting from the sum of breeding values (obtained from single- or multiple-trait BLUP) that were weighted by a factor. This weighted factor was calculated following Smith (1936) and Hazel (1943) and was obtained by multiplying the inverse of the phenotypic variance–covariance matrix among traits with the genotypic variance–covariance matrix and economic weights. Bernardo (1991) has suggested an alternative approach using retrospective index weights that were derived using the selection differential (the difference between the mean of the selected lines and the population mean). That approach is useful when small population sizes cause large errors in estimation of genotypic covariance among traits, but is not needed for simulated data that can be expected to be consistent. In our work the total merit index resulted from the weighted sum of BLUP breeding values and not from the weighted sum of phenotypic performance of the traits as in the standard Smith–Hazel selection index. This is an important difference because BLUP allows the genetic relatedness among the lines to be taken into account as a random factor in the statistical model. Including pedigree information in addition to the observation values of the traits can greatly enhance the selection response.

As we generated a "virtual" population by computer simulation, we were able to assume that the pedigree information was accurate. In practice, errors in the pedigree can occur, and these could lead to errors in the genetic

Table 2 Overall standard error of difference of single- and multiple-trait BLUP-breeding values for two traits with different heritabilities (h^2) considering varying genetic (r_g) and residual (r_e) correlation coefficients among traits

Correlation scenario	Single-trait BLUP	Multiple-trait BLUP
$r_g = r_e = 0$	6.64[a]	6.25
	11.93[b]	
$r_g = r_e = -0.8$	6.64	4.46
	9.83	
$r_g = r_e = -0.4$	6.64	5.82
	11.53	
$r_g = r_e = +0.4$	6.64	6.45
	11.55	
$r_g = r_e = +0.8$	6.64	6.55
	9.83	
$r_g = -0.2$, $r_e = +0.4$	6.64	6.36
	11.54	
$r_g = +0.4$, $r_e = +0.8$	6.64	6.50
	9.87	
$r_g = +0.8$, $r_e = +0.4$	6.64	6.50
	11.50	
$r_g = -0.8$, $r_e = -0.4$	6.64	5.67
	11.46	

[a] Overall standard error of difference of the analysis of trait *v* ($h^2 = 0.7$)

[b] Overall standard error of difference of the analysis of trait *w* ($h^2 = 0.3$)

relationship matrix. We were also able to expect the data to be consistent, without measurement error. In practical breeding, measurement error can result in outlier observations that will bias estimates. To address this, Jamrozik et al. (2007) suggested a robust estimation procedure using a multiple-trait BLUP model in which outlier observations were corrected in the iteration process for solving the MME. Applying this method in breeding Canadia Jersey cowes, they obtained similar breeding values as in a standard BLUP model.

Our research considered the simultaneous improvement of two or more traits. In practice, this is often desired. For example, breeders may want to increase both grain yield and protein content. In contrast, Satoh (2004) considered improvement of one trait with another trait held at its current level through the use of a restricted BLUP imposing constraints on some members of the population.

Disadvantages of multiple-trait BLUP are the high costs of computing and slower convergence of REML log-likelihood than when using single-trait BLUP. According to Mehrabani-Yeganeh et al. (1999) multiple-trait BLUP requires a large number of iterations because traits pull in different directions. Further, the use of a less stringent convergence criterion affects selection response more than under single-trait BLUP (Mehrabani-Yeganeh et al. (1999). In our study, 1 GB RAM on a Pentium IV processor was needed to compute a multiple-trait analysis of at least two correlated traits. Thus, a multiple-trait analysis of a high number of correlated traits could be computationally demanding.

In further research it would be interesting (1) to determine the influence of genetic correlations differing across environments and populations, and (2) to examine what happens if genes affecting a trait have different effect sizes and allele frequencies.

In conclusion, selecting potential parental lines that are characterized by a superior genetic disposition is an essential requirement in breeding self-pollinating crops. Poor decisions in parental selection will have major consequences for breeding success. Using multiple-trait breeding values seems to be an important tool for enhancing selection response in parental selection as economically relevant traits like grain yield and protein content, for example, are highly correlated among each other. Hence, we suggest the routine use of multiple-trait breeding values in selection decisions of parental inbred lines of self-pollinating crops whenever possible.

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Appendix

Mixed model equations (MME) of single-trait analysis

$$\begin{vmatrix} X'R^{-1}X & X'R^{-1}Z & X'R^{-1}S & X'R^{-1}T & X'R^{-1}V & X'R^{-1}W \\ Z'R^{-1}X & Z'R^{-1}Z+G^{-1} & Z'R^{-1}S & Z'R^{-1}T & Z'R^{-1}V & Z'R^{-1}W \\ S'R^{-1}X & S'R^{-1}Z & S'R^{-1}S+I\times\frac{1}{\sigma_s^2} & S'R^{-1}T & S'R^{-1}V & S'R^{-1}W \\ T'R^{-1}X & T'R^{-1}Z & T'R^{-1}S & T'R^{-1}T+I\times\frac{1}{\sigma_t^2} & T'R^{-1}V & T'R^{-1}W \\ V'R^{-1}X & V'R^{-1}Z & V'R^{-1}S & V'R^{-1}T & V'R^{-1}V+I\times\frac{1}{\sigma_v^2} & V'R^{-1}W \\ W'R^{-1}X & W'R^{-1}Z & W'R^{-1}S & W'R^{-1}T & W'R^{-1}V & W'R^{-1}W+I\times\frac{1}{\sigma_w^2} \end{vmatrix} \times \begin{vmatrix} \hat{b} \\ \hat{u} \\ \hat{o} \\ \hat{p} \\ \hat{q} \\ \hat{r} \end{vmatrix} = \begin{vmatrix} X'R^{-1}y \\ Z'R^{-1}y \\ S'R^{-1}y \\ T'R^{-1}y \\ V'R^{-1}y \\ W'R^{-1}y \end{vmatrix}$$

where: $\hat{b}$ = vector of fixed effect; $\hat{u}$ = vector of random additive genetic effect of the lines; $\hat{o}$ = vector of random year effect; $\hat{p}$ = vector of random location effect; $\hat{q}$ = vector of random block effect; $\hat{r}$ = vector of random genotype-by-environment interaction; y = vector of observation values; R = variance–covariance matrix of residual effects; I = identity matrix; $G = A\,\sigma_a^2$; A = genetic relationship matrix; $\sigma^2{}_a$ = additive genetic variance; $\sigma^2{}_s$ = variance of year effects; $\sigma^2{}_t$ = variance of location effects; $\sigma^2{}_v$ = variance of block effects; $\sigma^2{}_w$ = variance of genotype-by-environment interaction effects. X, Z, S, T, V, and W represent the corresponding design matrices. As in this study there is no fixed effect, X includes only an overall mean of $\mu = 1$.

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