Multi-trait BLUP in half-sib selection of annual crops

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Abstract

The Best Linear Unbiased Prediction (BLUP) methodology, which is widely used in animal and forestry genetic evaluation, can also be applied to annual crop breeding. The objective of this study was to compare the accuracy and efficiency of among- and within-half-sib family selection through the use of single- and multi-trait BLUP, and BLUE/ANOVA methods. Expansion volume and yield data from two recurrent selection cycles of a popcorn population were analyzed. Progeny tests were designed as a lattice. To maximize accuracy of the prediction of breeding values, the BLUP analyses included phenotypic values of the two cycles. All BLUP analyses were performed using the ASReml software. The multi-trait BLUP method demonstrated greater accuracy and efficiency in family selection. In the case of within-family selection, both accuracy and efficiency of multi- and single-trait BLUP methods were equivalent. The selection efficiency of the multi-trait BLUP was dependent on the estimated genetic parameters, particularly the difference between the genetic and environmental correlations of the traits.

Key words: sire model — animal model — genetic evaluation

Accurate prediction of the additive genetic values of individuals under selection is desirable in any breeding programme. Henderson (1974) stated that accuracy, or the correlation between the predicted and true breeding values, is maximized through use of the Best Linear Unbiased Prediction (BLUP) with pedigree information. In breeding programmes, superior individuals are normally selected based on traits that can be correlated, due to pleiotropism, genetic phase disequilibrium, and the common influence of the environment. A bias in selection of the correlated traits can occur if those traits are analyzed individually, especially with sequential selection (Pollak et al. 1984). To avoid this type of bias, and to obtain more precise and accurate predictions of breeding values, Henderson and Quas (1976) proposed the multi-trait BLUP method. This analysis tends to present greater accuracy because it simultaneously considers a greater amount of data and uses the genetic and residual correlations among the traits.

Multi-trait BLUP has been used in forestry and other perennial crops breeding with consistently favourable results. In a study on peach tree progenies derived from crosses involving 42 parents, De Souza et al. (1998a,b) used multi-trait BLUP to estimate genetic and phenotypic correlations. Costa e Silva et al. (2000) used single- and multi-trait BLUP in an analysis of Norway spruce (Picea abies) progenies derived from open pollination and controlled crosses. The results of their study strengthened the breeding strategy used in Denmark, based on a large central population and some small specialized populations. Multi-trait BLUP has also been used in Walnut (Juglans regia) breeding and was found to be superior to phenotypic selection (Aleta et al. 2004). In a simulation study involving two traits with different heritabilities (0.7 and 0.3), under equal, different and nil genetic and environmental correlation scenarios, and with no fixed effects and several random effects, Bauer and Léon (2008) verified greater efficiency in identifying genotypically superior pure lines and more accurate predictions through the use of multi-trait BLUP. Based on their review of the use of BLUP in plant breeding, Piepho et al. (2008) stated that multi-trait BLUP is most advantageous when the traits analyzed are highly correlated. The limitations of this technique are a greater demand for computer processing, due to the slow convergence of the REML process (Piepho et al. 2008), and low parsimony, which is mainly a concern when more than three traits are considered simultaneously (Resende 2007).

The objective of this study was to compare the accuracy and efficiency of single- and multi-trait BLUP, and BLUE/ANOVA methods in annual crop breeding, using half-sib families.

Materials and Methods

Experimental data: Data from two cycles of half-sib selection in the popcorn population Viçosa were analyzed for among- and within-selection. Each cycle consisted of evaluation of 196 families in a replicated trial, selection of the best 20 progenies, recombination of these families in isolated area (recombination plot), using remnant seeds, and selection of 196 superior plants for the next cycle. The tests were designed as a 14 × 14 simple lattice and carried out in the experimental station of the Federal University of Viçosa (UFV) in Coimbra, Minas Gerais, Brazil, in the 1999/2000 and 2001/2002 growing seasons. The following traits were assessed in each experimental plot: final stand (covariate), yield (kg/4.5 m²), grain moisture (%), covariate) and expansion volume (EV; ml/g), assessed in a hot air popcorn machine (1200 w) using a 30 g sample. The recombination plots (areas of crosses between selected families) were conducted at the experimental station of UFV in Ponte Nova, Minas Gerais, Brazil, in the 2000/2001 and 2002/2003 growing seasons. Twenty selected families were planted, intercalating one row of male plants every four rows of female plants. Two rows were also planted with the IAC 112 single hybrid (control). Each row was 20 m long, with up to 100 plants. The rows of females and the control were detasseled at flowering. Twenty plants were measured in each progeny and five to 10 plants in each row of the IAC 112. Each plant was measured for yield, in g/0.18 m², and EV, measured in a hot air popcorn machine using a 10 g sample. In the two cycles among- and within-selection were based on the Mulamba and Mock index, with weights 3 for EV and 1 for yield.

BLUP/REML analysis: The use of BLUP for among- and within-half-sib family selection aims to predict the additive genetic values of the
common parents of the progenies and of the individuals in the recombination plot. The models for family and individual data are both commonly used in animal genetic evaluation ('sire model' and 'animal model', respectively). When there are not phenotypic values of individuals within families in the progeny test, none additional genetic variance component can be isolated from the error variance. As in any cycle with half-sib progenies the dominance genetic relationship matrix for the individuals in the recombination plot is an identity matrix, it is not possible to fit the animal model with dominance, even by combining two or more cycles. Each element in the dominance relationship matrix is the probability that the two corresponding individuals have genotypes identical by descent (Mrode 2005).

Assuming the variance of the residual vector as \( R = \sigma^2_e I \), as the variance of the vector of due-to-dominance genetic values equal to \( \sigma^2_d I \), where \( \sigma^2_d \) is the dominance genetic variance, there is no convergence in the REML process. Then the error variance includes the dominance variance. The impossibility of adjusting the additive-dominant model is common in practically all breeding experiments, including those with animal, forestry and other perennial species. In general the data permits only the adjustment of the additive model.

If \( f \) families and \( p \) individuals were measured for \( t \) traits, then, assuming, in each cycle, assessment of the progenies in a lattice design with fixed effect of replication and random effect of blocks within replication (analysis with recovery of the interblock information), and assessment of plants in the recombination plot in the completely random design, with a genetically uniform common check (a single hybrid), the models for the analysis of the data of families and plants in the recombination plot, are given by:

\[
y = X\beta + Z_1 u_1 + Z_2 u_2 + \varepsilon
\]

\[
y = X\beta + Zu + \varepsilon,
\]

where \( y \) is the vector of phenotypic values, \( X \) is the incidence matrix of the fixed effects, \( \beta \) is the fixed effects vector, \( Z_1, Z_2 \) and \( Z \) are the incidence matrices of the random effects, \( u_1 \) is the vector of block/replication/generation effects, \( u_2 \) is the vector of the additive genetic values of the common parents of the families divided by 2, \( u \) is the vector of the additive genetic values of the individuals in the recombination plot, and \( \varepsilon \) is the residual vector, all relative to the \( t \) traits. Both models include a fixed effect of generation (confounded with the effect of year). In relation to the analysis of individual data, the model includes a fixed effect of population and a fixed effect of interaction population x generation. The ASReml programs are presented in the Appendix.

The criterion used to obtain the best linear unbiased predictor of a random vector is the maximization of the joint probability density function of the random vector(s) and the model, \( \text{Prob}(\mathbf{y}|\mathbf{X}). \) Alternatively the predictors can be obtained by maximizing the joint probability density function of the random vector(s) and \( \text{Prob}(\mathbf{y}|\mathbf{X}) \) relative to the number of generations; and \( G^T \), the restricted maximum likelihood estimator of the additive variance (Mrode 2005).

Assuming population in Hardy–Weinberg equilibrium the mean of the population obtained by mass selection on only one gender can be expressed as (Viana et al. 2009):

\[
M_1 = M + (1/2)E(A_s),
\]

where \( M \) is the mean of the base population and \( E(A_s) \) is the expectation of the additive genetic values of the selected individuals. In the case of among half-sib selection, with recombination of all progenies, the mean of the improved population can be expressed as (Viana et al. 2009):

\[
M_1 = M + (1/2)E\left(\frac{1}{2}A_s\right).
\]

Assuming, as Eberhart (1970), that the expected genetic gain with selection on both genders is twice the expected gain with selection on only one gender, the predicted genetic gain can be computed from parental control (c) and the predicted breeding values of the selected individuals (\( A_s \)) by:

\[
\Delta M_G = c \left( \frac{1}{n_i} \sum_{i=1}^{n_i} \lambda A_s \right).
\]

where \( n_i \) is the number of selected families or plants (20 and 196, for among- and within-selection), and \( c = 1 \) and \( k = 1/2 \) for family selection, or \( c = 1/2 \) and \( k = 1 \) for selection in the recombination plot.

This function is also obtained by an equivalent derivation of that used by Eberhart (1970), assuming that the predicted gain is proportional to a selection differential based on predicted breeding values (\( \Delta M_G = b(A_s - \overline{A}) \)), where \( \overline{A} \) is the mean of the breeding values of the selected individuals and \( \overline{A} \) is the mean of the predicted breeding values. Considering mass selection on only one gender and that the coefficient of proportionality is the regression coefficient of the genotypic value of half-sib family in the improved population (\( A_s \)) as a function of the additive genetic value of its common parent (selected individual), we have:

\[
b = \text{Cov}(A_s, \overline{A}) V(\overline{A})
\]

Assuming irrelevant changes in gene frequencies, \( b = 1/2 \). In general, \( b = 2r\lambda_X \), where \( r \) is the coefficient of relationship, \( X \) is selected individual and \( Y \) is its descendant in the improved population. With half-sib selection on only one gender, \( b = 1/4 \).

The derived function of predicting response to selection is more biased with selection on both genders, since with mass selection before flowering and half-sib selection with recombination only of selected progenies the mean of the improved population are, respectively:

\[
M_1 = M + (1/2)E(A_s) + E(f)
\]

\[
M_1 = M + (1/2)E\left(\frac{1}{2}A_s\right) + E(f')
\]

where the expectations of \( f \) and \( f' \) are functions of \( \Delta p \) (change in the favourable gene frequency), \( u \) (difference between the genotypic value of the homozygote of greater expression and the mean of the genotypic values of the homozygotes (m)), \( d \) (difference between the genotypic value of the heterozygote and \( m \)), and \( p \) (frequency of favourable gene) [only \( E(f') \)], for each gene. For a gene the parametric values of \( f \) and \( f' \) are:
Multi-trait BLUP in half-sib selection

\[ f = \Delta p(a - d) \text{ or } \Delta p(a) \text{ or } \Delta p(a + d) \]
\[ f' = \Delta p(a - pd) \text{ or } \Delta p(a + 0.5(1 - 2pd)) \text{ or } \Delta p(a + (1 - p)d) \]

if the common parent is homozygous for the gene that increase trait expression, heterozygous or homozygous for the gene that decrease trait expression, respectively.

The function of response to selection based on predicted breeding values was used to predict direct and indirect gains with selection on EV and, with multi-trait BLUP, with selection based on the rank values was used to predict direct and indirect gains with selection on trait expression, respectively.

EV and, with multi-trait BLUP, with selection based on the rank values was used to predict direct and indirect gains with selection on trait expression, heterozygous or homozygous for the gene that decrease trait expression, obtained from the average pairwise prediction error variance (average predicted gain is calculated from a generalized measure of heritability, \( f \)).

\[ \text{Heritability} = \frac{1}{P} \text{SD} \]

Other functions of response to selection were proposed by Cullis et al. (2006) and Piepho and Mühring (2007). In the former paper the predicted breeding values for EV and yield were 3 and 1.

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The estimates of the additive (four times the genotypic variance) and residual variances were very close between the multi-trait and single-trait BLUP analyses (Table 1).

The multi-trait BLUP gave superior accuracy compared with the single-trait analysis and BLUE/ANOVA. Compared with the single-trait BLUP, the multi-trait analysis presented accuracy values 5.9 and 4.8% superior for EV and yield, respectively.

The accuracy of this analysis is the square root of the residual variance. The accuracy of this analysis is the square root of the residual variance. The accuracy of this analysis is the square root of the residual variance. The accuracy of this analysis is the square root of the residual variance. The accuracy of this analysis is the square root of the residual variance.

Results

Among family selection ( sire model)

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Regarding the coincidence of the 20 families selected in the second cycle by the multi-trait and single-trait predictions of the breeding values and by phenotypic means based on the estimated family mean, differences were observed among the methods. Seventy-five and 80% of the families selected based on EV and on yield by the multi-trait analysis were also selected by the single-trait analysis. Based on phenotypic means, however, only 60% of the families selected based on

Table 1: Estimates of genetic and non-genetic parameters from BLUP/REML and BLUE/ANOVA (fixed model) using family data

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Multi-trait BLUP (2 cycles)</th>
<th>Single-trait BLUP (2 cycles)</th>
<th>BLUE/ANOVA (cycle 2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EV (ml/g)</td>
<td>Yield (kg/ha)</td>
<td>EV (ml/g)</td>
</tr>
<tr>
<td>Genotypic variance</td>
<td>1.8702 1.0025</td>
<td>102.179.0 0.0017</td>
<td>1.7520.0043</td>
</tr>
<tr>
<td>Block Rep. Gen. var.</td>
<td>1.8779</td>
<td>41.3922</td>
<td>1.8672</td>
</tr>
<tr>
<td>Residual variance</td>
<td>0.9120</td>
<td>539.872.0</td>
<td>10.0063</td>
</tr>
<tr>
<td>Heritability</td>
<td>0.3244</td>
<td>0.3294</td>
<td>0.2875</td>
</tr>
<tr>
<td>Accuracy</td>
<td>0.5786</td>
<td>0.5864</td>
<td>0.5461</td>
</tr>
<tr>
<td>Direct gain</td>
<td>0.75</td>
<td>-127.86</td>
<td>1.41</td>
</tr>
<tr>
<td>Indirect gain</td>
<td>0.37</td>
<td>-125.71</td>
<td>1.25</td>
</tr>
<tr>
<td>Gain w/sel. index</td>
<td>1.43</td>
<td>-39.134</td>
<td>-0.0093</td>
</tr>
<tr>
<td>Genetic correlation</td>
<td>-0.3934</td>
<td>-0.3934</td>
<td>-0.3934</td>
</tr>
<tr>
<td>Residual correlation</td>
<td>-0.3541</td>
<td>-0.3541</td>
<td>-0.3541</td>
</tr>
<tr>
<td>Phenotypic correlation</td>
<td>-0.2332</td>
<td>-0.2332</td>
<td>-0.2332</td>
</tr>
</tbody>
</table>

1Generalized measure of heritability for BLUP analysis; 2from Cullis et al. (2006); 3absolute value > 1; 4Mulamba and Mock (1978).
EV and 45% of those selected based on yield were also selected by the multi-trait BLUP.

**Within-family selection (animal model)**

The estimates of the additive and residual variances were also very similar between the multi-trait and single-trait BLUP analyses (Table 2). The accuracy and selection efficiency of the multi- and single-trait BLUP analyses were equivalent. Compared with BLUE/ANOVA, however, the accuracy values of the two BLUP methods were inferior for EV. In the BLUP analyses the genetic correlations were reduced (0.02 and 0.03 approximately) and the residual (0.11 and 0.10 approximately) correlations were superior to the genetic correlations. The predicted gains in EV by single- and multi-trait BLUP analyses were approximately equal (Table 2), and about 15% superior to the gain obtained with BLUE/ANOVA. The indirect gains for yield were irrelevant in the BLUP analyses. It is interesting to note that in the case of within-family selection the expected gains based on the generalized measure of heritability were, in general, 52–140% superior to the expected gains based on the predicted breeding values. With multi-trait BLUP analysis, the best predicted gains were also obtained with selection based index. The value predicted for EV is 98% of the maximum value, associated with positive gain in yield.

In relation to the coincidence involving the 196 individuals selected in the second cycle recombination plot, 98 and 99.5% of the individuals selected by the multi-trait analysis based on EV or on yield respectively, were also selected by the single-trait analysis. The multi-trait BLUP and the BLUE/ANOVA were also equivalent. The coincidences of selected individuals were 98 and 99% for EV and yield.

**Discussion**

**Among-family selection (sire model)**

The greater accuracy and selection efficiency of the multi-trait BLUP method, as compared with the single-trait analysis, was mainly due to the difference between the genetic and the environmental correlations relative to yield and EV (Table 1). According to Schaeffer (1984) and Thompson and Meyer (1986), the increase in accuracy obtained by using multi-trait BLUP is proportional to the absolute difference between the genetic and environmental correlations of the traits. When the heritability of the traits are equal, the selection efficiency of multi-trait BLUP, compared with single-trait analysis, depends only on the absolute difference between the genetic and environmental correlations of the variables analyzed (Resende 2007).

Our results corroborate those obtained by Bauer and Léon (2008) and by Persson and Andersson (2004). In the second study, the authors used Monte Carlo simulation to compare the prediction of the breeding values via multi-trait and single-trait BLUP, considering different values of genetic and environmental correlations and heritabilities. The authors observed that the multi-trait predictors resulted in a smaller average bias, and were therefore considered to be more accurate. Greater accuracy and efficiency of the multi-trait BLUP were also reported by Da Costa et al. (2002) in rubber tree breeding (*Hevea brasiliensis*), as well as by Kerr (1998) in the selection of open and controlled cross pollination cultivars in forestry breeding. These authors reported that an increase in the number of traits considered as selection criteria gave a greater advantage to the multi-trait analysis. When three traits were used as selection criteria, the increase in accuracy of the multi-trait analysis was less than 1% for all cultivars. However, when five traits were used as selection criteria, the increase in accuracy of the multi-trait analysis was 3% for the open pollination cultivars and 1.3% for the controlled pollination cultivars. Kadarmideen et al. (2003) compared the prediction accuracy of the breeding values for fertility by single-trait BLUP with the accuracy of the multi-trait analysis with fertility and milk production traits in dairy cattle. Both the predicted breeding values and the ranking of the animals were significantly different between the two analyses. The multi-trait analysis improved the accuracy of the predicted breeding values for each trait involved by reducing the prediction error variance. Multi-trait BLUP analysis of fertility and milk production was recommended by the authors, who argued that this analysis is efficient for traits that present unfavourable genetic correlation. Another advantage of the multi-trait BLUP observed in this study is the fact that this analysis permits prediction of the breeding values of individuals for a trait that was not assessed (fertility) through the assessment of a correlated trait (milk production). This extension allowed for prediction of the breeding values for fertility to be obtained for animals assessed only for milk production.

Compared with single-trait BLUP based only on the second cycle family test (not published), the multi-trait analysis

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Table 2: Estimates of genetic and non-genetic parameters from BLUP/REML and BLUE/ANOVA (fixed model) using individual data

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Multi-trait BLUP (2 cycles)</th>
<th>Single-trait BLUP (2 cycles)</th>
<th>BLUE/ANOVA (cycle 2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EV (ml/g)</td>
<td>Yield (g/0.18 m²)</td>
<td>EV (ml/g)</td>
</tr>
<tr>
<td>Additive variance</td>
<td>16.8423 ± 4E-8</td>
<td>221.5740 ± 0.0017</td>
<td>16.5041 ± 1.3E-7</td>
</tr>
<tr>
<td>Residual variance</td>
<td>11.1404</td>
<td>619.276</td>
<td>11.3845</td>
</tr>
<tr>
<td>Heritability</td>
<td>0.5301</td>
<td>0.2989</td>
<td>0.5221</td>
</tr>
<tr>
<td>Accuracy</td>
<td>0.7955</td>
<td>0.8755</td>
<td>0.7892</td>
</tr>
<tr>
<td>Direct gain</td>
<td>2.62</td>
<td>1.69</td>
<td>2.57</td>
</tr>
<tr>
<td>Indirect gain</td>
<td>-0.17</td>
<td>0.10</td>
<td>0.24</td>
</tr>
<tr>
<td>Gain w/selection Index</td>
<td>1.67</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td>Genetic correlation</td>
<td>0.0162</td>
<td>0.0262</td>
<td></td>
</tr>
<tr>
<td>Residual correlation</td>
<td>0.1080</td>
<td>0.1008</td>
<td></td>
</tr>
<tr>
<td>Phenotypic correlation</td>
<td>0.0121</td>
<td>0.0121</td>
<td></td>
</tr>
</tbody>
</table>

1 Generalized measure of heritability for BLUP analysis; 2 from Cullis et al. (2006); 3 Mulamba and Mock (1978).
considering the first two cycles gave more accurate breeding values for yield (0.87 vs. 0.37), greater predicted gain in EV (1.48 ml/g vs. 0.40 ml/g) and greater negative indirect gains in yield (−172.86 vs. −12.42 kg/ha).

Under lower selection intensity (40 selected families), the coincidences among the families selected by the different analyses were greater for EV (90%) and yield (82.5%), for the single-trait and multi-trait BLUP. In relation to BLUE/ANOVA, 72.5% of the families selected for EV and 57.5% of the families selected for yield would also be selected by the multi-trait analysis.

Within-family selection (animal model)
The multi-trait BLUP demonstrated accuracy equivalent to the single-trait analysis, showing that under the conditions studied, multi-trait analysis was not advantageous (Table 2). As emphasized, the decision to use multi-trait BLUP rather than a single-trait analysis would depend mainly on the heritabilities and correlations of the traits. Depending on the combination of these parameters, the efficiency of these two models may be similar. Thus, in situations where all the traits are observed for each plant, the heritabilities of the traits are similar, and all traits are favourably correlated, analysis with a model that considers multiple traits may not provide a substantial increase in the accuracy of the predicted breeding values (Schaeffer 1984). As the difference between the genetic and environmental correlations for EV and yield was reduced, no advantage was demonstrated by using multi-trait BLUP. Jain and Sadana (2000) compared accuracy and selection efficiency in bulls, using conventional, single-trait and multi-trait BLUP methods, following the animal model. Their results showed that multi-trait analysis can be either more or less accurate than the single-trait analysis, depending on the genetic parameters estimated.

For within family selection, multi-trait analysis combining the first two cycles surpassed the single-trait analysis using data from only the second cycle (not published), relative to EV predicted gain (1.71 ml/g vs. 0.98 ml/g). The estimated indirect gains in yield were different in magnitude and sign (−0.17 g/0.18 m² vs. 0.85 g/0.18 m²). The accuracy of prediction was inferior with multi-trait BLUP, for both traits.

Acknowledgements
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Appendix

ASReml code for the single-trait BLUP analysis

Single-trait BLUP analysis, family data, two cycles (title line)
gen 2 # generation, two levels
rep 2 # replication, two levels
blo 28 # block, 28 levels
fam 392 # family
ev # expansion volume
y # yield
z != ev !+ y # to permit estimation of correlations/covariances
pedf.txt # pedigree file
c12f.asd # data file

ASReml code for the multi-trait BLUP analysis

Multi-trait BLUP analysis, family data, two cycles

generation, two levels
rep 2 # replication, two levels
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