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PREVIEW

ESTIMATION OF GENETIC PARAMETERS FOR PRODUCTION TRAITS OF
CORN AND DUAL PURPOSE SHEEP

by

Christina Magdalena van Zyl

A DISSERTATION

Presented to the Faculty of
The Graduate College at the University of Nebraska

In Partial fulfillment of Requirements

For the Degree of doctor of Philosophy

Major: Animal Science

Under the Supervision of Professor L. Dale Van Vleck

Lincoln, Nebraska

February, 1998

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DISSERTATION TITLE

Estimation of genetic parameters for production traits

of corn and dual purpose sheep

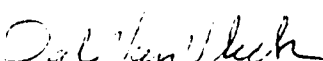
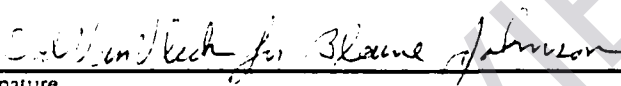
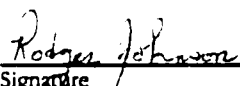

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ESTIMATION OF GENETIC PARAMETERS FOR PRODUCTION TRAITS OF CORN AND DUAL PURPOSE SHEEP

Christina Magdalena van Zyl, Ph.D.

University of Nebraska. 1998

Advisor: L. Dale Van Vleck

Phenotypic data were obtained for eight production traits from matings of seven unique sets of four fully inbred lines of each of two different heterotic groups of corn. Estimates of variance components due to line effects were obtained with derivative-free restricted maximum likelihood. Comparisons of estimates of variance due to line effects with and without taking relationships into account indicated that when relationships among lines are ignored, potential estimates of variance are less than when relationships are considered. When multiple covariates for marker alleles were included in the model, estimates of variance due to line effects increased for most traits when marker alleles were included in the analysis in contrast to what was expected.

Genetic parameters for Columbia, Polypay, Rambouillet and Targee sheep were estimated using REML with animal models for fertility, growth and wool traits, and litter weight weaned. Heritability estimates ranged from .03 to .11 for fertility traits, from .07 to .26 for growth traits and from .25 to .53 for wool traits. Heritability estimates ranged from .03 to .12 for litter weight weaned.

Estimates of direct genetic correlation among fertility traits and among growth traits

were positive and ranged from .58 to 1.00 and .18 to 1.00, respectively. Estimates of direct genetic correlation between fleece weight and staple length were positive (.50 to .70), but were negative between fleece weight and fleece grade (-.60 to -.34) and between staple length and fleece grade (-.72 to -.40). Fertility and wool traits were essentially uncorrelated. Growth and fertility traits were slightly positively correlated. Growth traits had a moderate positive direct genetic correlation with fleece weight and staple length, but were not correlated with fleece grade. Litter weight weaned had a moderate positive genetic correlation with fertility and growth traits, but was not correlated with wool traits. Genetic parameters can be used in deriving economic indexes for selection of dual purpose sheep.

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Without the grace of God, I would not have been able to conduct the research that was part of this dissertation, but he restored my health and renewed my strength. All glory be to God, for from him and through him and to him are all things. To him be the glory forever (Romans 12:14).

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Ek dra hierdie verhandeling op aan my wonderlike ouers

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Chapter 1

Estimation of Variance Components in Corn Due to Line Effects from F1 Performance With and Without Pedigree Relationships Among Lines

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ABSTRACT

Phenotypic data were obtained for eight traits from design II matings of seven unique sets of four fully inbred lines of each of two different heterotic groups of corn with a total of 112 crosses grown in up to 20 locations in two years. In the first model, lines within each heterotic group were considered random and unrelated to compare with a model with numerator relationships among lines included. The second set of comparisons was similar to the first, but with effects of lines in the first heterotic group considered as fixed in both models. For the third set of comparisons, effects of lines in the second heterotic group were considered as fixed in both models. Estimates of variance components due to line effects were obtained with derivative-free restricted maximum likelihood. Estimates of variance due to line effects with lines assumed unrelated divided by estimates taking relationships into account were as follows: 1) with both sets of lines considered random, ratios ranged from 0.50 to 0.87 with average of 0.67 for SSS lines and from 0.62 to 1.00 with average of 0.82 for NSS lines, 2) with effects of lines in the NSS heterotic group considered fixed, ratios ranged between 0.59 and 0.89 with average of 0.68 and 3) with effects of lines in SSS heterotic group considered fixed, the ratios ranged between 0.68 and 0.94 with average of 0.82. This reduction indicates potential gain from selection would be more than predicted from estimates of variance due to line effects ignoring relationships among lines.

INTRODUCTION

The design II or factorial mating design of Comstock and Robinson (1948) is used to estimate components of genetic variance, based upon covariances among relatives determined by the matings. Estimates of variance components under the original Comstock and Robinson model are based on the assumption of random choice of parents from the population. In applied maize breeding, choice of parents is rarely random. Inbred parents typically originate from different heterotic groups, and varying degrees of relatedness may exist among parents used in the matings. Animal geneticists regularly utilize genetic relationship matrices when estimating genetic components of variance. In dairy cattle, Dong and Van Vleck (1989) noted that ignoring existing relationships usually resulted in a reduction in estimates of genetic variance. A relationship matrix other than the identity matrix was necessary to eliminate confounding between additive genetic and environmental effects with an individual animal model. Ignoring some relationships also resulted in a reduction in estimates of genetic components of variance. Naciri and Gallais (1994) showed that simultaneous analysis of $S_0 \times S_0$ crosses and of S_1 progenies provides estimates of variance components within as well as among lines. The objective of this study was to compare estimates of components of variance, using data obtained from a design II mating in corn, for models which included and models which ignored the relationship matrix among lines.

MATERIALS AND METHODS

Phenotypic data were obtained for eight traits from a design II mating design (Comstock and Robinson , 1948). Progeny were obtained by crossing seven different sets of four inbred lines per set from the Iowa Stiff Stalk Synthetic heterotic group (SSS) at random with seven sets of four completely inbred lines unrelated to SSS (designated NSS), resulting in sixteen single-crosses per set (Table 1). Replicates of each set were cultivated over twenty locations and two years. Performance data were obtained from the resulting 4480 plots for the 112 single-cross hybrids although no traits were measured for all plots (Table 2).

Brittle snap was not originally planned as a trait but interest in this trait developed at one location. Two additional locations were grown with the intent to measure artificial brittle breakage. Natural storm pressure occurred before scheduled artificial breakage causing expression in both plantings resulting in the information analyzed. Measurements from these locations were analyzed separately for brittle breakage and excluded in analyses of the other traits. Brittle snap was measured as percentage of plants snapped at or below the ear node. Plant and ear heights were measured at 15.5-cm increments from ground to tip of a tassel or ear node, respectively. Root lodging was measured as the percentage of plants not root lodged in a plot. Stalk lodging was the percentage of plants not stalk lodged in a plot. Days to pollen shed were recorded as growing day units (gdu) from planting to when 50% of the plants were shedding. Days were calculated between 30°C maximum and 10°C minimum gdu. Yield was recorded as pounds of grain and converted to metric tons per hectare at 15.5%

moisture. Moisture of grain at harvest was electronically collected during harvest and recorded as the yield to moisture ratio of kg.ha^{-1} to kg.moisture^{-1} (%). Data characterization for traits measured is reported in Table 2.

Analyses for single traits were based on the following model:

$$y = X\beta + Zu + e.$$

where

β = vector of fixed effects associated with records in y by X . Fixed effects were environment (year by location), and with some models, parental lines were specified as fixed:

u = vector of random effects associated with records in y by Z (random effects were effects of parental lines not specified as fixed), for example

$u = (u_1 \ u_2)'$ with both parental lines considered random, and

e = vector of random residual effects.

The first and second moments are: $E[y] = X\beta$

and
$$V \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = G = \begin{pmatrix} A_{SSS}\sigma_1^2 & 0 \\ 0 & A_{NSS}\sigma_2^2 \end{pmatrix}$$

$$V[e] = R = I_n\sigma^2$$

where

A_{SSS} = numerator relationship matrix among SSS lines.

A_{NSS} = numerator relationship matrix among NSS lines.

σ_1^2 = variance of effects for SSS lines,

σ^2_{L} = variance of effects for NSS lines, and

σ^2 = residual variance.

The first model accounted for all relationships and lines were considered random. This model was compared to a similar model with pedigree information ignored but with lines considered random (Table 3). The second comparison was similar to the first, but with lines in the first heterotic group (SSS) considered as fixed in both models. The third comparison was similar to the second, but with lines in the second heterotic group (NSS) considered as fixed in both models. Calculations pretending effects of one set of lines are fixed removes potential associations between lines in one group and lines in the other groups which otherwise may bias estimates of variance components (e.g., Henderson, 1973).

To avoid confusion in terminology used to define genetic likeness, in these analyses the convention of animal breeders was followed to use the numerator relationship matrix, A , as a measure of genetic likeness among lines. Some plant breeding papers (e.g., Bernardo, 1994) have used instead, the matrix of coefficients of coancestry F which is $.5A$. With a sire and dam model corresponding to lines in heterotic groups SSS and NSS, the sire and dam components of variance in the absence of maternal effects, are estimates of one-fourth of additive genetic variance. Henderson (1977), however, presented a formula that indicated that with non-related and 100% inbred lines that the line component of variance estimates one-half of additive genetic variance.

A final complexity arose when instead of A, F was used for these analyses in the MME. With F, the estimate of line variance was within rounding exactly twice the estimate with A, the log likelihoods were exactly the same, and the fixed effects solutions with comparable constraints were also exactly the same. This result implied that the models with A and F are equivalent (see Henderson, 1985). The question then became what is the genetic explanation of the line component of variance when inverses of A or F are used in the mixed model equations? The answer became apparent based on reflection of what A and F are when lines are unrelated and 100% inbred; 2I and I, respectively. With F = I, the MME reduce to the MME used by Henderson (1977) to predict line effects. The original analyses that compared estimates with and without relationships used inverses of A and I when inverses of A and 2I should have been used. With F, each of the estimates of line variance is one-half additive genetic variance (Henderson, 1977) and with A, each estimate is one-fourth of the additive genetic variance ($\sigma_g^2/4$) as with sire models. Obviously these are equivalent models as the genetic part of the variance of the observation vector, y, (measurements on the F_1) with A is:

$$Z_1 A_{SSS} Z_1' \sigma_g^2/4 + Z_2 A_{NSS} Z_2' \sigma_g^2/4 \text{ and with F is}$$

$$Z_1 F_{SSS} Z_1' \sigma_g^2/2 + Z_2 F_{NSS} Z_2' \sigma_g^2/2 \text{ for the case when line variances are the same}$$

within SSS and NSS and where Z_1 and Z_2 are the model matrices for line effects and A_{SSS} and A_{NSS} (F_{SSS} and F_{NSS}) are the numerator relationship (coefficients of coancestry) matrices for lines in SSS and NSS with zero relationships between SSS and NSS lines. For non-zero relationships between SSS and NSS, then additional terms are required such as

$$Z_1 A_{SSS,NSS} Z_2' \sigma_g^2/4.$$

Thus, when the comparison was made correctly, the original expectation was fulfilled. In general, estimates of line variance increased when relationships were considered, either with A and 2I or with F and I.

Estimates of variance components due to line effects were obtained with a derivative-free restricted maximum likelihood program (MTDFREML; Boldman et al., 1995). The MTDFREML package is a set of programs using numerator relationships and a derivative-free algorithm to obtain REML estimates of variance and covariance components. These programs can be used to obtain solutions for fixed effects, breeding values and other random effects, as well as sampling variances of solutions to MME and expected values of the solutions. Fixed effects, covariates and other random effects can be specified separately for each trait. With the derivative-free algorithm, convergence for variance and covariance component estimation occurs when the global maximum of the log likelihood function is found. The simplex (polytope) method described by Nelder and Mead (1965) is the procedure used to locate the minimum with respect to the variance components of -2 times the logarithm of the likelihood (-2Λ) which corresponds to the maximum of the logarithm of the likelihood. With MTDFREML, $-2\Lambda = \text{constant} + \log |R| + \log |G| + \log |C| - y'Py$ with C a full-rank portion of the coefficient matrix of the mixed model equations and $\log |G| = \log |A_{SSS}| + q_1 \log(\sigma_1^2) + \log |A_{NSS}| + q_2 \log(\sigma_2^2)$ where q_1 is the order of A_{SSS} (number of SSS lines), q_2 is the order of A_{NSS} , σ_1^2 is the variance of effects due to SSS lines and σ_2^2 is the variance of effects for NSS lines, and $y'Py$ is the generalized residual sum of squares (Harville, 1977; Smith and Grazer, 1986; Meyer, 1989). The derivative-free method

tries different R and G (e.g., σ^2 of $R = I_N \sigma^2$, σ_1^2 of $A_{SSS} \sigma_1^2$, σ_2^2 of $A_{NSS} \sigma_2^2$) until the combination that maximizes Λ (or minimizes -2Λ) is found for the data, y . The simplex algorithm is not guaranteed to converge to a global maximum. The variance of the simplex, which is an intermediate convergence criterion, depends on the current simplex and becomes small even if convergence is to a local minimum. Therefore the program is restarted with estimates at apparent convergence as initial values until a global maximum is found (e.g., -2Λ not changing to third decimal in consecutive restarts). Note that a smaller $-2 \log$ likelihood indicates a better fit of the model.

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RESULTS AND DISCUSSION

The log likelihoods multiplied by -2 for the models with and without pedigree information are shown in Table 4. In the comparison with effects of lines within both heterotic groups considered random. Model 1a with lines assumed unrelated was compared to Model 1b with pedigree information included. The -2log likelihood improved for all eight traits after pedigree relationships were included. The changes in -2Δ were generally small.

When effects of lines of the NSS heterotic group were considered as fixed in the second comparison (Model 2a with Model 2b), the -2Δ were essentially the same although -2Δ improved slightly for seven of the eight traits after pedigree information was included. Similarly when effects of lines in the SSS heterotic group were considered as fixed in the third comparison (Model 3a with Model 3b) the -2Δ improved for all eight traits when pedigree information was included.

Comparisons of estimates of variance due to effects of SSS lines are shown in Table 5 when lines in the SSS heterotic group were considered as random. Estimates of variance due to effects of NSS lines for models with lines in the NSS heterotic group considered as random are reported in Table 6.

The ratio of the estimate of line variance with pedigree information included in the model to the estimate of line variance with pedigree information included was calculated for each

analysis. The ratios also are shown in Tables 5 and 6. In all comparisons the estimates of variance due to effects of lines increased after pedigree information was included except for one trait with lines in NSS assumed random.

With both sets of lines considered to be random, the ratios of estimated components of variance due to effects of lines in SSS ranged from 0.51 to 0.87 with an average of 0.67 (Table 5: Model 1a vs Model 1b). With effects of lines of the NSS heterotic group considered as fixed and SSS lines as random, the estimated ratios ranged between 0.59 and 0.89 with an average of 0.68 (Model 2a vs Model 2b).

For all traits except days to shed estimates of variance due to effects of lines in the NSS heterotic group increased after pedigree information was included (Table 6). With effects of lines in the SSS heterotic group also considered as random, the ratios of estimates of variance due to effects of NSS lines, ranged between 0.62 and 1.00 with an average of 0.82 (Model 1a vs Model 1b). When effects of lines of the SSS heterotic group were considered as fixed in the second comparison (Model 3a vs Model 3b) the ratio of estimates of variance ranged between 0.69 and 0.94 with an average of 0.82 which indicates an average increase in estimates of variance due to line effects after pedigree information was included.

The original expectation in these analyses was that including relationships in the mixed model equations (MME) would increase the estimates of additive genetic variance as has generally been reported for analyses of milk yield for sire models in dairy cattle (e.g., Dong and Van Vleck, 1989; Hudson and Van Vleck, 1982).

When one heterotic group is considered as fixed, effects of any confounding of lines in that heterotic group on estimated variance due to line effects of the heterotic group considered as random should be eliminated. Estimates of variance due to effects of lines in the SSS heterotic group decreased for seven of eight traits when NSS lines were considered to be fixed rather than random (Model 1b vs. Model 2b and Model 1a vs Model 2a in Table 5). When effects of lines in the NSS heterotic group were considered as random, estimates of variance also decreased for seven of eight traits when SSS lines were considered to be fixed rather than random (Model 1b vs Model 3b in Table 6) and for all eight traits for Model 1a vs Model 3a (Table 6).

Estimates of residual variance are reported in Table 7. For all traits and all comparisons, the estimates of residual variance did not change much after pedigree information was included or when effects of lines in one or the other heterotic group were considered as fixed.

The increase in variance due to line effects after including numerator relationships among the lines, indicates that potential gain from selection would be underpredicted if estimates of variance due to line effects are used and relationships among lines are ignored. The results

also suggest that partial confounding of lines from one heterotic group in the mating set may bias estimates of variance due to effects of lines in the other heterotic group. Gain from selection would be more than predicted from estimates of variance due to line effects, ignoring relationships among lines.

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