Genetic Parameters for Test-Day Electrical Conductivity of Milk for First-Lactation Cows from Random Regression Models

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ABSTRACT

Electrical conductivity (EC) of milk has been introduced as an indicator trait for mastitis during the last few decades. The correlation of EC to mastitis, easy access to EC data, and the low cost of recording are properties that make EC a good indicator trait for mastitis. In this study, EC was measured daily during the lactation and available from 2101 first-lactation Holstein cows in 8 herds in the United States. Data were analyzed with an animal model that included herd-test-day, age at calving and days in milk (DIM) as fixed effects, and random additive genetic and permanent environmental effects. A repeatability model and 5 random regression (RR) models with increasing order of Legendre polynomials were used. The goodness of fit for the different models was evaluated based on several tests. Our results indicate that the best model was a RR model with a fourth-order Legendre polynomial for both additive genetic and permanent environmental effects. Heritability estimates obtained with this model were from 0.26 to 0.36. Due to the relatively high heritability obtained for EC of milk, EC might be a potential indicator trait to use in a breeding program designed to reduce the incidence of mastitis.

(Key words: dairy cattle, electrical conductivity, mastitis, random regression model)

Abbreviation key: $2\ln A$ = twice the log restricted likelihood, **AG** = additive genetic, **AIC** = Akaike information criterion, **BIC** = Bayesian information criterion, **EC** = electrical conductivity, **MSEP** = mean square error of predictions, **PE** = permanent environment, **COP** = the correlation between observed and predicted value, **RR** = random regression.

INTRODUCTION

Electrical conductivity (**EC**) of milk was introduced as an indicator trait for mastitis in the 1970s and has been used since then for detection of mastitis (Hamann and Zecconi, 1998). Electrical conductivity is dependent on the concentration of anions and cations, with Na^+ , K^+ , and Cl^- being the most important. If a cow has mastitis, the concentration of Na^+ and Cl^- in the milk increases, which leads to increased EC of milk from infected quarters (Kitchen, 1981). Using current technology like automatic milking systems, EC can be measured cheaply and easily. Records of EC are available within a few seconds after milking, thus information on EC is useful for early detection of mastitis. From an animal welfare point of view, a system for on-line monitoring of udder health status is crucial in automatic milking systems. In addition to using EC as a management tool, it might be possible to use EC as an indicator trait for mastitis resistance in an udder health index for genetic improvement of dairy cattle. Today, selection for mastitis resistance is, with a few exceptions, based on SCC information that is normally recorded only every 4 to 8 wk. This means that most of the clinically infected cows do not have SCC record from the period when the cow is infected. Due to the possibility of daily recording of EC, it may be a valuable source of information about the cow's udder health. However, to be included in a breeding program, the trait must express genetic variation and be correlated with the breeding goal trait, in this case mastitis resistance. Estimates of genetic parameters for EC are scarce, though Goodling et al. (2000) presented promising results. Their work indicated that the heritabilities for lactation averages of EC were in the range from 0.27 to 0.39 for first-lactation cows. Several investigations have been carried out to verify phenotypic association between EC and mastitis (Nielen et al., 1992; DeMol et al., 1999; Norberg et al., 2004), but not much information exists on genetic correlation between EC

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and clinical mastitis. However, Goodling et al. (2001) found a regression of daughter EC on sire PTASCS on 0.8 for first lactation cows. Furthermore, preliminary results indicated that the genetic correlation between EC and clinical mastitis for first-lactation cows is about 0.65 (Rogers, 2002).

Test-day models for estimation of genetic parameters for production traits (Ptak and Schaefer, 1993; López-Romero and Carabaño, 2003) and SCS (Reents et al., 1994; Mrode et al., 2003) have been investigated in numerous studies, and a test-day model for EC can be considered for estimation of genetic parameters. In the simplest case, a repeatability model can be used to model test-day EC without computational difficulties. However, the repeatability model assumes both the additive genetic (**AG**) and permanent environmental (**PE**) variance to be constant throughout the lactation. It is also assumed that genetic and PE correlations between records at different stages of lactation are unity. Reents et al. (1994) and Haile-Mariam et al. (2001) showed that these assumptions do not hold for test-day analysis of SCS. Alternatively, records at different DIM could be regarded as separate traits and be analyzed using multivariate methodology. This would require estimation of (co)variance components for all DIM which is computationally very demanding. Random regression (**RR**) models are a combination of these 2 alternative approaches mentioned above. Such models may be well suited for analysis of longitudinal traits because the random regression coefficients induce a covariance structure along a given trajectory (Van der Werf et al., 1998). However, the choice of functions for modeling AG and PE effects will influence the estimated (co)variance components. Thus, different models must be carefully evaluated.

Genetic parameters for test-day EC records are unknown, therefore, the objective of this study was to estimate variances and heritabilities for test-day EC in first lactation cows. Various test-day models were evaluated, starting with a simple repeatability model, continuing with RR models with various standardized Legendre polynomials for modeling AG and PE effects. Due to the lack of information on variance components and genetic parameters for EC, the emphasis in this paper will be on the biological interpretation of the results and the possible use of EC as an indicator trait for mastitis in a breeding program.

MATERIALS AND METHODS

Data

Data consisted of daily records of EC collected in the period from June 1994 through June 1998 from 8 high-producing dairy herds in New York, South Carolina,

California, and Florida, with herd size ranging from 600 to 3600 cows. Only records from first-lactation Holstein cows, calving from age 20 to 32 mo were included in the study. Records from d 6 to 305 after calving were considered. Only cows from sires having more than 2 daughters were included. Descriptive statistics of the data are presented in Table 1.

Electrical conductivity was measured in millimho (mmho) in composite milk from every milking with the Afikim computerized milking and management system (SAE Afikim, Kibbutz Afikim, Israel), and daily averages for EC were recorded. The data were obtained directly from the farm. Obvious recording errors were omitted prior to the genetic analysis (less than 0.01% of the data). The distribution of the EC records were close to normal, and EC was not transformed prior to the analysis.

Models

The following animal model was used:

$$Y_{ijkp} = A_i + HTD_j + DIM_k + \sum_{n=0}^r p e_{pn} Z_{kn} + \sum_{n=0}^t a_{pn} Z_{kn} + e_{ijkp}$$

where

Y_{ijkp} = observation of test-day record of EC,

A_i = fixed effect of age at first calving class i ($i = 1, \dots, 12$),

HTD_j = fixed effect of herd-test-day class j ($j = 1, \dots, 4225$),

DIM_k = fixed effect of DIM class k ($k = 1, \dots, 300$),

Z_{kn} = polynomial n for DIM k , where $n = \{0, \dots, r\}$ for PE effects and $n = \{0, \dots, t\}$ for AG effects,

$p e_{pn}$ = random regression coefficient on Z_{kn} , for the permanent environmental effect of cow p ,

a_{pn} = random regression coefficient on Z_{kn} , for the additive genetic effect of animal p , and

e_{ijkp} = random residual.

Dam pedigree information was unavailable, so a pedigree including only sire of cows was used. A total of 16 models with various combinations of Legendre polynomials from zeroth- to fourth-order were attempted. For the AG effects, only polynomials with equal or lower order fit than for the PE effects were tested, because modeling the PE curve with a lower order of fit than the genetic curve may cause overestimation of the heritabilities (Pool and Meuwissen, 1999; Kettunen et al.,

Table 1. Descriptive statistics of the data.

Description	Value
EC ¹ records	419,048
Cows	2101
Mean EC records per cow	199.5
Sires	172
Mean daughters per sire	12.2
Mean records per herd-test-day class	99.2
Mean records per DIM	1396.8
EC, ² mean (SD)	11.7 (1.4)

¹Electrical conductivity.²In millimho in composite milk, daily averages.

2000). In this study, models with unequal order of fit for the AG and PE effect did not converge; therefore only results from models with equal order of fit will be presented and discussed.

The models were abbreviated as follows: the repeatability model = G0P0, the model with a first-order Legendre polynomial used for both AG and PE effects = G1P1, etc., and up to the model with a fourth-order Legendre polynomial for both AG and PE effects = G4P4. In addition to the test-day models considering all EC records for a cow, the lactation was divided into 30-d periods, and variance components were estimated within each period with a repeatability model.

Estimation of (co)variance components for all models was carried out using the AI-REML algorithm (Madsen et al., 1994; Johnson and Thompson, 1995) included in the DMU-package (Madsen and Jensen, 2000). Homogeneous residual variance was assumed for all models.

Additive genetic ($\sigma_{a_k}^2$) and PE ($\sigma_{pe_k}^2$) variances and heritabilities at DIM k (h_k^2) were calculated as:

$$\begin{aligned}\sigma_{a_k}^2 &= \mathbf{z}_k' \mathbf{G} \mathbf{z}_k \\ \sigma_{pe_k}^2 &= \mathbf{z}_k' \mathbf{P} \mathbf{z}_k \\ h_k^2 &= \frac{\sigma_{a_k}^2}{(\sigma_{a_k}^2 + \sigma_{pe_k}^2 + \sigma_e^2)}\end{aligned}$$

where

$\mathbf{z}_k$ = vector of polynomials in the model for DIM k ,
 $\mathbf{G}$ = (co)variance matrix for AG RR coefficients,
 $\mathbf{P}$ = (co)variance matrix for PE RR coefficients,
 and
 σ_e^2 = residual variance.

Comparison of Models

Models were compared based on twice the log-restricted likelihood ($2\ln\Lambda$), the residual variance, the ability to predict randomly excluded observations

[mean square error prediction (**MSEP**) and the correlation between observed and predicted EC values (**COP**)]. Values of $2\ln\Lambda$ for all models were given relative to the repeatability model. Nested models were compared using the likelihood ratio test. The likelihood tends to favor complex models with many parameters, so the Akaike information criterion (**AIC**) (Akaike, 1973) and the more conservative Bayesian information criterion (**BIC**) (Schwarz, 1978) were also used.

The likelihood-ratio test statistic for 2 models i and j , where i is nested within j is given by:

$$-2\ln\Lambda = 2\ln \frac{L(i)}{L(j)} \sim \chi_{v_j-v_i}^2$$

AIC and BIC are defined as:

$$\text{AIC} = 2 \left[\ln \frac{L(i)}{L(0)} - (v_i - v_0) \right]; \text{ and}$$

$$\text{BIC} = 2\ln \frac{L(i)}{L(0)} - (v_i - v_0) \ln(N - p);$$

where $L(0)$ and v_0 are the restricted likelihood and number of parameters of the repeatability model, N is the number of observations, and p is the rank of fixed effects incidence matrix.

Predictive ability was estimated by prediction of randomly excluded observations. Three different data sets with 10% of the observations excluded were generated. For all data sets MSEP was calculated as:

$$\text{MSEP} = \frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2,$$

where y_i is an observed test-day record in the excluded dataset, $\hat{y}_i$ is the prediction of the observation, and n is the total number of observations. The mean of MSEP in the 3 data sets was calculated. (Co)variance components estimated based on the remaining data set were used as the true parameters. Additionally, the variance components obtained in the 30-d periods were compared with parameter trajectories obtained in RR models.

RESULTS AND DISCUSSION

Lactation Curve for Electrical Conductivity

Mean test-day EC by DIM are given in Figure 1. Electrical conductivity decreased the first 50 d after calving, and increased slightly the rest of the lactation. The same trend was found by Sheldrake et al. (1983), but Maatje et al. (1992) found a decreasing level of EC in milk from uninfected quarters as lactation pro-

Figure 1. Mean test-day electrical conductivity (EC) of milk for all cows by DIM.

gressed. In our study both healthy and infected cows were included and EC increased in the beginning and the end of the lactation when the cows are most susceptible to infections. The shape of the curve resembles the lactation curve for SCC (Sheldrake et al., 1983; Schutz et al., 1995; Schepers et al., 1997). For individual cows, curves will show a peak when the cow gets mastitis, and the increase usually happens 1 or 2 d before the cow receives a treatment.

Estimation of Variance Components for Electrical Conductivity

Estimated AG variance by DIM is given in Figure 2. Additive genetic variance for the G0P0 model was approximately 0.6. For all of the RR models, the AG variance was higher than for the G0P0 model during

Figure 2. Daily additive genetic variance of electrical conductivity estimated with a repeatability model for 30-d periods during the lactation (×), for the whole lactation (+), and with 4 different random regression models using the following order of Legendre polynomials for both additive genetic and permanent environmental effects: first order (■), second order (◆), third order (▲), and fourth order (●).

the first 50 DIM. The nadir for the AG variance was reached after approximately 80 DIM for all RR models, and then stayed relatively stable for the next 16 wk. After about 180 DIM, the AG variance increased for all RR models, but especially for the G2P2 and the G4P4 models. The AG variance from the G3P3 model was approximately the same as the AG variance from the G0P0 model. Additive genetic variance estimated for the 30-d periods was highest in early lactation as well, and showed the same pattern as the RR models until 180 DIM. After 180 DIM, the AG variance decreased compared with the RR models and stayed lower than the AG variance modeled with the G0P0 model until 280 DIM.

Cows are more likely to get mastitis in the beginning of the lactation (Rajala-Schultz et al., 1999). Due to the binary properties of the trait, a larger genetic variation is expected in this period. This agrees well with the estimates we obtained in different parts of the lactation. Similar analysis for test-day EC was not found in the scientific literature, which makes comparison of results impossible. However, several investigations have been carried out with SCS and RR models. Ødegård et al. (2003) presented results for test-day SCS recorded bi-monthly and analyzed with an RR sire model using the same polynomial and order of fit as in our study. Contrary to the pattern obtained for test-day EC, the genetic variance was lowest in the beginning of the lactation for SCS. This may be due to the less frequent recording of SCC compared to EC.

The shape of the curves will depend on the order of the polynomial and biological interpretations of the pattern are difficult. Less information at the end of lactation due to drying off cows may result in less accurate estimates for this period. Although the observed pattern of the curves might be partially explained by larger variability, the RR models can lead to spurious estimates of genetic variance obtained at the edges of the trajectory (Van der Werf et al., 1998). Pool and Meuwissen (1999) showed that the length of the lactation affected the parameter estimates at the end of the trajectory as well. Further, López-Romero and Carabaño (2003) pointed out that problems associated with polynomials are more severe for higher orders of fit and variance components estimated with complex models are likely to be overestimated at the edges of the lactation. Our study showed the same in the beginning of the lactation, with larger variance estimates from models with higher order of fit.

Estimated PE variance is given in Figure 3. The shape of the curve is similar to the curve for AG variance. Compared with the G0P0 model, the RR models showed higher PE variance during the whole lactation. As for the models G2P2 and G4P4, AG variation in-

Figure 3. Daily permanent environmental variance of electrical conductivity estimated with a repeatability model for 30-d periods during the lactation (x), for the whole lactation (+), and with 4 different random regression models using the following order of Legendre polynomials for both additive genetic and permanent environmental effects: first order (■), second order (◆), third order (▲), and fourth order (●).

creased drastically also after 180 DIM. The G3P3 model showed a pattern closest to the G0P0 model. Estimated PE variance for the 30-d periods were larger than for the RR models until 180 DIM. The patterns for the 30-d periods followed approximately the same pattern as the G3P3 model. The increase in PE variance estimated with the RR models compared to the G0P0 model may be due to the larger flexibility of RR models and the assumption of homogenous residual variance. More flexible models for the PE effect will, at least to some extent, capture changes in the residual variance during the lactation (Ødegård et al., 2003).

Heritabilities for test-day EC by DIM are given in Figure 4. Using a simple repeatability model, estimated

Figure 4. Daily heritability of electrical conductivity estimated with a repeatability model for 30-d periods during the lactation (x), for the whole lactation (+), and with 4 different random regression models using the following order of Legendre polynomials for both additive genetic and permanent environmental effects: first order (■), second order (◆), third order (▲), and fourth order (●).

heritability was 0.28. This agrees well with Goodling et al. (2000), who estimated heritability for lactation averages of EC of milk from first-lactation cows to be between 0.21 and 0.29. For all RR models, estimates were higher in the beginning of the lactation compared to results from the G0P0 model. Heritabilities ranged from 0.32 to 0.37 at d 6 in lactation for the RR models, while the heritability for the first 30-d period was 0.30. The heritabilities for the G2P2, G3P3, and G4P4 models showed a wavy pattern during the lactation, and the estimates diverged at the end of the lactation. In mid-lactation (until 180 DIM) the estimates ranged from 0.24 to 0.28. For the 30-d periods, the heritability dropped after 30 DIM, and then increased again after 60 DIM. Highest heritabilities were obtained from 130 to 160 DIM (0.32). After 180 DIM, the heritability dropped to 0.26, then stayed lower than the heritability for the G0P0 model for the rest of the lactation. The pattern for heritability estimates for SCS using the same RR models (Ødegård et al., 2003) showed a different shape compared with the pattern for heritabilities for EC.

In our study, homogenous residual variance was assumed mainly due to software limits. However, results presented by Ødegård et al. (2003) showed that trajectories of sire variance and heritabilities were similar for SCS regardless of assuming either homogenous or heterogeneous variance structure. They found that the PE effect absorbed most of the heterogeneity of the residual variance, particularly for the more complex models.

The absolute level of EC of milk may, to some degree, be influenced by factors other than bacterial infections, e.g., content of fat and protein. This may partly explain the relatively high heritabilities obtained for EC compared with clinical mastitis and SCS. Lund et al. (1999) and Heringstad et al. (2001) estimated heritabilities for clinical mastitis with a threshold model in the range from 0.06 to 0.12. For SCS, heritabilities are found to be in the range from 0.07 to 0.12 (Reents et al., 1995; Mrode and Swanson, 2003; Ødegård et al., 2003). However, estimating genetic parameters for indicator traits is only of interest if the traits are genetically correlated with the breeding goal, in this case mastitis. Genetic correlation between SCS and mastitis has been estimated to range from close to zero (Coffey et al., 1986) to close to unity (Lund et al., 1994). Weller et al. (1992) found a correlation of 0.3 between SCC and clinical mastitis, and Mrode and Swanson (1996) concluded that the genetic correlation between clinical mastitis and SCS, based on values from the literature, was about 0.7. Moderate to high (0.65) genetic correlations between mastitis and EC for first lactation cows has been found (Rogers, 2002), but further research to obtain estimates is strongly needed.

Table 2. Estimates of twice the log restricted likelihood ($2\ln\Lambda$), Akaike information criterion (AIC), Bayesian information criterion (BIC), residual variance (σ_e^2), mean squared error of predictions (MSEP), and correlation between observed and predicted EC values (COP) for a repeatability test-day model (G0P0) and for 4 different random regression models using the following order of Legendre polynomials for both additive genetic and permanent environmental effects: first order (G1P1), second order (G2P2), third order (G3P3), and fourth order (G4P4).

Model	$2\ln\Lambda^1$	AIC ¹	BIC ¹	σ_e^2	MSEP	COP
G0P0	0	0	0	0.9015	0.8512	0.74
G1P1	44,425	44,417	44,373	0.7954	0.8154	0.77
G2P2	65,316	65,296	65,186	0.7471	0.7695	0.78
G3P3	76,004	75,968	75,771	0.7233	0.7504	0.79
G4P4	81,634	81,578	81,272	0.7096	0.7384	0.80

¹The values of $2\ln\Lambda$, AIC and BIC are presented as deviates from values of the G0P0 model.

Comparison of Models

The diverging estimates for variance components and heritabilities in this study show the necessity of being careful when models are selected. Model comparison based on $2\ln\Lambda$, AIC, BIC, residual variance, and MSEP are presented in Table 2. For all models, residual variance decreased as the number of parameters in the models increased. Based on the model selection criteria that are dependent on the likelihood ($2\ln\Lambda$, BIC, and AIC), a significant improvement was achieved when the order of fit was increased. This corresponds well with results presented by other authors who have used RR models to estimate genetic parameters for other dairy cattle traits (Pool and Meuwissen, 1999; López-Romero and Carabaño, 2003; Ødegård et al., 2003). In some cases, the BIC will penalize models with many parameters and favor less complex models, but in our study BIC ranked the models in the same order as the other criteria. Values for the model selection criteria increased most from a repeatability model to a model with first-order polynomials for both random effects. The ability of a model to predict excluded observations should be considered when models are selected. By estimating the correlation between the observed and the predicted values, one gets a clear impression of how the models fit the data. The MSEP decreased and COP increased when more complex models were used. For the repeatability model, COP was 0.74, while a model with fourth-order fit on both additive genetic and permanent environmental effect showed a COP of 0.80. The largest increase in COP was found by going from the G0P0 model to the G1P1 model. Based on these results, a model with a fourth-order Legendre Polynomial for both AG and PE effect should be applied. But looking at the AG variance solely, the estimates from the RR models and the repeatability models were about the same for the first 200 DIM. In this study, a relatively small number of animals with records were available. This may lead to less accurate estimates and higher

standard errors compared to analysis where records from the whole population are available. However, the standard error of the heritability estimated with the repeatability model was 0.06, which is quite low. Electrical conductivity was recorded every day during the lactation, so the number of records per cow was high. This will contribute to increase the accuracy of the estimates. Recording of EC on the farm is increasing, and models should be validated on a larger data set in the future if possible.

Practical Implications

Due to the relatively high heritabilities obtained for EC of milk in this study and the genetic correlation reported in the literature between EC and mastitis (Rogers, 2002), EC might be a potential indicator trait in a breeding program where selection for reduced mastitis frequency is desired. Heritability estimates for most udder health traits are low, which will limit successful selection for these traits. Currently, breeding schemes including selection for improved udder health are mainly based on SCC in milk.

In the future, monitoring udder health of dairy cows is likely to change due to the use of more automated sensor-based systems, especially in automatic milking systems. Today, such systems are typically based on information on EC of milk. Measurements are recorded at every milking and information about the udder health status is obtained, even on individual quarters if needed. No additional costs are connected to registration of EC if equipment is originally installed, which it is in most automated milking systems and some other new manual milking systems. In contrast, analysis of SCC in milk is normally performed at an interval of 4 to 8 wk, and cows may have mastitis in this period without showing an increased SCC level. If in-line recordings of EC are sufficient to manage the udder health status of cows, analysis of SCC on individual cows may be redundant. However, breeding organizations are de-

pendent on information about udder health from producers to be able to include mastitis in the breeding goal. If recording of SCC decreases, other information sources such as EC, should be made available to the breeding organizations. However, data has to be transferred from the farmer to the national recording system, and some extra technology will be required to accomplish that.

In our study, equal distribution of EC for all cows was assumed. It is known that the distribution of SCC in milk from infected cows will diverge from the distribution of SCC in milk from healthy cows, and, to account for this, a mixture model could be applied (Detilleux and Leroy, 2000). Electrical conductivity data from healthy and infected cows show to some degree a different distribution and a mixture model could be considered in further analysis.

CONCLUSIONS

Electrical conductivity of milk showed the same pattern during the lactation as SCC, with the highest level for EC at the beginning and at the end of the lactation. A random regression model with a fourth-order Legendre polynomials for both additive and permanent environmental effects fitted the data best in our study. Heritability estimates were near 0.36 at the beginning and the end of the lactation, and about 0.26 in midlactation. The correlation between estimated and observed EC values was 0.80 for the chosen model. Due to the possibility of frequent recording of EC, the relatively high heritability, and the genetic correlation between EC and mastitis reported in the literature, EC might be a potential indicator trait to use in a breeding program designed to reduce the incidence of mastitis.

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