https://doi.org/10.17221/254/2020-CJAS

Additive genetic and permanent environmental correlation between different parts of lactation in moderate and cold regions

Farzad Atrian Afiani[1], *Sahereh Joezy-Shekalgorabi*[2], *Mehdi Amin-Afshar*[1]*, *Ali-Asghar Sadeghi*[1], *Just Jensen*[3]

[1]*Department of Animal Science, Science and Research Branch, Islamic Azad University, Tehran, Iran*

[2]*Department of Animal Science, Shahr-e-Qods Branch, Islamic Azad University, Tehran, Iran*

[3]*Center for Quantitative Genetic and Genomics, Aarhus University, Tjele, Denmark*

**Corresponding author: aminafshar@gmail.com*

Citation: Afiani F.A., Joezy-Shekalgorabi S., Amin-Afshar M., Sadeghi A.A., Jensen J. (2021): Additive genetic and permanent environmental correlation between different parts of lactation in moderate and cold regions. Czech J. Anim. Sci., 66: 112–121.

Abstract: The objective of this study was to investigate genotype by environment interaction as well as genetic parameters for somatic cell score (SCS) in first lactation Holstein cows in Iran. Data were collected by the National Animal Breeding Centre of Iran during 2003 to 2018. Data consisted of 1 031 885 SCS test-day records of 145 817 first lactation Holstein cows. Records were classified into the cold and moderate climate on data of synoptic stations. Variance components and genetic parameters were estimated using a random regression model and restricted maximum likelihood method. The analyses were performed using the AI-REML algorithm of the DMU package. The mean SCS was 1.859 (1.598) and 1.823 (1.522) for the cold and moderate climate, respectively. Genetic variance of SCS was lower than the corresponding permanent environmental variance. The permanent environmental variance in the moderate climate was higher than that of the cold climate during lactation. The highest values of heritability were observed in the early stage of lactation. However, the estimates of heritability during the lactation curve were low. The estimates of heritability for the entire 305-day lactation were higher in the cold climate than those in the moderate climate. Genetic correlation between the cold and moderate climate ranged from 0.25 to 0.81. The results indicated the existence of genotype × environment interaction and hence the need for different breeding program for SCS in the studied climates.

Keywords: G × E interaction; genetic analysis; SCS; test day; cow

Over the past few decades, the average milk production and milk components have been improved by genetic selection and by the improvement of nutritional, health, and management conditions on individual farms. Concurrently with increasing milk production in dairy herds, new problems, such as reduced fertility, reduced longevity and worse health of livestock and higher prevalence of diseases like mastitis have been observed. These effects are more pronounced in developing countries with sperm imports from other countries and inducing a sudden increase in livestock production capacity, which caused many problems to livestock farmers. These events have made animal health traits, including somatic cell score, more important in breeding programs over the past two decades (Berglund 2008). Mastitis is the most serious disease associated with milk production in dairy industry and in many countries, like Iran, information on clinical mastitis is not available but somatic cell counts are re-

https://doi.org/10.17221/254/2020-CJAS

corded. Considering the strong genetic correlation between milk somatic cell count and clinical mastitis, indirect selection for somatic cell count could be applied in order to reduce mastitis (Mrode and Swanson 2003). In Iran, dairy processors, besides milk volume, pay for milk based on two factors, i.e. fat percentage and somatic cell count. This indicates the importance of somatic cells in breeding programs in Iran. Genetic correlations between parities have demonstrated that genes that control somatic cell score (SCS) in various parities are the same and selection of animals for SCS in the first parity would affect the SCS in other parities (Zavadilova et al. 2011; Kheirabadi and Alijani 2014), whereas the incidence of mastitis increases with age and parity of cows. Genotype by environment interaction exists when the capacity to alter the phenotype in response to changes in the environment differs among animals (Falconer and Mackay 1996). Genotype by environment interaction is defined by genetic correlations less than unity between the same traits expressed in different environments. Genetic correlations of production traits between environments are usually high. However, genetic correlations between trait expressions in different environments are lower for functional traits than for production traits (Mulder et al. 2004). When different genotypes react differently in different environments, genotype by environment interaction can cause re-ranking of animals across environments (Lynch and Walsh 1998). Previous studies on somatic cell score in Iran have mainly focused on the estimation of variance and covariance component (Kheirabadi and Alijani 2014; Faraji-Arough et al. 2015). For SCS there exists no estimation of variance component due to genotype by environment interaction under different geographical conditions. Holsteins are the predominant dairy breed in Iran except in the very hot southern provinces. The aim of this study was to determine genetic parameters and genotype by environment interaction of somatic cell score of Holstein cattle in different geographical regions of Iran.

MATERIAL AND METHODS

Data set

Data were provided by the National Animal Breeding and Milk Improvement Center of Iran and these were data from the period March 2003 to January 2018. The test days (TD) ranged from five to 305 days in milk (DIM). A minimum of three TD records were required for a cow to be included in the analysis. The first monthly test had to be less than 90 days in milk and the difference between any two test-day records should be greater than 15 days. The number of cows per herd was more than 150. The number of first lactation cows per herd-year of calving had to be at least 10. Sires with at least 10 daughters in three different herds were taken into account. The final data set for SCS consisted of 1 031 885 test-day records of 145 817 first lactation Iranian Holstein dairy cows, housed in 102 herds, located in different geographical regions of Iran (Table 1). The number of utilized test days along the lactation curve, and for the studied climatic regions, is illustrated in Figure 1. In order to maximize connections between regions, the pedigree was traced as far back as possible. Ultimately, the pedigree for the data set included 275 103 dams and 7 301 sires with birth year from 1950 to 2016.

Table 1. Classification of geographical condition and descriptive statistics of the data set

Description	Geographical condition		Total
	moderate	cold	
Average temperature	16.1	11.0	–
Maximum temperature	28.2	23.6	–
Minimum temperature	2.9	–3.0	–
Number of herds	77	25	102
Maximum number of observations in herds	80 317	52 515	–
Minimum number of observations in herds	945	1 675	–
Average number of observations in herds	9 620	11 939	–
Number of animals	105 087	40 730	145 817
Number of records	733 391	298 494	1 031 885
Average milk yield (SD)	36.1 (2.624)	35.1 (2.383)	34.1 (2.566)
Maximum herd yield	39.526	38.938	–
Minimum herd yield	27.377	29.377	–
Mean of herd yield	34.158	34.229	–
Maximum value for somatic cell score	6.321	6.321	–
Minimum value for somatic cell score	–3.643	–3.643	–
Mean somatic cell score (SD)	1.823 (1.522)	1.859 (1.598)	1.838 (1.561)

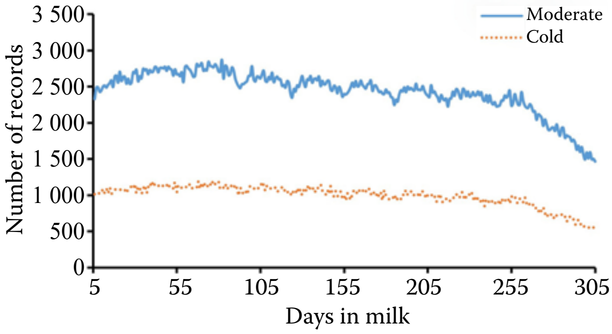

Figure 1. Distribution of records across the moderate and the cold regions

The average of milk production and SCS in days in milk ranged from 25 to 38 kg and 1.567 to 2.615, respectively (Figure 2). For obtaining the normal distribution of TD records, individual somatic cell count (SCC) records were transformed into SCS by [SCS = $\log_2$(SCC/100 000) + 3].

Records were classified into two areas, including cold and moderate regions based on synoptic weather station data (Bohlouli et al. 2014) considering the location of herds and in accordance with the climatic data presented in Table 1. Due to the insufficient data in the arid region, data from the arid region were not included in the model of evaluation.

Statistical model

Variance components and heritability were estimated using a random regression model and the restricted maximum likelihood algorithm. The analyses were performed using the AI-REML module of DMU package v6, release 5.2. (Madsen and Jensen 2013). Data were analysed using a bivariate RRM model.

The bivariate RR test-day model with different order Legendre polynomials was used for the SCS as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}a_1 & 0 \\ 0 & \mathbf{Z}a_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \\ + \begin{bmatrix} \mathbf{Z}pe_1 & 0 \\ 0 & \mathbf{Z}pe_2 \end{bmatrix} \begin{bmatrix} pe_1 \\ pe_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \quad (1)$$

where:

y_i – the vector of test-day records of SCS in i^{th} geographical location (i = 2);

X – the incidence matrix relating b to y;

b – the vector of cross-classified fixed effects (i.e. herd-test-day and DIM) with a class for every DIM from 5 to 305, in i^{th} geographical location);

Z*a* and **Z***pe* – the design matrices containing Legendre polynomial coefficients relating a to y;

a – the vector of random regressions (*LP0, LP1, LP2, LP3, LP4*) for the additive genetic effect in i^{th} geographical location;

pe – the vector of random regressions (*LP0, LP1, LP2, LP3, LP4*) for permanent environmental effects in i^{th} geographical location;

e_i – the vector of random residual effect in i^{th} geographical location.

The covariance structure of the model is:

$$V\begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} = [\mathbf{A} \otimes \mathbf{G}_0] \quad (2)$$

where:

A – the additive genetic relationship matrix;

$\otimes$ – the direct product operator;

$\mathbf{G_0}$ – the 10 × 10 matrix of additive genetic (co)variances.

The two 5 × 5 diagonal blocks correspond to additive genetic covariance within each region and the remaining block corresponds to additive genetic covariance between regions.

$$V\begin{bmatrix} \mathbf{pe}_1 \\ \mathbf{pe}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{I}_{im1} \otimes \mathbf{Pe}i_1 & 0 \\ 0 & \mathbf{I}_{im2} \otimes \mathbf{Pe}i_2 \end{bmatrix} \quad (3)$$

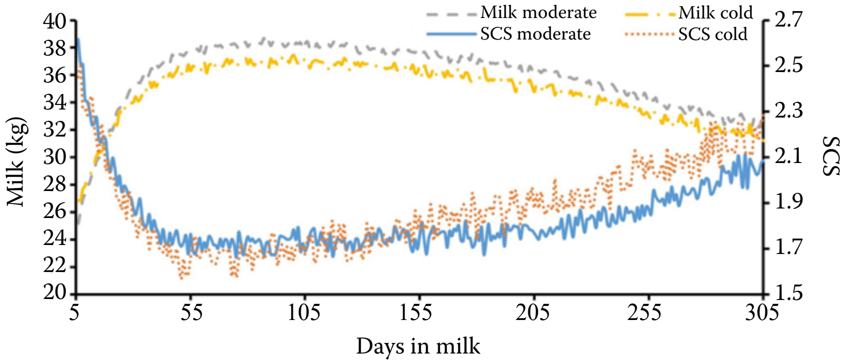

Figure 2. Milk production and somatic cell score (SCS) along the lactation curve across the moderate and the cold regions

where:

$\mathbf{I}_{im}$ – the $m \times m$ identity matrix of dimensions equal to the number of cows in i^{th} geographical location (im is the number of cows with records in i^{th} geographical location);

$\mathbf{Pe}_i$ – the 5 × 5 matrix of random regression coefficient in i^{th} geographical location.

No covariance existed for permanent environments across climate zones as no cows moved between moderate and cold regions.

The residual variance was obtained as:

$$\mathbf{R} = \begin{bmatrix} \mathbf{c}_{i1s1}\sigma^2_{i1s1} & 0 \\ 0 & \mathbf{c}_{i2s2}\sigma^2_{i2s2} \end{bmatrix} \tag{4}$$

where:

$\mathbf{c}_i$ – the $s \times s$ identity matrix of the residual effect in i^{th} geographical location (is the number of observations with records for i^{th} geographical location).

In this study we assumed homogeneous residual variance along the lactation curve. Therefore the heterogeneity of residual variance is picked up by the permanent environmental effect.

Heritability of SCS [$h^2_{(in)}$] for the n^{th} test day and i^{th} geographical location was calculated as follows (Bohlouli et al. 2014):

$$h^2_{(in)} = \frac{\sigma^2_{a(in)}}{\sigma^2_{a(in)} + \sigma^2_{pe(in)} + \sigma^2_{e(in)}} \tag{5}$$

where:

$\sigma^2_{a(in)}$ – the additive genetic variance for test day n in i^{th} geographical location;

$\sigma^2_{pe(in)}$ – the permanent environmental variance for test day n in i^{th} geographical location;

$\sigma^2_{e(in)}$ – the residual variance for SCS in i^{th} geographical location.

For SCS heritability of 305 day by lactation sums of variance and covariance component was calculated as follows:

$$h^2_{(305d)} = \frac{\sigma^2_{a(305d)}}{\sigma^2_{a(305d)} + \sigma^2_{pe(305d)} + 305 \times \sigma^2_e} \tag{6}$$

In the above equation $\sigma^2_{a(305d)}$ and $\sigma^2_{pe(305d)}$ were calculated as follows:

$$\sum(q') \times \mathbf{K}_i \times \sum(q) \tag{7}$$

where:

$\mathbf{K}_i$ – the (co)variance matrix for additive genetic or permanent environmental effect within each region;

$\Sigma(q)$ – the sum of the random regression vectors.

Genetic correlation of SCS among geographical locations as the ratio of the genetic covariance between two environments was calculated as follows (Bohlouli et al. 2014):

$$r_{g(i,j)} = \frac{q'\mathrm{G}(i,j)q}{\sqrt{q'\mathrm{G}(i,i)q \times q'\mathrm{G}(j,j)q}} \tag{8}$$

where:

$\mathrm{G}(i,j)$ – the genetic covariance matrix for trait in i^{th} and j^{th} region;

$\mathrm{G}(i,i)$ and $\mathrm{G}(j,j)$ – the genetic covariance matrices of the same curve parameters in i^{th} and j^{th} region, respectively;

q – the vector of Legendre polynomial for considered days in milk.

Genetic correlations for 305-day yields in different geographical conditions were computed according to Hammami et al. 2008.

RESULTS

The averages of milk production along the lactation curve in the moderate climate were higher than those of the cold climate. The greatest means of milk production were observed between days 50 and 100 in both climates, whereas SCS values were the lowest in this period (Figure 2). The overall means of milk production were 36.1 and 35.1 kg (with a standard deviation of 2.624 and 2.383) in the moderate and cold climate, respectively (Table 1). The mean SCS in the studied herds was 1.838 with a standard deviation of 1.566. These values were 1.859 (1.598) and 1.823 (1.522) for the cold and moderate climate, respectively. SCS was higher in the cold climate by +0.036 compared to the moderate climate (Table 1).

Genetic and permanent variances

Genetic variance of SCS was lower than the corresponding permanent environmental variance.

https://doi.org/10.17221/254/2020-CJAS

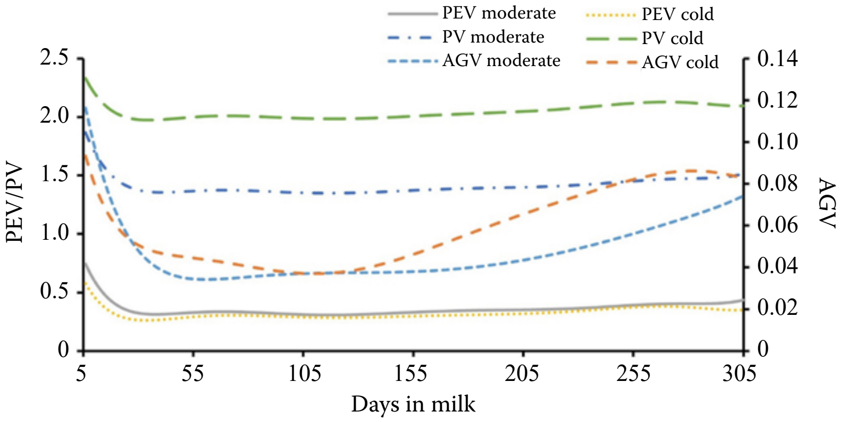

Figure 3. Permanent environment variances (PEV), phenotypic variances (PV) and additive genetic variances (AGV) of the somatic cell score during the lactation curve in moderate and cold regions

The genetic variance curve had a similar pattern like the permanent environmental variance curve. Genetic variances with a sharp decline at the beginning of lactation (first month) in the moderate climate were higher than those in the cold climate. Generally the level of genetic variance curve in moderate climate was lower than that of cold climate. Similar to genetic variances, permanent environmental variances showed a sharp decline at the beginning of lactation followed by a gradual increase to the end of lactation. Permanent environmental variance in the moderate climate was greater than that in the cold climate (Figure 3).

Heritability and repeatability

The highest values of heritability were observed in the early stage of lactation, although the estimates of heritability during the lactation were low. For both climates, heritability estimates with a decline at the beginning of lactation were more constant in the mid-lactation and then gradually increased to the end of lactation. The estimates of heritability during the lactation curve in the moderate climate were higher than those in the cold climate (Figure 4) whereas heritability for the entire lactation showed the highest value in the cold region with the highest genetic variances (Table 2). Furthermore, estimates of repeatability during the lactation curve are presented in Figure 4. The highest values of repeatability were observed in early lactation and gradually declined to the mid-lactation. The estimates of repeatability during the lactation curve in the cold climate were lower than those in the moderate climate.

Correlations and covariances

In the present study correlations between different parts of DIM were calculated for additive genetic and permanent environmental effects within each climate. Our results indicated the lowest correlations between the early and the late parts of lactation for both genetic and permanent environmental variances across the studied climates while the highest correlations were observed be-

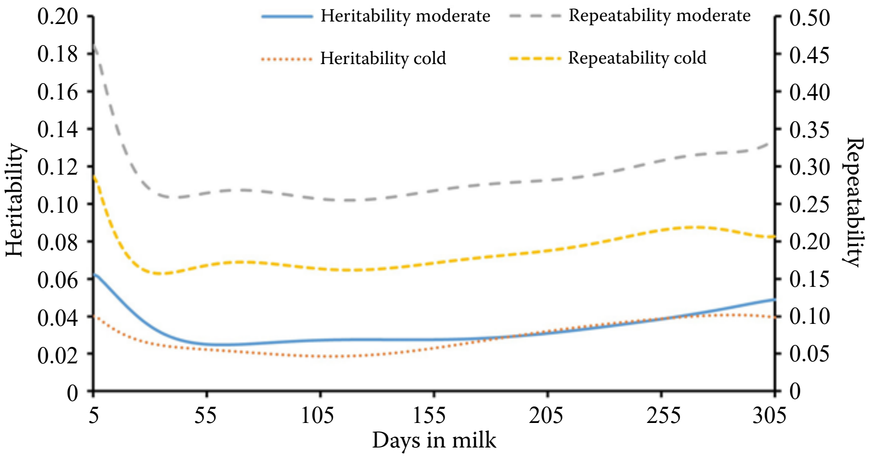

Figure 4. Heritability and repeatability estimates of the somatic cell score during the lactation curve in moderate and cold regions

Table 2. Variance components and heritability for entire 305-day lactation and genetic correlation between moderate and cold regions

Trait	Climate	Heritability	Genetic variances	Permanent environmental variances	Residual variances	Genetic correlation
Somatic cell score	moderate	0.13	2 887.24	18 274.56	302	0.82
	cold	0.16	3 497.89	16 622.44	499	

tween adjacent periods, especially in the mid-lactation (Table 3).

Furthermore, genetic correlations between test-day records at different DIM for SCS between cold and moderate climate are presented in Figure 5. Genetic correlations between different test-day records were less than unity, and the correlations gradually declined with increasing distance between test days. Genetic correlation between the cold and moderate climate ranged from 0.25 to 0.81. Genetic correlation had the lowest value at the beginning of lactation. This parameter increased until the third month, and then decreased until the end of lactation. Genetic correlation estimation of SCS 305-day between the moderate and cold region was 0.82, which was slightly higher than the ranging correlations along the lactation curve (Table 2). The genetic covariance matrix between the moderate and cold region and for different coefficients of random regression is presented in Table 4. The covariance matrix showed the highest value of the intercept between the cold and moderate region (0.058). Furthermore, the curve of genetic covariance between the moderate and cold region is presented in Figure 6. The genetic covariance curve showed the lowest value in early lactation and then gradually increased until the end of lactation.

Table 3. Additive genetic (lower left triangle) and permanent environmental (upper right triangle) correlation between different parts of lactation in moderate and cold regions

		Days in milk					
	Days in milk	1–50	50–100	100–150	150–200	200–250	250–300
Moderate region	1–50	1	0.61	0.31	0.14	0.11	0.08
	50–100	0.65	1	0.81	0.52	0.39	0.27
	100–150	0.44	0.93	1	0.89	0.69	0.45
	150–200	0.32	0.79	0.94	1	0.89	0.66
	200–250	0.18	0.62	0.82	0.95	1	0.91
	250–300	0.13	0.49	0.71	0.87	0.96	1
Cold region	1–50	1	0.61	0.31	0.13	0.11	0.11
	50–100	0.81	1	0.81	0.53	0.41	0.31
	100–150	0.57	0.85	1	0.89	0.66	0.45
	150–200	0.32	0.62	0.93	1	0.88	0.66
	200–250	0.15	0.54	0.84	0.95	1	0.91
	250–300	0.03	0.47	0.67	0.77	0.92	1

DISCUSSION

Somatic cell score is an important trait that has considerable effects on profitability of dairy cow production. A high SCS value is not only associated with milk loss, but also decreases the longevity

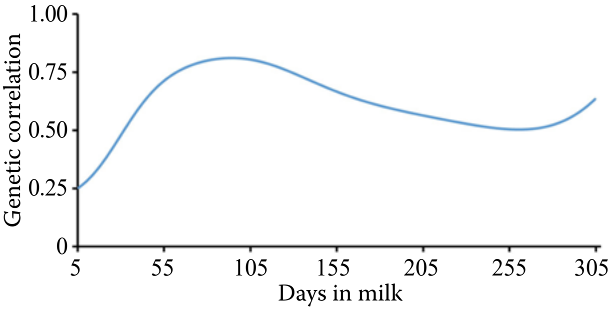

Figure 5. Genetic correlation of the somatic cell score (SCS) during the lactation between cold and moderate regions

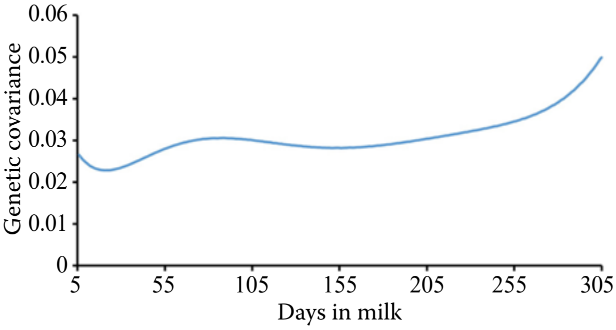

Figure 6. Genetic covariance of the somatic cell score (SCS) during the lactation between cold and moderate regions

Table 4. Genetic covariance matrix between moderate and cold regions for different random regression coefficients

		Moderate region				
		am_0	am_1	am_2	am_3	am_4
Cold region	ac_0	0.058 0	0.000 7	–0.001 9	0.003 5	–0.001 5
	ac_1	0.007 6	0.001 1	–0.001 5	0.002 2	–0.000 1
	ac_2	0.000 9	0.003 0	0.001 0	–0.001 2	0.000 7
	ac_3	–0.000 4	–0.001 2	0.000 4	0.000 8	0.000 1
	ac_4	–0.001 2	0.001 0	0.000 5	–0.000 8	0.000 1

ac_0 to ac_4 = different random regression coefficient in cold region; am_0 to am_4 = different random regression coefficient in moderate region

of dairy cows (Sewalem et al. 2006). Several studies have reported the negative effect of SCS on subsequent milk production (Durr et al. 2008; Rekik et al. 2008). The mean SCS value in the present study was 1.838. Different formulas applied for transforming somatic cell count to somatic cell score indicate that the mean of this trait may differ in different studies. Faraji-Arough et al. (2015) and Kheirabadi and Alijani (2014) reported the mean somatic cell score of the first lactation Iranian Holstein cows as 7.78 and 2.63, respectively. This difference could be due to the number of herds and cows considered in the model. Furthermore, negative phenotypic correlations between SCS and milk yield in Iranian Holstein and Finnish Ayrshire were reported previously (Koivula et al. 2005; Faraji-Arough et al. 2015). In our results, a higher level of herd production was observed in the moderate region while the highest mean SCS values were found in the cold region. Therefore, no negative relationship existed between the SCS and milk yield in our study.

Variances and heritability

The permanent environmental variances were higher than the additive genetic variances in both climates. These results were similar to the results published by Kheirabadi (2019) and Ptak et al. (2007). Except for the beginning of lactation, the increasing permanent environmental variance during lactation indicates the importance of non-genetic factors on SCS. The results of this study, similar to other studies (Koivula et al. 2005; Mulim et al. 2021), revealed that SCS is strongly affected by the temporary environmental variance.

Similar to our results, reported heritabilities of SCS on lactation days in Iranian Holstein cows were generally low (between 0.03 and 0.07) (Kheirabadi and Alijani 2014; Faraji-Arough et al. 2015). Mrode and Swanson (2003) and Rzewuska et al. (2011) estimated the heritability for SCS of Holstein-Friesian Cattle as 0.07 and 0.11, respectively, which were higher values than the estimated value in the present study. Low heritability estimates obtained in this study were related to the high environmental variation and low additive genetic variance in the first lactation. This indicates that SCS is mostly affected by environmental factors. Different model of analysis as well as different yield levels can cause differences in heritability estimates (De Veer and Van Vleck 1987). The shape of heritability curve obtained in our study (Figure 4) was in agreement with other sources (de Roos et al. 2003; Rzewuska et al. 2011; Kheirabadi 2019). Genetic variances and heritability estimates (Figure 3 and Figure 4) revealed the equal genetic expression of genes for this trait in the cold and moderate climate. Therefore, improvement of environmental conditions (i.e. nutrition, health and management) can reduce the environmental variance. For this reason heritabilities obtained from the data of one herd are often higher compared to estimated heritabilities of a great number of herds in different climates. In this study, estimates of heritability for 305-day were higher than those estimated along the lactation curve; which confirms the results of Strabel and Misztal (1999), who reported higher heritability estimates for 305-day compared to the heritability estimate for test-day records.

Genotype by environment interaction

Genetic correlation between traits measured in different environments can be used to express the level of G × E interaction. Estimates of genetic correlation lower than 0.8 indicate the existence of biologically significant G × E interaction (Robertson 1959). Existence of G × E interaction causes re-ranking of sires (Santana et al. 2012). G × E interaction can be measured by estimating the genetic correlation between the breeding values of related animals that produce in different environments. In this research, genetic correlation between the cold and moderate region for SCS ranged from 0.25 to 0.81 along the lactation curve and was 0.82 for the entire lactation. These results show the existence of G × E interaction between the two climates for SCC, so that they could be considered as different traits. A reason for the existence of G × E interaction and low genetic correlation between the moderate and cold climate is the influence of environmental effects on this trait especially in early lactation. Mulim et al. (2021) studied the effect of different environmental temperatures on genetic behaviour of the Holstein population. They reported high genetic correlations (i.e. close to unity) among their studied regions and concluded that there exists no significant genotype by environment interaction among the regions with different environmental temperature. Van der Laak et al. (2016) reported that genetic correlation of SCS between grazing and non-grazing Dutch Holstein-Friesian cows was close to unity and G × E was almost absent. Zwald et al. (2003) reported that bulls' daughters may act differently in herds with hot climate and in herds with cool climate. Ismael et al. (2016) concluded that genetic correlations of time from calving to first insemination were close to unity, indicating no genotype by environment interaction between different geographic locations. On the other hand, genetic correlations less than unity were reported between calving seasons for days open in the US Holstein cows (Oseni et al. 2004) and for age at first calving between Brazil and Colombia (Ceron-Munoz et al. 2004). Mulder et al. (2004) reported lower genetic correlations between automatic milking system farms and conventional milking system farms for SCS than for productive traits. Also, another study showed genetic correlation less than unity for production traits between the comfort and heat stress zone in the highest values of the temperature humidity index, which indicated the existence of genotype by environmental interaction (Santana et al. 2016). The results of this study showed that SCS in the moderate and cold climate are genetically different traits. This topic creates the need for a different breeding program for SCS or at least it might lead to selection of different sires in various climates. It is clear that responses to selection are dependent on the environment in which the animals are reared and evaluated (Santana et al. 2012).

CONCLUSION

In both climate zones, genetic variance and environmental variance had a sharp decline in the first month and then gradually increased till late lactation. The level of genetic variance and environmental variance was higher in the cold climate than in the moderate climate. Generally, in this study, the estimates of heritability were low in all parts of lactation but the highest heritabilities were observed in early lactation. Also, the estimate of heritability for the lactation sums was higher in the cold region. The lowest levels of genetic correlation were observed in early lactation and the highest levels were observed in the mid-lactation. The genetic correlation for SCS ranged from 0.25 to 0.81. The result in this research showed the existence of genotype by environmental interaction and the effect of this interaction should be considered for genetic selection of animals for resistance to mastitis.

Acknowledgement

The authors acknowledge the Animal Breeding Center of Karaj, Iran for providing the data.

Conflict of interest

The authors declare no conflict of interest.

REFERENCES

Berglund B. Genetic improvement of dairy cow reproductive performance. Repro Dom Anim. 2008 Jul;43:89-95.

Bohlouli M, Shodja J, Alijani S, Pirany N. Interaction between genotype and geographical region for milk production traits of Iranian Holstein dairy cattle. Livest Sci. 2014 Nov 1;169:1-9.

Ceron-Munoz MF, Tonhati H, Costa CN, Maldonado-Estrada J, Rojas-Sarmiento D. Genotype × environment interaction for age at first calving in Brazilian and Colombian Holsteins. J Dairy Sci. 2004 Aug 1;87(8):2455-8.

de Roos A, Harbers A, De Jong G. Genetic parameters of test-day somatic cell score estimated with a random regression model. Int Bull. 2003;31:97-101.

De Veer JC, Van Vleck LD. Genetic parameters for first lactation milk yields at three levels of herd production. J Dairy Sci. 1987 Jul 1;70(7):1434-41.

Durr JW, Cue RI, Monardes HG, Moro-Mendez J, Wade KM. Milk losses associated with somatic cell counts per breed, parity and stage of lactation in Canadian dairy cattle. Livest Sci. 2008 Sep 1;117(2-3):225-32.

Falconer DS, MacKay TFC. Introduction to quantitative genetics. 4th ed. Harlow: Pearson Longman; 1996.

Faraji-Arough H, Aslaminejad AA, Tahmoorespur M, Rokouei M, Shariati MM. Bayesian inference of (co) variance components and genetic parameters for economic traits in Iranian Holsteins via Gibbs sampling. Iran J App Anim Sci. 2015 Mar 1;5(1):51-60.

Hammami H, Rekik B, Soyeurt H, Bastin C, Stoll J, Gengler N. Genotype × environment interaction for milk yield in Holsteins using Luxembourg and Tunisian populations. J Dairy Sci. 2008 Sep;91(9):3661-71.

Ismael A, Strandberg E, Berglund B, Kargo M, Fogh A, Lovendahl P. Genotype by environment interaction for the interval from calving to first insemination with regard to calving month and geographic location in Holstein cows in Denmark and Sweden. J Dairy Sci. 2016 Jul 1;99(7):5498-507.

Kheirabadi K, Alijani S. Estimation of genetic parameters and genetic trends of somatic cell score in Iranian Holstein cows using test-day records. Iran J App Anim Sci. 2014 Dec 1;4(4):707-16.

Kheirabadi K. Estimates of genetic trends for daily milk yield and somatic cell score of primiparous Holstein cattle in Iran. J Appl Anim Res. 2019 Jan 1;47(1):467-73.

Koivula M, Mantysaari EA, Negussie E, Serenius T. Genetic and phenotypic relationships among milk yield and somatic cell count before and after clinical mastitis. J Dairy Sci. 2005 Feb 1;88(2):827-33.

Lynch M, Walsh B. Genetics and analysis of quantitative traits. Sunderland (MA): Sinauer Associates, Inc. Publishers; 1998. p. 535-57.

Madsen P, Jensen J. A user's guide to DMU: A package for analysing multivariate mixed models. Version 6, release 5.2. Tjele (Denmark): University of Aarhus; 2013 Nov. p. 8830-40.

Mrode RA, Swanson GJ. Estimation of genetic parameters for somatic cell count in the first three lactations using random regression. Livest Prod Sci. 2003 Feb 1;79(2-3):239-47.

Mulder HA, Groen AF, De Jong G, Bijma P. Genotype × environment interaction for yield and somatic cell score with automatic and conventional milking systems. J Dairy Sci. 2004 May 1;87(5):1487-95.

Mulim HA, Pinto LF, Valloto AA, Pedrosa VB. Genotype by environment interaction for somatic cell score in Holstein cattle of southern Brazil via reaction norms. Anim Biosci. 2021 Apr;34(4):449-505.

Oseni S, Misztal I, Tsuruta S, Rekaya R. Genetic components of days open under heat stress. J Dairy Sci. 2004 Sep 1;87(9):3022-8.

Ptak E, Brzozowski P, Jagusiak W, Zdziarski K. Genetic parameters for somatic cell score for polish black-and-white cattle estimated with a random regression model. J Anim Feed Sci. 2007 Sep 6;16(3):357-69.

Rekik B, Ajili N, Belhani H, Gara AB, Rouissi H. Effect of somatic cell count on milk and protein yields and female fertility in Tunisian Holstein dairy cows. Livest Sci. 2008 Jul 1;116(1-3):309-17.

Robertson A. The sampling variance of the genetic correlation coefficient. Biomet. 1959 Sep 1;15(3):469-85.

Rzewuska K, Jamrozik J, Zarnecki A, Strabel T. Genetic parameters of test-day somatic cell scores for the first three lactations of Polish Holstein-Friesian cattle. Czech J Anim Sci. 2011 Jan 1;56(9):381-9.

Santana Jr ML, Eler JP, Cardoso FF, Albuquerque LG, Bignardi AB, Ferraz JB. Genotype by environment interaction for birth and weaning weights of composite beef cattle in different regions of Brazil. Livest Sci. 2012 Nov 1;149 (3):242-9.

Santana ML, Bignardi AB, Pereira RJ, Menendez-Buxadera A, El Faro L. Random regression models to account for the effect of genotype by environment interaction due to heat stress on the milk yield of Holstein cows under tropical conditions. J App Gen. 2016 Feb 1;57(1):119-27.

Sewalem A, Miglior F, Kistemaker GJ, Van Doormaal BJ. Analysis of the relationship between somatic cell score and functional longevity in Canadian dairy cattle. J Dairy Sci. 2006 Sep 1;89(9):3609-14.

Strabel T, Misztal I. Genetic parameters for first and second lactation milk yields of Polish Black and White cattle with random regression test-day models. J Dairy Sci. 1999 Dec 1;82(12):2805-10.

Van der Laak M, van Pelt ML, De Jong G, Mulder HA. Genotype by environment interaction for production, somatic cell score, workability, and conformation traits in Dutch Holstein-Friesian cows between farms with or without grazing. J Dairy Sci. 2016 Jun 1;99(6):4496-503.

Zavadilova L, Wolf J, Stipkova M, Nemcova E, Jamrozik J. Genetic parameters for somatic cell score in the first three lactations of Czech Holstein and Fleckvieh breeds using a random regression model. Czech J Anim Sci. 2011 Jan 1; 56(6):251-60.

Zwald NR, Weigel KA, Fikse WF, Rekaya R. Identification of factors that cause genotype by environment interaction between herds of Holstein cattle in seventeen countries. J Dairy Sci. 2003 Mar 1;86(3):1009-18.

Received: October 3, 2020
Accepted: February 15, 2021