Genotype-environment interaction between Chile and North America and between Chilean herd environmental categories for milk yield traits in Black and White cattle*

Hugo H. Montaldo[1]**, Héctor Castillo-Juárez[2], Carlos Lizana[3],
Carlos Trejo[3], Eugenia G. Cienfuegos-Rivas[4], Alejandra Pelcastre-Cruz[1]

[1] Department of Genetics and Biostatistics, School of Veterinary Medicine
  and Animal Husbandry, National Autonomous University of Mexico, Ciudad Universitaria,
  04510, Distrito Federal, Mexico

[2] Department of Agricultural and Animal Production,
  Autonomous Metropolitan University-Xochimilco.
  Calzada del Hueso 1100, 04960, Distrito Federal, Mexico

[3] Agriculture and Service Cooperative, COOPRINSEM,
  Manuel Rodríguez 1040, Osorno, Región de Los Lagos, Chile

[4] Autonomous University of Tamaulipas, 87030, Ciudad Victoria, Tamaulipas, Mexico

In order to evaluate the expression of sire genetic evaluations obtained in North America for Chilean Black and White Cattle, genetic correlations were estimated for milk (MY), fat (FY) and protein (PY) yields, and for fat (F%) and protein (P%) contents between Chile, Canada and the US, from predicted transmitting abilities of common sires in two countries. Moreover, genetic correlations for the same traits were estimated between herd environmental categories formed according to MY levels, using bivariate analyses. Genetic correlation estimates for MY, FY, and PY between Chile-Canada (0.80, 0.61, and 0.70), and between Chile-US (0.79, 0.68, and 0.77), were lower than values obtained by simulation, assuming sire selection of the best 50%, and were also lower than the genetic correlations between Canada-USA, which were close to 1, suggesting a moderate genotype

by country interaction. All genetic correlation estimates between countries for F% and P% were close to 1. No evidence of genotype-environment interaction was found for any trait between High and Low Chilean herd environmental categories based on MY, (genetic correlation estimates ≥0.96; not statistically different from 1). Results indicate that a single national dairy genetic improvement programme incorporating international evaluations could be implemented in southern Chile, rather than separate programmes for specific herd MY environments. Moderate genotype-environmental interaction between North American and Chilean environments was found for MY, FY, and PY. Results from across and within country analyses indicate that sire selection in North America for milk solids yield will produce relatively high correlated genetic responses for the southern Chile dairy production system characterized by grazing and a temperate climate.

KEY WORDS: across country selection / Chile /dairy sires / genotype-environment interaction / milk yield traits / North America

The Black and White dairy population of southern Chile originates from old Chilean Black and White (Friesian) cattle, plus the incorporation of Holstein genes through the use of AI bulls evaluated mainly in North America – Canada and US – [Elzo *et al*. 2004]. Total Chilean cow´s milk production by 2009 was around 2.4 million ton from about 480 000 cows [ODEPA 2010]. Mean annual increment rate in milk production between years 2000-2009 was 3.8% [ODEPA 2010]. Most of the Chilean milk in 2010 (82.9 %) was produced in the oceanic temperate climate area of southern Chile (from 36° to 44° latitude south) in production systems based mainly on grazing, with different levels of technological components, such as concentrate supplementation and mashine milking parlors [ODEPA 2010].

Holstein is the breed with the largest worldwide use of imported semen, mainly from Canada, US and the Netherlands. However, the percentage of foreign Holstein bulls varies from 65% to 95% for many countries including those at organization Interbull [Dürr and Jakobsen 2009]. For this reason, studies have been performed to estimate the genetic correlations (r_g) and to determine whether there is a genotype-environmental interaction (GEI) for dairy traits between North America and regions such as Mexico [Cienfuegos-Rivas *et al*. 1999], Brazil [Costa *et al*. 2000] and other countries [Zwald *et al*. 2003]. Also, studies within Canada [Boettcher *et al*. 2003], the US [Castillo-Juarez *et al*. 2002], Italy [Raffrenato *et al*. 2003] and New Zealand [Bryant *et al*. 2007] for dairy traits in Holstein cattle in different herd environments or management levels have been carried out. Although Chilean Black and White producers have been using mostly Holstein semen imported from North America [Elzo *et al*. 2004], no studies have been developed to estimate genetic correlations (r_g) to determine if there is genotype-environment interaction for dairy traits between two countries. There are also rather few studies worldwide involving North America and grazing systems in temperate climates outside New Zealand and Europe. In general, there are no studies indicating whether genotype-environment interaction exists for dairy traits between herds differing on management levels for this Chilean population.

The objective of this study was to estimate genetic correlations between milk traits for Chile-Canada and for Chile-US, and to estimate genetic correlations for these traits between High and Low Chilean herd environmental categories defined

on the basis of milk yield. This knowledge may help in estimating to what degree sires genetically evaluated in North America are suitable in the context of breeding programs in grazing production systems such like those in the southern Chile, and to determine if different genetic evaluations might be needed for Chilean herds with different production systems classified by using average milk production level as a surrogate.

Material and methods

Genetic correlations between countries

Chilean data. Chilean PTA were obtained from univariate models at convergence, where $PTA_i = \frac{1}{2}u_i$, with u_i as the i-th solution for animal effects. Mature equivalent, 305-d milk (MY), fat (FY), and protein (PY) yields, and fat (F%) and protein (P%) contents records for the Black and White dairy population of southern Chile were obtained by the Cooperativa de Servicios Agrícolas [COOPRINSEM), from dairy herds in an extensive geographic area, covering three geographical Chilean political regions of La Araucanía), Los Lagos, and Los Ríos.

Milk records were from cows calving from 1997 to 2008. The final data set was from a multibreed population and it was comprised by three genetic groups: 1) Holstein (HH) with 103 517 lactations; 2) Holstein-Friesian crossbreed cows (HF) with 106 931 lactations; and 3) Friesian cows (FF) with 32 686 lactations.

All records for MY, FY and PY ≤80-d were adjusted to 305-d mature equivalent with methods developed and validated for this population by COOPRINSEM. Data were adjusted for variance heterogeneity by geographic region, production period, and cow genetic group with the method suggested by Hill [1984], which is based on standardizing phenotypic variances across genetic groups to a base value. Correlations between adjusted and non-adjusted records were >0.98 but heritabilities for unadjusted data were slightly higher (data not shown). Data were edited to include only records with milk yield ≥1000 kg, from cows' records with a known sire ID. Sires were required to provide records from at least four daughters. Based on this, approximately 20% of the original data was excluded. Most of the sires excluded are natural service sires with a small number of daughters in just one herd. Pedigree information was available from animals born from 1970 to 2008, and the relationship matrix **A** included the cow, sire, and dam ID´s.

Model and analysis

Univariate repeatability models were used to estimate variance components and to perform genetic evaluations for the Chilean population. Fixed effects included herd-year-season of calving (three seasons were considered: January to April, May to August, and September to December), calving season-parity effects, the covariates breed direct effect (Holstein = 1, Holstein × Friesian = 0, Friesian = -1), heterosis effect (0 for Holstein and Friesians, 1 for Holstein × Friesian). Random effects were

animal, permanent environment, sire-herd and residual. Crossbreeding effects were included to reduce possible biases in the estimates of genetic parameters caused by possible breed differences and heterosis.

In matrix notation the model used was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wp} + \mathbf{Ks} + \mathbf{e}$$

where:

$\mathbf{y}$ – vector of record observations (milk yields and composition traits);

$\mathbf{X}$ – fixed effects incidence matrix;

$\mathbf{b}$ – vector of fixed effects;

$\mathbf{Z}$ – incidence matrix for animal additive genetic effects;

$\mathbf{u}$ – vector of random animal additive genetic effects;

$\mathbf{W}$ – incidence matrix for permanent environmental effects;

$\mathbf{p}$ – vector of permanent environmental random effects;

$\mathbf{K}$ – incidence matrix for random sire-herd effects;

$\mathbf{s}$ – vector of sire-herd random effects;

$\mathbf{e}$ – vector of random residual effects.

Expectations and variances for model effects were:

$E(\mathbf{y}) = \mathbf{Xb}$; $E(\mathbf{u}) = E(\mathbf{p}) = E(\mathbf{s}) = E(\mathbf{e}) = \mathbf{0}$;
$var(\mathbf{u}) = \mathbf{A}\sigma_u^2$; $var(\mathbf{p}) = \mathbf{I}\sigma_u^2$; $var(\mathbf{s}) = \mathbf{I}\sigma_u^2$; $var(\mathbf{e}) = \mathbf{I}\sigma_u^2$.

Estimates of (co)variance components and solutions for animal effects were obtained by REML, with ASReml programme [Gilmour *et al*. 2009].

Canadian data. Official genetic evaluations of Canada were obtained from the web site of the Canadian Dairy Network [CDN 2009] for 9 084 bulls born from 1969 to 2006. Canadian breeding value evaluations were expressed as PTAs by multiplying them by 0.5.

US Data. Official PTAs of the US bulls were obtained from the web site of the Laboratory of Animal Improvement of the Department of Agriculture of the United States [USDA-ARS 2009] for 202 630 bulls born from 1950 to 2001.

PTAs for yield traits for all countries were expressed in kg, while those for milk content traits were expressed in percentage units. Data from bulls with evaluations in Chile-Canada and Chile-US were edited in a file that included common sires with a reliability ≥0.90 for the Chilean PTA for PY. This was done to reduce the downward bias in calculating the r_g [Montaldo and Pelcastre-Cruz 2012]. The genetic evaluations were from 40 common sires in Chile-Canada, 111 common sires in Chile-US and 40 common sires in Chile-Canada and Canada-US. The reliability was defined as the estimated $r^2_{T,PTA}$, where T is the true transmitting ability of the sire. The estimated r_g between countries were approximated from the observed correlations among the

PTAs of each bull in two countries and their average reliabilities, according to the following formula [Calo *et al*. 1973]:

$$r_g = \frac{r_o}{\sqrt{arel_i \times arel_j}}$$

where:

r_g – estimated genetic correlation;

r_o – observed correlation between PTAs of two countries;

$arel_i$ – average reliability of the PTAs in country i;

$arel_j$ – average reliability of the PTAs in country j.

Estimates of genetic correlations between PTAs in Chile-Canada and Chile-US were compared to genetic correlations which were obtained by simulation, using the same number of sires and PTAs reliability for obtaining r_g without genotype-environment interaction effects in order to account for possible underestimation related to data structure and sire selection [Montaldo and Pelcastre-Cruz 2012]. This was made using methodology described by Montaldo and Pelcastre-Cruz [2012] with a sire model with 10 000 replicates, using only PTAs from the top 50% sires' in their country of origin.

Estimates of r_g between herd environmental categories were considered lower than 1 (P<0.05) when the parameter estimate was smaller than twice the value of the standard error of the estimate. This is an approximate rule that is valid for significance testing of parameters estimated using large samples such as in this case, by assuming normal distribution of the estimates [see for example Akesson *et al*. 2008].

Analyses for environmental categories of the herds

Herds were classified in two environmental categories according to their MY average, as a proxy for the management level. Herds above general mean were considered as high environmental category (High) and those below, as low environmental category (Low). Descriptive statistics regarding the number of herds, sires, cows, records and the studied traits for the complete southern Chilean population and within herd environmental category for the studied traits are shown in Table 1. The r_g between herd environmental categories for each trait were estimated by using bivariate models containing the same effects as the already described for single-trait analyses.

Results and discussion

Chilean phenotypic and genetic parameters. Means for the Chilean population for the studied traits are shown in Table 1. Means for MY, FY, and PY were lower to corresponding means for recorded US Holsteins for the same period (USDA-ARS 2009) by 31, 31 and 25%, respectively. Means for F% and P% were 0 and 8% larger

Table 1. Descriptive statistics for the complete dataset and within herd environmental category for the studied traits in the Chilean Black and White dairy cattle population

Item	Complete data set		High environmental category		Low environmental category	
Herds (n)	446		210		236	
Sires (n)	1900		1608		1452	
Cows (n)	107002		70269		36733	
Lactations (n)	243134		158253		84881	
Average milk yield/herd (kg)	7603		9081		6287	

Trait	Mean	SD	Mean	SD	Mean	SD
Milk yield (kg)	8082	2316	8933	2158	6496	1680
Fat yield (kg)	291	76	316	73	243	58
Protein yield (kg)	260	74	288	69	209	54
Fat content (%)	3.64	0.52	3.59	0.52	3.74	0.50
Protein content (%)	3.23	0.24	3.23	0.24	3.24	0.24

Table 2. Genetic parameters for the studied traits in the Chilean Black and White dairy cattle population for the complete data set

Trait	Phenotypic SD[a]	Sire-herd[b]	Heritability	Repeatability
Milk yield (kg)	1550	0.04±0.002	0.19±0.006	0.43±0.003
Fat yield (kg)	54	0.04±0.002	0.21±0.006	0.44±0.003
Protein yield (kg)	48	0.04±0.002	0.15±0.006	0.41±0.003
Fat content (%)	0.46	0.03±0.002	0.55±0.007	0.75±0.002
Protein content (%)	0.21	0.02±0.001	0.55±0.007	0.73±0.002

[a]Phenotypic variance = animal + sire-herd + permanent environment + error variances.
[b]As a fraction of phenotypic SD.

than the corresponding means for recorded US Holsteins for the same period (USDA-ARS 2009). This is a consequence of the production system of southern Chile, mainly based on grazing, compared to mostly conventional systems in the US. Chilean means for MY, FY, PY, and F% were lower than the corresponding means for recorded Canadian Holsteins for the period 2001-2008 by 16, 19, 16 and 2% respectively, and 1% larger for P% (ICAR 2013) indicating a similar general trend with respect to Canada.

Heritability estimates (Tab. 2) for MY, FY, PY, F% and P% (0.19, 0.21, 0.15, 0.55 and 0.55 respectively) were smaller for MY, FY and PY but similar for F % and P % to those estimated using US Holstein data by Castillo-Juarez *et al*. [2002] as 0.28, 0.27, 0.26, 0.56 and 0.56 respectively, by Chauhan and Hayes [1991] as 0.29, 0.31, 0.25, 0.65 and 0.61 respectively and by Boettcher *et al*. [2003] for the Canadian Holstein grazing management systems (0.31, 0.35, 0.30, 0.70 and 0.61 respectively).

Similar heritability estimates were reported for yield traits in the Australian Black and White breed as 0.17, 0.15 and 0.13 for MY, FY and PY respectively, by Meyer [1985], in US Holstein by Schutz *et al*. [1990] (0.16, 0.16 and 0.13 respectively) and in the Mexican Holstein population by Montaldo *et al*. [2010] using first lactation data (0.17, 0.17 and 0.18 respectively). Previous heritability estimates for MY, FY and PY for the same Chilean Black and White population using smaller samples were larger (0.31, 0.29 and 0.24 respectively) [Elzo *et al*. 2004]. The smaller heritabilities found in our study could be due to changes in the genetic make-up of the population and in the management systems across time, but also may reflect differences in the size and edition of the datasets, models and algorithms used for variance component estimation.

Genetic correlations between countries. Genetic correlations for milk production and milk composition traits for US-Canada, Chile-Canada and Chile-US are shown in Table 3. Genetic correlations estimates between Canada and US showed higher values for F% and P% (about 0.99)

Table 3. Genetic correlations for milk production and composition traits Canada-US, Chile-Canada and Chile-US[a]

Country	Trait	Number of common sires	Average reliability Country 1	Average reliability Country 2	Expected correlation	Observed correlation	Genetic correlation estimated	Genetic correlation simulated
Canada-US	Milk yield (kg)	40	0.97	0.99	0.98	0.91	0.92±0.07	-
Canada-US	Fat yield (kg)	40	0.97	0.99	0.98	0.92	0.94±0.06	-
Canada-US	Protein yield (kg)	40	0.97	0.99	0.98	0.92	0.94±0.06	-
Canada-US	Fat content (%)	40	0.99	0.99	0.99	0.98	0.99±0.03	-
Canada-US	Protein content (%)	40	0.99	0.99	0.99	0.98	0.99±0.03	-
Chile-Canada	Milk yield (kg)	40	0.93	0.97	0.95	0.76	0.80±0.05	0.92±0.05
Chile-Canada	Fat yield (kg)	40	0.93	0.97	0.95	0.58	0.61±0.05	0.92±0.05
Chile-Canada	Protein yield (kg)	40	0.91	0.97	0.94	0.66	0.70±0.06	0.91±0.05
Chile-Canada	Fat content (%)	40	0.97	0.99	0.98	0.92	0.94±0.03	0.96±0.02
Chile-Canada	Protein content (%)	40	0.97	0.99	0.98	0.92	0.94±0.03	0.96±0.03
Chile-US	Milk yield (kg)	111	0.93	0.99	0.96	0.76	0.79±0.03	0.94±0.02
Chile-US	Fat yield (kg)	111	0.94	0.99	0.96	0.65	0.68±0.03	0.94±0.02
Chile-US	Protein yield (kg)	111	0.92	0.99	0.95	0.73	0.77±0.03	0.93±0.03
Chile-US	Fat content (%)	111	0.98	0.99	0.98	0.93	0.94±0.02	0.97±0.01
Chile-US	Protein content (%)	111	0.98	0.99	0.98	0.93	0.94±0.02	0.97±0.01

[a]From sires with reliabilities 0.90 for protein yield PTAs in Chile.

compared to yield traits (from 0.92 to 0.94), but with smaller differences compared to Chile-Canada and Chile-US (Table 3). Genetic correlations between Canada and US were high for all traits (0.92 to 0.98) (Table 3) and contain 1 in their approximate 95% confidence intervals, similar to those found by Weigel *et al*. [2001] between US-Canada (0.95) and to those observed by Jamrozik *et al*. [2002] for milk yield between Australia and Canada (0.96) and between New Zealand and Canada (0.93). Nevertheless, our estimate was higher than the one estimated by Weigel *et al*. [2001] for milk yield

Table 4. Genetic parameters for the studied traits in the Chilean Black and White dairy cattle population for the High and Low herd environmental categories

Trait	Herd Environmental Category				Genetic correlation[b]
	high		low		
	heritability	phenotypic SD[a]	heritability	phenotypic SD[a]	
Milk yield (kg)	0.21±0.01	1673	0.20±0.01	1286	0.97±0.02
Fat yield (kg)	0.22±0.01	58	0.21±0.01	46	0.98±0.02
Protein yield (kg)	0.17±0.01	51	0.15±0.01	40	0.96±0.02
Fat content (%)	0.56±0.01	0.44	0.56±0.01	0.47	0.99±0.01
Protein content (%)	0.58±0.01	0.20	0.54±0.01	0.21	1.00±0.01

[a]Phenotypic variance = animal + sire-herd + permanent environment + error variances.
[b]$P>0.05$, do not rejecting Ho: $r_g = 1$

between Australia and Canada (0.82), using an international sire evaluation model. Genetic correlations for PY and FY, in the present study, between Chile-Canada and Chile-US (0.61 to 0.68 for FY and 0.70 to 0.77 for PY) were somewhat lower to those found between either Canada or US and other 15 countries, which ranged from 0.80 to 0.96 for FY and from 0.85 to 0.95 for PY [Weigel *et al*. 2001]. Other studies of genetic correlations between US and Western European Countries for milk yield traits have shown similar values with an average of 0.92 [Mark, 2004]. More recent estimates used by International Bull Evaluation Service (Interbull) [Interbull 2013] indicate lower genetic correlations for yield traits between grazing systems in New Zealand than those from other countries with conventional production systems (0.75-0.76) when compared to those observed for Canada-USA (0.92-0.94). This and the results of our study may indicate a degree of sire by production system (grazing *vs*. conventional) interaction for MY, FY and PY.

Genetic correlations between High and Low Herd environmental categories Genetic parameters between Chilean High and Low herd environmental categories for the studied traits are shown in Table 4. Herds from the High category had on average 335 cows versus 156 in the Low category (Tab. 1). Heritability estimates were similar for all the traits in the High and Low herd environmental categories, in spite of large differences for phenotypic variance estimates, and consequently, additive genetic and environmental variances. Heritability estimates within herd environmental categories were similar to the observed for the complete dataset (Tab. 2). The r_g for milk traits between Chilean herd environmental categories varied from 0.96 to 1.00 (Tab. 4) and were not different from 1 ($P>0.05$) indicating that milk production and composition traits did not show GEI between herds grouped according to milk production level. Similar to our findings, Castillo-Juarez *et al*. [2002] found $r_g \geq 0.97$ for mature equivalent milk, fat and protein yields, and for fat and protein contents between high and low herd environmental categories in the US based on an

index that weight milk production and variability, indicating that breeding values and ranking of the sires based on them for these traits would, under single trait selection, be essentially the same in the two yield environment classes. The r_g estimates between herd environmental categories found in our study were slightly larger than the estimates of r_g between conventional and grazing environments observed in Canada by Boettcher *et al*. [2003] for milk traits, including composition traits that were mostly also close to 1, varying from 0.88 to 0.96. They also found similar heritability estimates between grazing and the (conventional) high producing level in Canada. Bryant *et al*. [2007] used the mean of the sum of fat and protein yields to classify New Zealand herds into four environmental levels and found no evidence of GEI for any dairy trait, with most r_g estimates ≥ 0.90 between environmental levels. They did not find differences between heritabilities across levels. Conversely, Raffrenato *et al*. [2003] in Italy, found r_g estimates statistically smaller than 1 (0.48 to 0.66) for yield traits using two environment opportunity categories based on within herd-year-season standard deviation for MY, a criterion which is closely related to the herd average for MY used in our study. They did not find differences in heritabilities between categories. In this sense, Castillo-Juarez *et al*. [2002] did not find differences in genetic parameter estimates when defining environmental opportunity levels either based on herd-year-standard deviations, or using a combination of herd-year-mean milk yield and herd-year-standard deviations for milk yield.

General discussion. Regarding the estimates of genetic correlations among countries, and using the criteria by Mulder *et al*. [2006], there is no need to develop a breeding programme for the Chilean Black and White population separated from the North American Holstein population, because the estimates were all above 0.60. However, values of genetic correlation indicate that local programmes would be more competitive with North American breeding programmes when compared to situations with larger genetic correlation estimates. Results indicate that studies to compare the profitability of dairy selection programmes for Chile, versus semen importation [see for example Vargas and Van Arendonk 2004], should be undertaken.

Genetic correlation estimates between MY herd environmental categories close to 1 indicate the advantage of using a single Chilean dairy genetic programme for the Black and White dairy population, rather than having separate programmes for specific herd environments.

REFERENCES

1. AKESSON M., BENSCH S., HASSELQUIST D., TARKA M., HANSSON B., 2008 – Estimating heritabilities and genetic correlations: Comparing the 'animal model' with parent-offspring regression using data from a natural population. Accessed Jul. 23, 2009. http://www.plosone.org/article/info: doi%2F10.1371%2Fjournal.pone.0001739.

2. BOETTCHER P.J., FATEHI J., SCHUTZ M.M**.,** 2003 – Genotype × environment interactions in conventional versus pasture-based dairies in Canada. *Journal of Dairy Science* 86, 383-389.

3. BRYANT J.R., LÓPEZ-VILLALOBOS N., PRYCE J.E., HOLMES C.W., JOHNSON D.L., GARRICK D.J., 2007 – Environmental sensitivity in New Zealand dairy cattle. *Journal of Dairy Science* 90, 1538–1547.

4. CALO L.L., MCDOWELL R.E., VAN VLECK L.D., MILLER P.D., 1973 – Genetic aspects of beef production among Holstein-Friesians pedigree selected for milk production. *Journal of Animal Science* 37, 676-682.

5. CASTILLO-JUAREZ H., OLTENACU P.A., CIENFUEGOS-RIVAS E.G., 2002 – Genetic and phenotypic relationships among milk production and composition traits in primiparous Holstein cows in two different herd environments. *Livestock Production Science* 78**,** 223-231.

6. CDN, 2009 - Official Genetic Evaluations. Accessed Jan. 8, 2009. http://www.cdn.ca/files_ge_ articles.php

7. CHAUHAN V.P.S., HAYES J.F., 1991 – Genetic parameters traits for Holsteins for first lactation milk production and composition using multivariate restricted maximum likelihood. *Journal of Dairy Science* 74, 603-610.

8. CIENFUEGOS-RIVAS E.G., OLTENACU P.A., BLAKE R.W., SCHAWEGER S.J., CASTILLO-JUAREZ H., RUIZ F.J., 1999 – Interaction between milk yield of Holstein cows in Mexico and the United States. *Journal of Dairy Science* 82, 2218–2223.

9. COSTA C.N., BLAKE R.W., POLLAK E.J., OLTENACU P.A., QUAAS R.L., SEARLE S.R., 2000 – Genetic analysis of Holstein cattle populations in Brazil and the United States. *Journal of Dairy Science* 83**,** 2963-2974.

10. DÜRR J.W., JAKOBSEN J.H., 2009 – Country profiles regarding the use of imported dairy bulls. *INTERBULL Bulletin* 40, 259-266. Accessed Jul. 15, 2011.

11. http://www-interbull.slu.se/bulletins/bulletin40/Durr.pdf.

12. ELZO M.A., JARA A., BARRIA N., 2004 – Genetic parameters and trends in the Chilean multibreed dairy cattle population. *Journal of Dairy Science* 87, 1506–1518.

13. GILMOUR A.R., GOGEL B.J., CULLIS B.R., THOMPSON R., 2009 – ASReml user guide. Release 3.0.VSN International Ltd, U.K.

14. HILL W.G., 1984 – On selection among groups with heterogeneous variance. *Animal Production* 39, 473-477.

15. ICAR 2013 – Yearly milk enquiry. International Committee for Animal Recording, Rome, Italy. Accessed May 29, 2013. http://www.survey-icar.org/cow_survey/Canada/043_main_breeds_cows, can1_interface/Results/results_page.asp.

16. INTERBULL 2013 – Interbull Routine Genetic Evaluation for Dairy Production Traits. April 2013. International Bull Evaluation Service, Uppsala, Sweden. Accessed May 29, 2013. http://www-interbull.slu.se/eval/prod-appen1-131.pdf.

17. JAMROZIK J., SCHAEFFER L.R., WEIGEL K.A., 2002 – Genetic evaluation of bulls and cows with single- and multiple-country test-day models. *Journal of Dairy Science* 85, 1617-1622.

18. MARK T., 2004 – Applied genetic evaluations for production and functional traits in dairy cattle. *Journal of Dairy Science* 87, 2641-2652.

19. MEYER, K., 1985 – Genetic parameters for dairy production of Australian Black and White cows. *Livestock Production Science* 12, 205-219.

20. MONTALDO H.H., CASTILLO-JUÁREZ H., VALENCIA-POSADAS M., CIENFUEGOS-RIVAS E.G., RUIZ-LÓPEZ F.J., 2010 − Genetic and environmental parameters for milk production, udder health, and fertility traits in Mexican Holstein cows. *Journal of Dairy Science* 93, 2168-2175.

21. MONTALDO H.H., PELCASTRE-CRUZ A., 2012 – Factors affecting genetic correlation estimates from dairy sires' genetic evaluations to assess genotype-environment interaction. ***Animal Science Papers and Reports*** 30, 309-315.

22. MULDER H.A., VEERKAMP R.F., DUCRO B.J., VAN ARENDONK J.A.M., BIJMA P., 2006 – Optimization of dairy cattle breeding programs for different environments with genotype by environment interaction. ***Journal of Dairy Science*** 89, 1740-1752.

23. ODEPA 2010 – Dairy Bulletin -Year 2010. Ministry of Agriculture, Chile. Pages 1-51. Accessed Mar. 29, 2011 http://www.odepa.cl/wp-content/uploads/2013/09/boletin_Leche-2010.pdf

24. RAFFRENATO E., BLAKE R.W., OLTENACU P.A., CARVALHEIRA J., LICITRA G., 2003 – Genotype by environment interaction for yield and somatic cell score with alternative environmental definitions. ***Journal of Dairy Science*** 86, 2470-2479.

25. SCHUTZ M.M., HANSEN L.B., STEUERNAGEL G.R., RENEAU J.K., 1990 – Genetic parameters for somatic cells, protein, and fat in milk of Holsteins. ***Journal of Dairy Science*** 73, 494-450.

26. USDA-ARS 2009 – Official Genetic Evaluations. Accessed Mar. 8, 2009 http://www.aipl.arsusda.gov/eval.htm

27. VARGAS B., VAN ARENDONK J.A.M., 2004 – Genetic comparison of breeding schemes based on semen importation and local breeding schemes: framework and application to Costa Rica. ***Journal of Dairy Science*** 87, 1496-1505.

28. WEIGEL K.A., REKAYA R., ZWALD N.R., FIKSE W.F., 2001 – International genetic evaluation of dairy sires using a multiple-trait model with individual animal performance records. ***Journal of Dairy Science*** 84, 2789-2795.

29. ZWALD N.R., WEIGEL K.A., FIKSE W.F., REKAYA R., 2003 – Identification of factors that cause genotype by environment interaction between herds of Holstein cattle in seventeen countries. ***Journal of Dairy Science*** 86**,** 1009-1018.