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The Resilient Dairy Genome Project – a general overview of methods and objectives related to feed efficiency and methane emissions

Nienke van Staaveren,1* Hinayah R. Oliveira,12* Kerry Houlahan,1* Tatiane C. S. Chud,[1] Gerson A. Oliveira Jr.,[1] Dagnachew Hailemariam,[3] Gerrit Kistemaker,[2] Filippo Miglior,12 Graham Plastow,[3] Flavio S. Schenkel,[1] Ronaldo Cerri,[4] Marc-André Sirard,[5] Paul Stothard,[3] Jennie Pryce,67 Adrien Butty,[8] Patrick Stratz,[8] Emhimad A. E. Abdalla,[9] Dierck Segelke,910 Eckhard Stamer,[11] Georg Thaller,[10] Jan Lassen,[12] Coralia Ines V. Manzanilla-Pech,[13] Rasmus B. Stephansen,[13] Noureddine Charfeddine,[14] Aser Garcia-Rodriguez,[15] Oscar González-Recio,[16] Javier López-Paredes,[17] Ransom Baldwin,[18] Javier Burchard,[19] Kristen Gaddis,[19] James E. Koltes,[20] Francisco Peñagaricano,[21] José Eduardo P. Santos,[22] Robert J. Tempelman,[23] Michael VandeHaar,[23] Kent Weigel,[21] Heather White,[21] and Christine F. Baes124*

[1]Centre for Genetic Improvement of Livestock, Department of Animal Biosciences, University of Guelph, Guelph, ON N1G 2W1, Canada
[2]Lactanet Canada, Guelph, ON N1K 1E5, Canada
[3]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, AB T6G 2R3, Canada
[4]Applied Animal Biology, Faculty of Land and Food Systems, University of British Columbia, Vancouver, BC, Canada V6T 1Z4
[5]Department of Animal Sciences, Laval University, Qubec G1V 0A6, QC, Canada
[6]School of Applied Systems Biology, La Trobe University, Bundoora, Victoria 3083, Australia
[7]Agriculture Victoria Research, LaTrobe University, Bundoora, Victoria 3083, Australia
[8]Qualitas AG, 6300 Zug, Switzerland
[9]Vereinigte Informationssysteme Tierhaltung w.V. (vit), Heinrich-Schröder-Weg 1, 27283, Verden, Germany
[10]Institute of Animal Breeding and Husbandry, Christian-Albrechts-University, 24098, Kiel, Germany
[11] TiDa Tier und Daten GmbH, 24259 Westensee/Brux, Germany
[12]Viking Genetics, Ebeltoftvej 16, 8960 Assentoft, Denmark
[13]Center for Quantitative Genetics and Genomics, Aarhus University, PO Box 50, DK-8830 Tjele, Denmark
[14]Spanish Holstein Association (CONAFE), Ctra. Andalucía km 23600 Valdemoro, 28340 Madrid, Spain
[15]Department of Animal Production, NEIKER—Basque Institute for Agricultural Research and Development, 01192 Arkaute, Spain
[16]Department of Animal Breeding, Instituto Nacional de Investigacion y Tecnologia Agraria y Alimentaria (INIA-CSIC), 28040 Madrid, Spain
[17]Federación Española de Criadores de Limusín, C/Infanta Mercedes, 31, 28020 Madrid, Spain
[18]Animal Genomics and Improvement Laboratory, Agricultural Research Service, USDA, Beltsville, MD 20705, USA
[19]Council on Dairy Cattle Breeding, Bowie, MD 20716, USA
[20]Department of Animal Science, Iowa State University, Ames, IA 50011, USA
[21]Department of Animal and Dairy Sciences, University of Wisconsin-Madison, Madison, WI 53706, USA
[22]Department of Animal Sciences, University of Florida, 2250 Shealy Drive, Gainesville, FL, 32611, USA
[23]Department of Animal Science, Michigan State University, East Lansing MI 48824, USA
[24]Vetsuisse Faculty, Institute of Genetics, University of Bern, 3012 Bern, Switzerland

ABSTRACT

The Resilient Dairy Genome Project (**RDGP**) is an international large-scale applied research project that aims to generate genomic tools to breed more resilient dairy cows. In this context, improving feed efficiency and reducing greenhouse gases from dairy is a high priority. The inclusion of traits related to feed efficiency (e.g., dry matter intake [**DMI**]) or greenhouse gases (e.g., methane emissions [$\mathbf{CH_4}$]) relies on available genotypes as well as high quality phenotypes. Currently, 7 countries, i.e., Australia [**AUS**], Canada [**CAN**], Denmark [**DNK**], Germany [**DEU**], Spain [**ESP**], Switzerland [**CHE**], and United States of America [**USA**] contribute with genotypes and phenotypes including DMI and CH_4. However, combining data is challenging due to differences in recording protocols, measurement technology, genotyping, and animal management across sources. In this study, we provide an overview of how the RDGP partners address these issues to advance international collaboration to generate genomic tools for resilient dairy. Specifically, we describe the current state of the RDGP database, data collection protocols in each country, and the strategies used for managing the shared data. As of February 2022, the database contains 1,289,593 DMI records from 12,687 cows and 17,403 CH_4 records from 3,093 cows and continues to grow as countries upload new data over the coming years. No strong genomic differentiation between the populations was identified in this study, which may be beneficial for eventual across-country genomic predictions. Moreover, our results reinforce the need

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*Corresponding author: Christine F. Baes, Centre for Genetic Improvement of Livestock, Department of Animal Biosciences, University of Guelph, 50 Stone Road East, Guelph N1G 2W1, Ontario, Canada, Phone: +1 (519) 824-4120 ext. 53363, cbaes@uoguelph.ca

to account for the heterogeneity in the DMI and CH_4 phenotypes in genomic analysis.
Keywords: resilience, feed efficiency, dairy cattle breeding, methane, dry matter intake

INTRODUCTION

Dairy farming success relies on the ability of cows to produce milk, while minimizing environmental impact, as well as enhancing animals' health and welfare, within socially acceptable standards (Cardoso et al., 2016; Brito et al., 2021). Breeding goals in dairy cattle have thus shifted from a focus on production to a more balanced and comprehensive goal with emphasis on traits related to longevity, fertility, calving, health and welfare, workability, milk quality, environmental efficiency, and overall resilience (Calus et al., 2013; Miglior et al., 2017; Mulder and Rashidi, 2017; Herzog et al., 2018; Berghof et al., 2019; Seymour et al., 2019; König and May, 2019; Adriaens et al., 2020; Brito et al., 2021; Manzanilla-Pech et al., 2021; Ouweltjes et al., 2021; Zhang et al., 2022). In Canada, the Resilient Dairy Genome Project (**RDGP**; http://www.resilientdairy.ca) is a continuation of the Efficient Dairy Genome Project (**EDGP**; https://genomedairy.ualberta.ca/). The overarching goal of the RDGP is to generate genomic tools to breed more resilient dairy cows. Resilience can be defined in different ways (Colditz and Hine, 2016), but within the RDGP it is defined as the capacity of the animal to adapt rapidly to changing environmental conditions, without compromising its productivity, health or fertility while becoming more resource-efficient and reducing its environmental burden.

Within this context, 2 main components that play a crucial role are feed efficiency and CH_4 emissions. Feed accounts for the largest proportion of operational costs in a dairy farm. Additionally, CH_4, formed during enteric fermentation, is a source of feed energy loss (Johnson et al., 1994) and a major greenhouse gas. While CH_4 has a 28 times greater global warming potential than carbon dioxide (**CO_2**), it has a shorter half-life, which may reduce its overall impact on global warming (IPCC, 2014; Knapp et al., 2014; Liu et al., 2021). While the relationship between feed efficiency and CH_4 emissions is not fully elucidated (Løvendahl et al., 2018), evidence suggests that genetic improvements in feed efficiency could reduce methane emissions (Yan et al., 2010; Waghorn and Hegarty, 2011; Basarab et al., 2013; Hayes et al., 2013; Knapp et al., 2014; Difford et al., 2020; Manzanilla-Pech et al., 2021). This simultaneous benefit can be achieved when nutrient utilization is optimized to achieve a greater productive output per animal (under the same input) and fewer animals are needed to produce the same amount of milk (Knapp et al., 2014). Furthermore, producers' profit can be maximized not only by saving on feed costs, but through financial benefits provided by, for example, governmental programs related to emissions trading markets (Zhang et al., 2021).

Improvements in feed efficiency and methane emission through selective breeding are permanent and cumulative (Lassen and Difford, 2020; de Haas et al., 2021); however, results depend on several factors such as trait definitions, economic weights, and selection strategies used in breeding programs (González-Recio et al., 2020; de Haas et al., 2021; Houlahan et al., 2021; Manzanilla-Pech et al., 2021). Moreover, there is a need for clearly defined and standardized phenotypes that can be cost-effectively recorded on a large number of animals, which is especially challenging for traits related to feed efficiency and methane emissions. Advancements in genomics allow breeding values to be accurately predicted for selection candidates without phenotypes, if a sufficiently large and diverse training population is available (Miglior et al., 2017). For instance, it has been suggested that a training population of over 30,000 animals is needed to achieve desired reliabilities for feed efficiency related traits such as residual feed intake (reviewed by Brito et al., 2020). Similarly, de Haas et al. (2021) suggested that methane records would be needed for an average of 150 cows at over 100 farms for a minimum of 2 years to achieve desired reliabilities for genomic predictions.

The size of the training population for feed efficiency and methane emissions can be increased through collaboration at national and international levels (Berry et al., 2014; de Haas et al., 2015; Tempelman et al., 2015; Lassen and Difford, 2020; Manzanilla-Pech et al., 2021). Consequently, several major countries, including Australia, United States of America, Denmark, Norway, Finland, Sweden, New Zealand, The Netherlands, United Kingdom, and Canada, have now included feed efficiency as a selection criterion in their breeding programs (reviewed by Brito et al., 2020; Houlahan, 2021; Stephansen et al., 2021). In contrast, to the best of our knowledge, no official genomic evaluations have been performed for methane emissions yet despite on-going efforts (González-Recio et al., 2020; Manzanilla-Pech et al., 2021; Richardson et al., 2021b). Australia recently released a Sustainability Index which does not include methane directly, but instead places emphasis on traits associated with methane emissions (Richardson et al., 2021a). Moreover, Canada has launched the first official genomic evaluation for methane efficiency in April 2023, but using an approach that predicts methane using a relatively small reference population and artificial neural networks (Lactanet Canada, 2023). This is likely due to the difficulty in collecting these data but also

because methane emissions currently have little direct economic value to farmers (Boaitey et al., 2019; Lassen and Difford, 2020), which is expected to change in the next few years as several global initiatives are being implemented to reduce greenhouse gas emissions (Global Dairy Platform, 2021; Dairy Farmers of Canada, 2022; Oliveira et al., 2022a).

A larger training population can increase the accuracy of genomic estimated breeding values and enable genetic progress for feed efficiency and methane emission traits worldwide. One of the specific objectives within the RDGP is to enlarge the training population for genomic evaluations of feed efficiency and methane emissions by expanding on the international database established as part of the EDGP. Currently, 7 countries namely Australia [**AUS**], Canada [**CAN**], Denmark [**DNK**], Germany [**DEU**], Spain [**ESP**], Switzerland [**CHE**], and United States of America [**USA**] have contributed with genotypes and phenotypes for feed efficiency and methane emissions. However, combining data is challenging due to differences in recording protocols, measurement technology, genotyping (e.g., densities of single nucleotide polymorphism [**SNP**] panels), management and nutrition across data sources (de Haas et al., 2015; Hristov et al., 2018; Manzanilla-Pech et al., 2021). The aim of this study was to overcome these obstacles and provide the basis for future research and genomic evaluations using data contributed by the partners in this project. More specifically, this study aimed to: 1) describe the data currently available in the RDGP database, as well as the data collection protocols in each country; and 2) define the methods currently used for managing the shared data.

MATERIALS AND METHODS

Data Collection

Data were collected as part of the global Resilient Dairy Genome Project (2020 to 2023, http://www.resilientdairy.ca/), which is a continuation of the Efficient Dairy Genome Project (2015 to 2020, https://genomedairy.ualberta.ca/). All traits were collected from dairy herds of research or commercial partners in Australia (1 herd), Canada (3 herds), USA (8 herds), Denmark (1 herd), Switzerland (2 herds), Germany (5 herds), and Spain (22 herds). Thus, data were provided from experiments according to local guidelines and regulations. The database built through this project is updated with new data 3 times per year to align with national evaluations, and hence, it is continuously expanding. The data presented here consist of the last extraction in February 2022. Data consist of pedigree, calving, production, feed efficiency, environmental emissions, genotype, and milk mid-infrared spectral files and are merged to provide a database containing all records from each country. One record could be uploaded for each individual cow on a specific date, with countries providing daily, weekly, or monthly averages depending on the data collection methods as described further.

The main traits recorded in the database include among others milk yield (**MY**, g), fat yield (**FY**, g), protein yield (**PY**, g), lactose yield (**LY**, g), somatic cell count (**SCC,** 10^3/mL divided by 1,000), milk urea nitrogen (**MUN**, g), milk β hydroxybutyrate (**BHB**, mmol/L multiplied by 1,000), milk mid-infrared spectral data (**MIR,** cm^{-1}), dry matter intake (**DMI**, g/day), body weight (**BW**, kg), body condition score (**BCS,** 1 to 5 scale), CH_4 emission (g/day), and CO_2 emission (g/day). Units provided are those as required in the database to ensure standardized traits. The number of cows for each trait provided by each country is shown in Figure 1. In order, traits with the total number of cows decreased from MY (15,577), PY (15,333), FY (15,332), DMI (12,687), BW (12,250), SCC (11,727), LY (11,474), BCS (8,476), MUN (8,153), CH_4 (3,093), MIR (3,015), BHB (2,238), to CO_2 (814).

Detailed information on data collection of all traits for each herd in the different countries is described in the Supplementary Material I. While some countries collected data on different cattle breeds, only data on Holstein dairy cows is considered in this paper. A general overview of the housing, management, and data collection in each country is shown in Table 1. With the exception of one herd in AUS and ESP who kept cows predominantly on pasture, all cows were housed indoors and on a partial or total mixed ration. Animals were milked using standard commercial practices i.e., 2 to 3 times a day in a parlor setting, or through a voluntary milking system (robot).

A main area of research within the RDGP is the genetic evaluation of feed efficiency and CH_4 emissions traits, and thus for conciseness, we will only discuss these 2 traits within this paper. Feed intake and CH_4 emission data were collected from 24 and 20 herds, respectively. Dry matter intake data collection ranged from 30 d before calving to 305 d in milk (**DIM**), while CH_4 emission data were collected only for lactating animals. Some countries focused on specific parities or time points within the lactation, while others collected data spanning the entire 305-d lactation in primiparous and multiparous cows (Supplementary Material I). All animals had *ad libitum* access to feed and water. Feed intake data were collected through a variety of methods. These methods included automated data collection (Insentec Roughage Intake Control feed bunks, Hokofarms Group B.V., Marknesse, The Netherlands;

	MY	FY	PY	LY	SCC	MUN	BHB	MIR	DMI	BW	BCS	CH4	CO2
AUS	576	576	576	576	0	0	0	226	576	576	494	464	385
CAN	1,786	1,780	1,780	186	1,789	197	1,621	1,615	1,810	1,574	1,029	661	410
CHE	189	188	188	188	95	95	0	91	206	206	72	94	19
DEU	1,796	1,795	1,796	1,796	1,796	1,796	0	0	1,810	1,816	0	0	0
DNK	2,034	2,020	2,020	809	721	0	0	220	823	822	809	246	0
ESP	2,423	2,218	2,218	2,073	1,459	70	617	659	645	450	0	1,625	0
USA	6,773	6,755	6,755	5,846	5,867	5,995	0	204	6,817	6,806	6,075	3	0

Figure 1. Number of cows provided for each trait by each country at the end of February 2022. Countries: Australia (AUS), Canada (CAN), Switzerland (CHE), Germany (DEU), Denmark (DNK), Spain (ESP), and United States of America (USA). Production traits: milk yield (MY, g), fat yield (FY, g), protein yield (PY, g), lactose yield (LY, g), milk mid-infrared spectral data (MIR, cm-1), somatic cell count (SCC, 10^3/mL divided by 1,000), milk urea nitrogen (MUN, g), and milk β hydroxybutyrate (BHB, mmol/L multiplied by 1,000). Efficiency traits: dry matter intake (DMI, g/day), live body weight (BW, kg), body condition score (BCS, 1–5 score), methane emission (g/day), carbon dioxide emission (CO_2, g/day).

GrowSafe ® dairy feed intake system, GrowSafe Calgary, Alberta, Canada; Waagen Döhrn, Wesel, Germany; and Landtechnick Weihenstephan, Weihenstephan, Germany) and manual weights, where feed offered was weighed at the time of feeding and the feed refused was weighed 24 h later with cows in tie-stall barns or in freestall barns equipped with individual feeding gates (e.g., American Calan Inc., Northwood, NH). Methane emissions were collected using 4 different methods, including respiration chambers (CHE), GreenFeed (C-Lock Inc., Rapid City, SD, USA; CAN, CHE and USA), sniffers (DNK and ESP), and modified SF6 tracer (AUS and CHE). All countries uploaded CH_4 production in g/d as the final trait. Depending on the herd, measurements could be taken at different frequency, with most of the herds collecting data daily during specific periods within a lactation (for full details see Supplementary Material I). Additionally, it should be noted that CHE (CH_4), DEU (DMI, BW), DNK (DMI, CH_4), and ESP (DMI, BW, CH_4) reported weekly averages.

Pedigree and Genotypes

Pedigree information was traced back to 1940 and available for 72,682 animals. Of this, a total of 11,819 cows were genotyped using 28 different SNP panels. The current number of genotyped cows per trait and a summary of the SNP panels included in the RDGP, split by country, are shown in the Supplementary Material II. All SNP marker positions were updated to the ARS-UCD1.2 bovine reference genome assembly (Rosen et al., 2020). Concordance between SNP panels used in the different countries was evaluated based on the Pearson correlation coefficient of allele frequencies, using the SNPs in common across all SNP panels (n = 3,888 SNPs) that remained after the quality control (as described in the "Genotypic quality control" topic). Allele frequencies were calculated using the–freq flag

available in the PLINK 1.9 software (Purcell et al., 2007).

Genotype imputation. Imputation of genotypes was performed with the objective that all cows in the RDGP database had the same SNP density. As most cows were genotyped using a version of a 50K SNP chip, this was the target density for the imputation process. The analyses were divided in 2 steps. First, all cows originally genotyped using panels with more than 45K SNPs were considered as the reference data set, comprising of 8,484 animals (approx. 72% of the available animals). After imputing this reference data set to 50K (54,015 SNPs), it was used to bring up lower-density panels to the same density. Genotype phasing and imputation were performed using the BEAGLE v5.3 (Browning et al., 2021). BEAGLE is a commonly used population-based imputation program (it does not rely on pedigree information) that adopts a stochastic procedure based on a Hidden Markov Monte-Carlo process to infer the probabilities of each haplotype/genotype. Only autosomes were considered. Imputation accuracy was assessed by Pearson correlation between imputed and observed genotypes. This was done by setting aside 100 randomly chosen animals that had their 50K genotypes masked to a lower density panel (i.e., 7K) of this study. These animals were then imputed to their original panel density (i.e., 50K), and the correlations were calculated using only the information of imputed markers.

Genotypic quality control. Genotypic quality control was performed before and after imputation within each country. In addition, extra quality control was performed considering all animals together, using the common SNP panel established. In general, SNPs with unknown genomic positions and/or located in the sex chromosomes, those with minor allele frequency (MAF) lower than 0.05, those with sample or SNP call rate lower than 95%, and extreme departure from Hardy Weinberg equilibrium ($p\text{-}value < 10^{-15}$) were excluded. Genotypic quality controls were performed using the PLINK 1.9 software (Purcell et al., 2007). The total SNPs and genotyped animals that remained after the quality control were 54,015 and 11,580, respectively (from which 557 were from AUS, 1,696 from CAN, 132 from CHE, 441 from DNK, 1,404 from ESP, and 4,409 from USA).

Population Characterization

To evaluate the level of relatedness between the animals in the different countries, the entire population was characterized using 2 criteria calculated using the imputed genotypes: 1) proximity in the principal component analysis (PCA), and 2) consistency of gametic phase.

PCA. Principal component analysis was performed to investigate the genomic similarities between genotyped cows from the different countries, using the–pca

Table 1. General overview of housing, management, and data collection of Holstein dairy cows in each country participating in the Resilient Dairy Genome Project

	AUS	CAN	CHE	DEU	DNK	ESP	USA
Farm							
Research	X	X	X	X	X	X	X
Commercial		X				X	
Housing							
Outdoor	X					X	
Tiestall		X	X			X	X
Freestall		X	X	X	X	X	X
Parity	1–9	1–10	1–8	1–11	1–6	1–9	1–8
Feed							
Pasture	X					X	
Partial mixed ration		X	X	X			
Total mixed ration		X		X	X	X	X
CH_4 method							
Chamber			X				
GreenFeed		X	X				X
SF6	X		X				
Sniffer					X	X	
Measurement frequency[1]							
DMI	d	d	d, w	d, w[2]	d, w[2]	d, w[2]	d
BW	d	d, w, m	d	w[2], m[2]	d	d, w[2]	d, w
CH_4	d	d	d, w[2]		d, w[2]	d, w[2]	d

Countries: Australia (AUS), Canada (CAN), Switzerland (CHE), Germany (DEU), Denmark (DNK), Spain (ESP), and United States of America (USA). Dry matter intake (DMI), body weight (BW), methane emission (CH_4).

[1]Frequency of measurement: daily (d), weekly (w), monthly (m).

[2]Measurements were used to calculate a weekly average which was uploaded to the database.

flag available in the PLINK 1.9 software (Purcell et al., 2007). Principal components were estimated based on the variance-standardized genomic relationship matrix (**G**), calculated as the first method shown in VanRaden et al. (2008).

Consistency of gametic phase. Across pairs of markers, genotypes coded as 0, 1, or 2 have a correlation r, which describes linkage disequilibrium (Hill and Robertson, 1968). The consistency of phase was measured as the correlation *rho* of these correlations r for 2 countries, across pairs of markers at similar distances (de Roos et al., 2008). Negative values imply that the most frequent haplotypes have recombined, whereas values close to 1 imply that ancestral haplotypes are conserved. Both metrics were calculated for the genotyped animals using the *–r2* and *–dprime-signed* flags available in the PLINK 1.9 software (Purcell et al., 2007).

Phenotypic Quality Control and Test of Homogeneity

Phenotypic quality control was performed independently for each trait within each country. Additional quality control on the RDGP database was performed to assess homogeneity of the traits. Phenotypes were discarded if they were lower or higher than the mean ± 3.5 standard deviations (SD) within contemporary group, or if they were out of a biologically reasonable range (e.g., less than 4 or more than 60 kg DMI/day). Contemporary groups were defined by the combination of herd, year, and season. In addition, it was required that each contemporary group contained at least 3 animals, and that all animals with phenotypic data had both birth date and calving date information. Animals with age at calving greater than 160 mo were removed from the data set.

To assure the homogeneity of the traits (i.e., to confirm that similar traits were measured in the different countries), possible differences in both means and variances among countries were tested using the Alexander-Govern test and the Levene′s test, respectively. Residuals were estimated after adjusting DMI and CH_4 records for the fixed effects that were significant ($P < 0.05$; i.e., herd-year of calving, year-season of calving, age at calving nested in lactation, and DIM) and used in the tests. Specifically, for DMI, the fixed effect of number of milkings per day nested within milking program (i.e., 24 h, AM/PM, automated milking machines, and robots) was also significant and therefore, it was included in the statistical model. Residuals were assumed independent, and normality was verified using the Kolmogorov-Smirnov test.

RESULTS AND DISCUSSION

Pedigree and Genotypes

The majority of sires with daughters with DMI records had US herd book registration numbers, followed by DEU and CAN herd book registrations (Table 2). The number of sires shared between countries was relatively low (275 shared sires). The pairs of countries which shared the most sires included DEU-USA, CAN-USA, and CAN-DEU which is in line with findings from Weigel et al. (2000). As shown in Table 2, a greater exchange of genetic material across countries is recommended to increase the genetic connectedness between the populations. In this context, the systematic use of shared sires could increase relatedness in populations, especially between countries with direct international trade (Zenger et al., 2007; Mrode et al., 2009). A better-linked pedigree between countries is helpful in accurately estimating genetic parameters (Manzanilla-Pech et al., 2021).

The concordance among SNP panels provided by different countries was assessed to determine if genotypes included in the data set were coded similarly. This is especially important when merging genomic data from multiple sources. One of the countries used the opposite reference allele compared with the other countries, and this was subsequently corrected. The correlations between allele frequencies estimated between countries after this correction are shown in Table 3. Among all, CHE seems to have the lowest correlation of allele frequencies compared with all other pair of countries, suggesting that there is simply lower sampling, slightly different emphasis on specific traits, or that some alleles might not be fixed in the CHE population as they are in the Holstein populations from other countries. This difference can be due to a variety of factors such as differences in selection goals and pressures, and/or gene flow. Regardless, correlations were overall high, showing that genomic data from different countries can be combined once corrected.

Imputation

Genotype imputation is a computational technique used to predict missing genotypes in large-scale genomic data sets. This technique allows to increase the density of genetic markers and improve the accuracy of genomic prediction models without any economic cost (Klímová et al., 2020). As mentioned by VanRaden et al. (2023), imputation strategies must balance accuracy with computational costs, while adapting to the properties of the input data such as array densities, error rates, and population structure. In this study, the

Table 2. Number of sires with daughters with dry matter intake (DMI) records. The number of sires from each country with daughters with DMI records are listed on the diagonal, sires shared between countries are listed above the diagonal and percentage of sires shared out of the total sires shared (n = 275) are listed below the diagonal

	AUS	CAN	CHE	DEU	DNK	ESP	USA
AUS	123	4	1	12	1	3	10
CAN	1.5%	426	8	30	0	15	46
CHE	0.4%	2.9%	152	13	0	3	12
DEU	4.4%	10.9%	4.7%	510	4	15	71
DNK	0.4%	0%	0%	1.5%	142	0	0
ESP	1.1%	5.5%	1.1%	5.5%	0%	311	27
USA	3.6%	16.7%	4.4%	25.8%	0%	9.8%	1,260

Countries: Australia (AUS), Canada (CAN), Switzerland (CHE), Germany (DEU), Denmark (DNK), Spain (ESP), and United States of America (USA).

overall imputation accuracy estimated was 0.98 ± 0.02, which was found to be similar to other recent studies using Holstein cattle (e.g., Al-Khudhair et al., 2021). Moreover, as expected, imputation accuracy tended to increase with higher minor allele frequencies (**MAF**) (Figure 2). However, even with low values of MAF (i.e.: < 0.05), the mean imputation accuracy was generally high (0.92 ± 0.14).

Population Characterization

PCA. Figure 3 illustrates the results of the principal component analysis (PCA) performed on the genomic relationship matrix after imputation, with a focus on the first 2 principal components. The lack of discernible clustering among genotypes from different countries indicates that there is considerable genetic similarity between Holstein populations across countries. This finding suggests that genetic exchange and therefore migration has occurred, resulting in the mixing of genotypes from diverse geographic locations. Furthermore, the first and second principal components explained 20.3% and 6.4% of the total genomic variance, respectively. The proportion of variance explained by the first 10 principal components is shown in the Supplementary Material II.

Consistency of the gametic phase. When markers are not in the same phase across 2 populations, the ability to combine them in the same genomic evaluation is hindered. The consistency of gametic phase between different countries is shown in Figure 4. All the 21 country-pair combinations showed a similar trend with higher correlations at shorter distances compared with larger distances, as also reported in other studies (de Roos et al., 2008; Larmer et al., 2014; Brito et al., 2017; Oliveira et al., 2020). The lowest consistency of gametic phase at the first distance bin (0 to 0.01 Mb) were between AUS and ESP (r = 0.68), DNK and ESP (r = 0.71) and CAN and ESP (r = 0.75), however, only the correlations between AUS – ESP and DNK – ESP remained the lowest over nearly all distances. On the other hand, the highest values were observed between CHE and USA (r = 0.91), DNK and USA (r = 0.89), and CHE and DNK (r = 0.87) at the first distance bin (0 to 0.01 Mb), with highest correlation being observed between DEU and USA across nearly all distances. Regardless, all correlations were moderate to high until a distance of 0.5 Mb. The correlations reported in the current study are in line with those reported by de Roos et al. (2008) when comparing Holstein dairy breeds from Australia, New Zealand, and the Netherlands.

The moderate-to-high consistency of the gametic phase and absence of stratification in the PCA suggests that Holstein populations from the countries participating in the RDGP (i.e., AUS, CAN, DNK, DEU, ESP, CHE, and USA) are overall genetically related, which is not unexpected due to the export of semen by different countries (Zenger et al., 2007). Moreover, our results also indicates that somewhat similar selection goals have been implemented in all analyzed populations, as no major distinction (and/or low consistency of the gametic phase) was observed. These results are promising for the RDGP, as they suggest that a joint genomic prediction can likely be successfully implemented for novel traits such as DMI and CH4.

Table 3. Correlations of allele frequencies estimated between the different countries after correction to the same reference allele for all countries

	AUS	CAN	CHE	DEU	DNK	ESP	USA
AUS	1						
CAN	0.82	1					
CHE	0.70	0.71	1				
DEU	0.83	0.92	0.71	1			
DNK	0.84	0.78	0.65	0.81	1		
ESP	0.85	0.91	0.70	0.89	0.81	1	
USA	0.88	0.94	0.70	0.91	0.86	0.92	1

Countries: Australia (AUS), Canada (CAN), Switzerland (CHE), Germany (DEU), Denmark (DNK), Spain (ESP), and United States of America (USA).

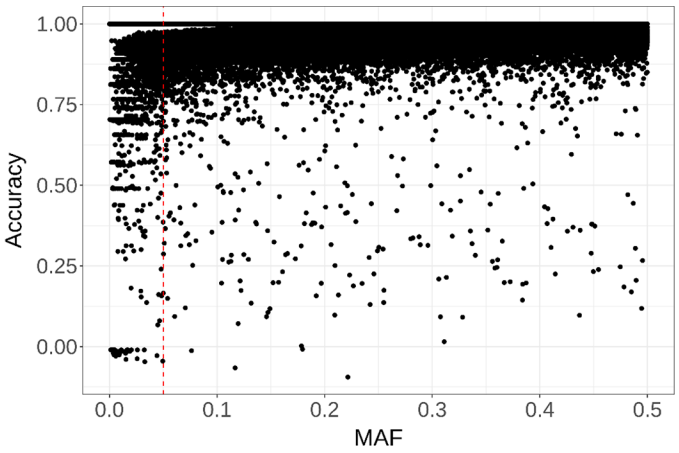

Figure 2. Relationship between SNP imputation accuracies at different levels of minor allele frequencies (MAF). The dashed red line represents MAF of 0.05.

Test of Homogeneity

Tests of homogeneity were performed for the main traits of interest in the RDGP, namely DMI and CH_4. Averages of DMI and CH_4 (Table 4) were in line with previous reported values for the respective countries (López-Paredes et al., 2020; Manzanilla-Pech et al., 2021; Negussie et al., 2022). The variances of DMI and CH_4 were not homogenous between countries as shown by the Levene's test (DMI: test statistic = 1,236.70, p-value < 2.2e-16; CH_4: test statistic = 296.44, p-value < 2.2e-16). Consequently, the Alexander-Govern test was used to assess differences of means when variances are not homogeneous. This showed that DMI (test statistic = 18,003.86, p-value = 0) and CH_4 emission (test statistic = 13,223.42, p-value = 0) were different between the countries. Similar variability has been reported for CH_4 emission between different countries (de Haas et al., 2012; Tempelman et al., 2015; Negussie et al., 2022). Our finding is therefore perhaps not surprising considering e.g., the different data collection protocols (Supplementary Material I), but it does highlight the importance of ensuring homogeneity of any trait before further analyses. If traits are determined to not be homogenous, standardization of traits is required (de Haas et al., 2012) or heterogeneity accounted for through different modeling approaches (Tempelman et al., 2015).

It is important to highlight, however, that estimating the genetic correlations across countries is the preferred method to accurately discern the extent of genetic similarity among traits recorded in different countries. Nevertheless, in this study, the restricted number of cows assessed for specific traits makes accurate estimations of genetic correlations for some pairs of countries and traits difficult. Consequently, combining all countries in a single training population may provide benefits. This is a question that requires further research.

Practical Implications

International collaboration has increased the size and quality of the available reference population for traits related to feed efficiency and methane emissions. Several countries participant in the RDGP either already include foreign data in their genetic evaluations for feed efficiency (e.g., CAN and USA) or are in the process of evaluating the inclusion of foreign data (e.g., CHE and DEU). The international exchange has improved the actual progress toward the launch of feed efficiency across many project partners, while the increase in data on methane emissions is paving the way for the development of new evaluations for this important trait. Through this process, genetic solutions can contribute to the selection of dairy cows that are more resource efficient and have a lower environmental burden.

CONCLUSIONS

In this study, a complete overview of the data collection protocols used in each partner country and the current state of the RDGP database was provided. Strategies used for managing the shared data were described, and some descriptive genomic and phenotypic analyses were presented. In this context, our results suggested that there is no strong genomic differentiation between the Holstein populations involved, which may be beneficial for potential across-country genomic predictions. Moreover, our results reinforce the need for accounting for the heterogeneity in the DMI and CH_4 phenotypes in genomic analysis.

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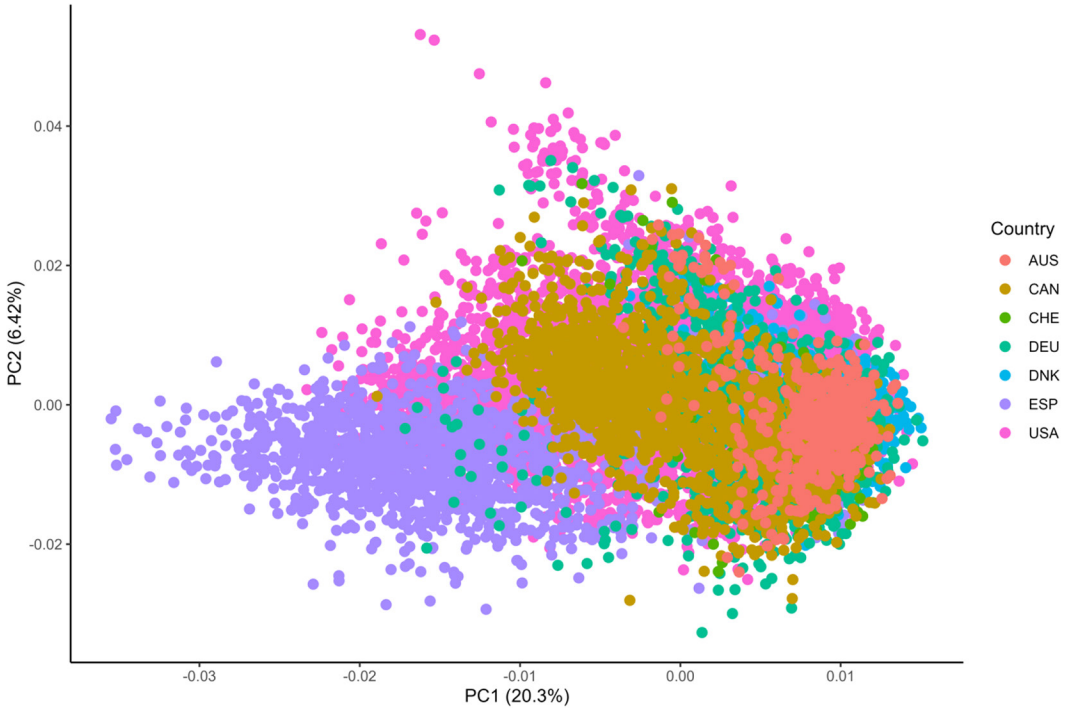

Figure 3. Principal component (PC) decomposition of the genomic relationship matrix after imputation colored by country. Countries placed in decreasing order to improve visibility. Countries: Australia (AUS), Canada (CAN), Switzerland (CHE), Germany (DEU), Denmark (DNK), Spain (ESP), and United States of America (USA).

Table 4. Descriptive statistics of dry matter intake (DMI) in grams per day and methane emissions (CH_4) in grams per day by country

	DMI (g/day)				CH_4 (g/day)			
	N (cows)	Mean	SD	CV (%)	N (cows)	Mean	SD	CV (%)
AUS	21,086 (551)	23,627	4,471	18.9	2,102 (463)	473	92	19.5
CAN	350,172 (1,783)	20,371	6,971	34.2	3,597 (654)	454	110	24.2
CHE	32,702 (190)	21,121	4,168	19.7	636 (86)	433	76	17.5
DEU	59,577 (1,799)	22,472	4,213	18.8	NA	NA	NA	NA
DNK	58,327 (823)	21,516	3,881	18.0	6,323 (276)	355	66	18.5
ESP	14,963 (641)	22,530	4,826	21.4	3,114 (1096)	200	70	35.1
USA	708,050 (6,737)	23,898	5,385	22.5	110 (3)	538	132	24.6

Countries: Australia (AUS), Canada (CAN), Switzerland (CHE), Germany (DEU), Denmark (DNK), Spain (ESP), and United States of America (USA).

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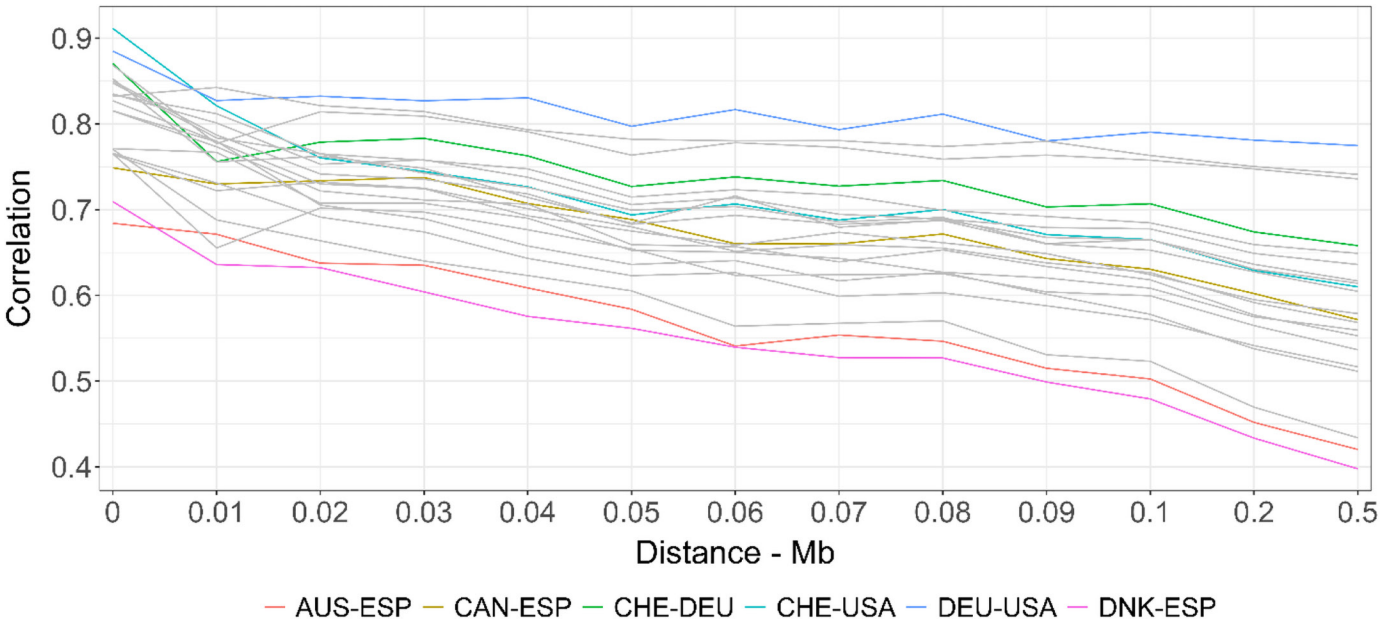

Figure 4. Consistency of the gametic phase at given distances between dairy cows from 21 country-pair combinations (7 countries). The 3 combinations with the lowest and the 3 combinations with the highest correlations at the shorter distance (0 to 0.01 Mb) are shown in color. Countries: Australia (AUS), Canada (CAN), Switzerland (CHE), Germany (DEU), Denmark (DNK), Spain (ESP), and United States of America (USA).

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