International cooperation: The pathway for cattle genomics

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Implications

- Genomic selection tools are radically changing the way dairy cattle genetics is organized worldwide by providing the means to reduce generation intervals and accelerate genetic progress. As a result, young genomically selected bulls are quickly replacing progeny-tested bulls in the top lists.
- To achieve moderate reliabilities in genomic predictions, large reference populations of progeny-tested animals have to be assembled, and this number increases dramatically for traits with low heritability. International cooperation becomes imperative, both for joining databases of genotypes and for obtaining phenotypic information translated into the respective national scale (Interbull multiple-trait across-country evaluation estimates).
- Keeping the Interbull conventional international evaluations (based on national conventional estimated breeding values) as a source of phenotypic information for the national genomic predictive models requires maintaining conventional evaluation models at the national level.
- Interbull is establishing a new framework to incorporate genomically enhanced multiple-trait across-country evaluations, Intergenomics, and a genomic data repository.

Key words: dairy genetics, data sharing, Interbull, marker genotype

International Cooperation in Dairy Cattle Genetics

Dairy breeds are among the domestic populations with the most extensive exchange of genetic material. The use of reproductive technologies, such as artificial insemination and embryo transfer, has made it possible for selected breeding stocks to contribute superior genes to herds located anywhere around the globe. The top bulls have been used extensively in many countries, thus establishing genetic links between populations. This internationalization of dairy breeds, however, has encountered a relevant obstacle: the absence of an effective method to compare the genetic merit of bulls selected in different exporting countries, as well as to express their estimated breeding values (EBV) in the scales adopted by the importing countries. Without a common basis for comparing breeding animals from different origins, the genetic merit of bulls used for artificial insemination has been derived from their progeny information, obtained, in most cases, only in the country of origin of the bull while ignoring differences in trait definition, evaluation model, measurement scale, management practices, environmental conditions, genetic makeup, and selection goals. Members of the scientific community and the dairy breeding industry acknowledged this challenge as early as 1975, and after years of cooperative work, the International Bull Evaluation Service (Interbull) was created in 1983 (Philipsson, 2005). The objective was to support the dairy industry with accurate genetic information on bulls of the major dairy breeds for use by importers and exporters, thereby facilitating selection of the best genetics for different countries, environments, or breeding goals.

Interbull was developed as a joint effort of the International Committee for Animal Recording; the European Federation of Animal Science, or EAAP; and the International Dairy Federation to become the main international forum for the development and standardization of methods and procedures in dairy cattle evaluation. The information exchange promoted by Interbull has clearly helped participating countries improve national systems and benefit greatly from the international genetic evaluations carried out by the Interbull Centre. As a cooperative action between the participating countries, Interbull does not compete with the national genetic evaluation centers, but is rather an auxiliary service. The authority over publication of breeding values in national scales remains with each of the countries. This very successful partnership among competitors, exporters, and importers is a result of permanent and intense networking, making all the actors involved jointly responsible for the choice of methods and for the quality of the results obtained.

The Interbull international evaluations are computed by a linear multiple-trait across-country evaluation (MACE) of national conventional EBV from the participating countries (Schaeffer, 1994). In MACE, bull progeny contributions from different countries are treated as different traits, with genetic correlations lower than unity. Consequently, the use of foreign information is accounted for by considering genotype-environment interaction, as well as differences in modeling, the genetic base, and trait definitions. Currently, Interbull MACE evaluations yield international EBV (IEBV) for a range of 34 traits and 6 breeds, expressed on as many as 30 national scales (currently, data from 73 populations are included) that are used extensively worldwide for semen marketing.

Interbull has been a reference for international cooperation since 1983 at both the scientific and the industry levels, but the dawn of genomic selection in dairy cattle has taken this cooperation to a completely new level. The aim of this article is to present how dependent the “genomic...
Impact of Genomic Information on Dairy Cattle Breeding

The recent availability of affordable single nucleotide polymorphism (SNP) panels and methods of estimating genetic merit based on these markers (Meuwissen et al., 2001; VanRaden, 2008; Aguilar et al., 2010; Habier et al., 2010; Croiseau et al., 2011) represent an actual revolution in the bovine breeding business, with an impact that is comparable with the introduction of artificial insemination. The following are expected gains from adopting genomic selection compared with conventional progeny testing (Schaeffer, 2006; Goddard and Hayes, 2007): a greater accuracy for the estimates of genetic merit, especially for traits with low heritability or ones that are difficult to measure; a greater proportion of the genetic variance explained by the SNP markers; a reduction in the generation interval resulting from selection and breeding at very young ages; and finally, much faster genetic progress, with a significant reduction in logistical costs. Figure 1 shows how marker genotypes from a reference population are being utilized in combination with phenotypes and pedigrees to estimate marker prediction equations that can be applied to predict, with reasonably good accuracy, the future performance of bulls and cows very early in life. In traditional progeny-testing schemes, a bull used for artificial insemination would receive its first reliable genetic evaluation only after a minimum number of its progeny had completed performance records (a minimum of 64 months), whereas when using genomic prediction equations, a calf can receive a reliable genetic evaluation as soon as it is genotyped. Therefore, selection can occur very early in life, greatly reducing the generation interval and testing costs.

Fast Implementation of Genomic Methods

Adoption of genomic tools by the breeding industry has been extremely fast. The Illumina BovineSNP50 BeadChip (Illumina Inc., San Diego, CA; Matukumalli et al., 2009; Illumina, 2011) features more than 54,000 evenly spaced SNP across the entire bovine genome and is by far the most widely used panel to date. It was released as recently as 2007, and already in January 2009, the United States was the first country to officially publish genomic evaluations for the Holstein breed, inaugurating a gold rush among breeding companies worldwide. Currently, the main Holstein populations and a few of the other dairy breeds have already published some sort of genomic estimates and routinely apply genomic prediction equations for young sire selection. In fact, the implementation has moved so quickly that some genomically selected bulls that are not yet progeny tested already have sons selected and used in the semen market. This dramatic amplification of selection intensity in such a short time raises some particular points of interest.

Sampling of Young Bulls. In some cases, the number of young bulls sampled (genotyped) has already increased dramatically, and there is a strong trend within breeding companies of buying bull dams to ensure exclusivity. The idea of reducing sampling costs, however, is still to be fully achieved because some companies are still reluctant to completely abandon progeny-testing schemes before the real impact of young bull genomic selection can be validated with data (Chesnais, 2010).

Inbreeding. Genomic selection can be a powerful tool to manage inbreeding if the sampling of young bulls is done to maintain diversity in addition to targeting the progress of economic traits (Simianer et al., 2011). However, it is also possible to dangerously speed up inbreeding by sampling only the most obvious families and promoting the most profitable matings in the short term. Simply judging by the small number of sires in the modern-day Holstein breed, there is a risk that this might be the case in some populations.

Preselection Bias. One of the risks with genomic selection is that the young bulls that have been tested but not selected may not be recorded (or reported) and consequently may not be included in the genetic evaluations. It has been shown that this leads to underestimated breeding values of preselected bulls and their daughters and overestimation of standard reliabilities (Patry and Ducrocq, 2011).

Phenotypic Data Collection. Ending the usual incentives for dairy breeders to use young, unproven bulls, which were an important part of the progeny-testing schemes, may pose a threat to phenotypic data collection, especially for conformation traits (Ducrocq and Santus, 2011). Not only keeping the existing phenotypic data flow, but also adding new and more accurate phenotypes to the system is fundamental for the success of genomic selection. The industry needs to consider this seriously.

Adoption by Farmers. Any new technology needs to overcome a credibility gap before the final users can completely replace the technology adopted at present. Genomically selected young bulls are taking a significant share of the bull top lists, and dairy breeders are getting used to mating their cows to bulls without a progeny test or without a picture from the best daughters of those bulls in the sire catalog. Another important development that speeds up adoption of genomic selection is the possibility of genotyping the cows with low-density SNP panels (Funk, 2011; Reents, 2011).

Genomics and International Cooperation

To obtain genomic prediction equations with an acceptable accuracy, it is necessary to assemble a large reference population of animals that...
have been genotyped and that possess accurate phenotypic records to be used as input information for the genomic prediction models. It is also important that the reference animals are closely related to the young animals whose genetic merits are to be predicted. The required size of the reference population is inversely proportional to the trait heritability and directly proportional to the effective population size (Goddard, 2009). Figure 2 illustrates that a given population may easily reach the minimum number of animals in the reference population by using only nationally available phenotypic data if the trait of interest has a high heritability, but the national database will not be sufficient for traits with moderate and low heritability. For these traits, national animal improvement programs need to include foreign bulls in their reference populations to achieve the minimum size for reliable genomic predictions. However, identifying influential foreign bulls and determining their marker genotypes adds no value to the reference population if phenotypic information is not also available for the animals, and the only useful phenotypes available for most foreign bulls is their deregressed MACE IEBV expressed on each national scale (Liu, 2011). Consequently, Interbull has become even more strategic in the genomic era as an indispensable data supplier for the national genetic improvement programs.

National evaluation centers need to maintain their conventional genetic evaluations based on progeny data for the purpose of supplying Interbull with genetic merit estimates free of genomic information. Otherwise, MACE estimates cannot be used as input for the national genomic predictions when foreign bulls need to be included in the reference population. Despite the costs of having 2 parallel evaluations, the risk of not being able to take advantage of phenotypic data generated in 30 different countries and available via Interbull is certainly more expensive. Therefore, it is very likely that the Interbull MACE based on progeny-tested bulls will remain an important tool for international trade of dairy genetics, even if the market eventually adopts the genomically enhanced breeding value (GEBV) as the standard way of expressing genetic merit.

The need for sufficiently large reference populations has already triggered the establishment of partnerships that would have been difficult to imagine in the pregenomics era. The first association formed to share genotypes and technical knowledge was between Canada and the United States, in 2008 (VanRaden et al., 2009; Muir et al., 2010). In 2011, Italy and Great Britain joined the North American consortium. The second big conglomerate was formed in 2009 by Denmark, France, Finland, Germany, Sweden, and the Netherlands, and the epithet Eurogenomics was adopted to identify the group (David et al., 2010). These 2 groups could be said to represent the main exporting Holstein populations. Some other initiatives involving smaller populations of mostly importing countries are also being organized. One example is the IGenoP project, which promotes the establishment of a common repository of genotypes to facilitate exchanges between participating countries (Cromie et al., 2010). In all the above-mentioned cases, the means of cooperation is the sharing of genotypes while maintaining the estimation procedures separately at the national centers. A different approach was chosen by the most important Brown Swiss populations (Austria, France, Germany, Slovenia, Switzerland, and the United States), not only creating a common reference population database, but also implementing a common estimation framework at the Interbull Centre. This project is known as Intergenomics and is in the final stages of becoming a regular service (Santus, 2011).

**Interbull Initiatives in Genomics**

The main actions that are ongoing at Interbull to prepare the framework for national and international implementation of genomic information are discussed below.

**Networking**

Since the Interbull Scientific Advisory Committee presented its first annual report on the potential impact of genomic information on dairy genetics at the 2007 Interbull meeting in Dublin, Ireland, Interbull has been the primary international forum for genomic developments in dairy cattle. In addition to establishing a task force of experts to propose priorities and a work plan around the theme, the use of genomic information for national and international genetic evaluations has been the focus of the Interbull annual meetings. Additionally, Interbull organized 3 international workshops (2009, 2010, and 2011) on genomics, and a fourth workshop is planned to take place in Verona, Italy, in February 2012. Communications through the Interbull discussion groups have been quite intense around the development of methods and the implementation of new procedures over the past 3 years.

**Validation of National Genomic Breeding Values**

Before accepting data from a country to include in the international genetic evaluation, Interbull requests that national centers implement 3 different trend validation tests (Boichard et al., 1995; Weller et al., 2003; Lidauer et al., 2005). This ensures that the MACE IEBV are based on unbiased input data with an acceptable standard of quality. Soon after the new genomic methods began to be adopted by the national programs, it became evident that a similar trend validation was needed for at least 2 reasons: to ensure data quality when an international comparison of GEBV is eventually established and to comply with the requirements of European Commission Regulation 427/2006 for wide use of semen also from young sires. A method was proposed (Mäntysaari et al., 2010) and implemented in August 2010. This action...
has greatly facilitated the trade of semen from genomically selected young bulls within Europe.

**International Comparison of Genomic Breeding Values**

Methods to implement an international comparison of GEBV similar to MACE have been proposed (Sullivan and VanRaden, 2009; VanRaden and Sullivan, 2010; Sullivan et al., 2011), and the essential difference between conventional and genomic MACE (GMACE) is the need to account for the fact that the same bulls are used as part of the reference population in different countries, which does not comply with the assumption of independence between records. Two pilot studies were already carried out, but there are still outstanding questions to be addressed before moving into service. The most probable scenario is the implementation of GMACE, which converts only the genomically enhanced genetic merit estimates expressed in young (unproven) bulls into the scales of other countries (Sullivan et al., 2011). Figure 3 represents the data flow between national and international conventional and genomic evaluations should Interbull implement GMACE.

**International Genomic Evaluations**

Using data from the 7 main Brown Swiss populations (Austria, France, Germany, Italy, Slovenia, Switzerland, and the United States), researchers at the Interbull Centre implemented the genomic best linear unbiased prediction methodology (VanRaden, 2008) to provide genomic prediction equations in all national scales when using a common reference population of genotyped animals and deregressed MACE IEBV as input phenotypes. The national evaluation centers will continue holding the responsibility of deciding how the direct genomic values will be blended with progeny-testing information to create publishable GEBV and publishing official estimates. This initiative is already becoming a service, and it establishes the grounds for genomic evaluations of minor breeds, which otherwise would be treated marginally to the Holstein developments or even excluded from the process because of the limited reference population size and eventually lack of infrastructure. Figure 4 shows how this approach differs from the GMACE approach.

**International Database of Genomic Information**

When the first organizations decided to invest significant amounts into genotyping dairy bulls and cows, the marker genotypes were treated as a private asset that represented a strategic advantage, and the will to share such data with other players was not present. As soon as the need to considerably increase the size of reference populations became evident, trading genotypes became not only a possibility, but also a necessity. Given the relevant decrease in the price of genotyping services, a clear evolution in the concept of sharing genotypes internationally is occurring, and most countries now recognize the need for a common repository of bovine genotypes at Interbull as the means to

- Facilitate exchanges between Interbull customers with well-established standards of formats and protocols.

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Figure 3. Information flow for implementation of national and international genetic evaluations [black arrows: national conventional estimated breeding values (EBV); red arrows: national genomic breeding values (GEBV), using international EBV as inputs for foreign bulls; blue arrows: international conventional EBV or multiple-trait across-country evaluations (MACE); green arrows: international GEBV or genomically enhanced MACE (GMACE)]. SNP = single nucleotide polymorphisms.
Reduction costs of and optimize investments in genotyping bovine animals by avoiding duplication.

2. Improve reference populations for predicting genomically enhanced genetic merit, especially for low-heritability health and functional traits, such as somatic cell count, mastitis, calving difficulty, longevity, and female fertility.

3. Make it possible to screen large populations for causative mutations. A good example is a recent study from North America that identified 5 lethal recessive genes by using this type of database (VanRaden et al., 2011).

4. Maintain a worldwide parentage verification database for Interbull customers, using the SNP-based methods that are about to be officially recommended by the International Society for Animal Genetics and the International Committee for Animal Recording.

5. Use the genomic data to study diversity within and among the bovine populations in a more complete way than is possible with the methods based on only pedigree information.

The idea is to continue providing supplemental services to the national organizations without overtaking their responsibilities or interfering with their commercial goals. The proposal is, in essence, to optimize the use of resources internationally and for Interbull to facilitate logistics.

Conclusions

Dairy geneticists and breeders live in a unique period of fast transformation. Genomics brings the perspective of finally combining the advances in molecular biology with the sophisticated statistics of quantitative genetics applied to animal breeding. It offers tools for selection early in life as a means to greatly accelerate genetic progress, and ideally to reduce the costs of genetic evaluation. However, the amount of information necessary to implement genomic selection schemes and the speed of the scientific developments in the field assume international cooperation as a prerequisite. The Interbull community has responded to this necessity by providing extensive networking opportunities, implementing a trend validation for national GEBV, developing methods for international comparison of national GEBV, establishing the framework for joint genomic evaluations for minor breeds, and initiating the groundwork for the organization of an international repository of genomic information.

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