

Interbull Developments, Global Genetic Trends and Role in the Era of Genomics

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Interbull secretary 1983-2011

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Abstract

Effects of animal breeding have historically been boosted at certain times by important technical discoveries or theoretical developments. The globalization of cattle breeding has been possible due to the possibility of using frozen semen of individual bulls across the world. Which are the best bulls to be used got a boost by the development of the mixed-model procedures (BLUP) supported by enormously enhanced computer capacity. The development of MACE enabled the opportunity to evaluate practically all AI bulls across countries. And now we are in the midst of a technical breakthrough where technology developments including sequencing of the cattle genome combined with use of quantitative genetic methods form the basis for genomic selection. During the past 20 years an enormous development has taken place in the major dairy breeds. Interbull has played an important role for this development as facilitator through delivery of genetic evaluations to be used across countries, so that all bulls are ranked correctly for the predominant environment of each country or region – a win-win situation for both importers and exporters of semen. The achievements, so far reaching 80 populations representing six breeds in 30 countries and more than 40 traits, have been supported by the collaborative research conducted by Interbull Center and its partners attracting top scientists around the world. The regularly arranged open seminars and technical workshops have laid the basis for a spirit of cooperation and freely sharing of research results and practical experiences. In the era of genomics experiences already show an increased need of cooperation and sharing of experiences for the industry to fully benefit from adoption of this new fast developing technology. Additional activities at the Interbull Center might include sharing of information on genotyped or sequenced bulls, estimation of SNP effects, and an increasingly important task of monitoring genetic trends, genetic diversity and inbreeding. But more than that, phenotypic information on production and functional traits for present and future breeding objectives are needed for international evaluations also in future in order to fully benefit from adoption of the new technologies.

Introduction

The development of sustainable breeding programs is historically characterized by the synergies of many different factors: research and discoveries in genetics and reproduction technologies as well as market developments and infrastructural arrangements at the implementation level are all equally important factors. We all know that the dairy breeding industry has undergone a tremendous change in the last 3-4 decades. The breeding of dairy cattle has become truly global, not only in the sense that semen by individual bulls is used globally, but also that objectives and harmonized methods and information are requested and used internationally. What were

the main drivers for this development? That the globalization of cattle breeding has been possible at all is due to the possibility of using frozen semen of individual bulls across the world. Then the issue of identifying which are the best bulls to be used got a boost by the development of the mixed-model procedures (BLUP) supported by the enormous computer capacity developments. Further developments (MACE) have enabled the opportunity to evaluate practically all AI bulls across countries. And now we are in the midst of a technical breakthrough where technology developments including sequencing of the cattle genome combined with use of quantitative genetic methods form the basis for genomic selection.

How did the Interbull concept develop to fit into this picture, and possibly contributed to a desired development? What lessons could be learnt and what would be the future role of Interbull? In the following some of these aspects will be discussed in more detail, while also key developments and results will be featured in light of opportunities for future.

The Interbull concept develops

The FAO-experiment in the 1970-ies in Poland with 10 strains of (Holstein) Friesian cattle became a starting point for much of the amazing development we have seen take place since then in dairy cattle breeding. This large-scale experiment provided invaluable information about the widely spread strains of the Friesian breed after its diversification following the export to different parts of the world 50-100 years earlier. The superior production shown in North-American Holstein cattle, also at moderate production levels, underpinned the increasing trade of semen, primarily from North-America to all other parts of the world. The corresponding FAO-trail with red dairy cattle breeds/strains in Bulgaria did not attract the breeding community as much. For most breeds many national breed comparisons were also made thanks to the increased trade of semen. However, very few direct comparisons were made whereby similarly selected animals were compared to achieve true population comparisons.

From visions.....

The increased opportunities for import and export of superior genetics, following the various experiments and strain comparisons, boosted the international trade of semen and the needs for comparison of sub-populations and individual bulls within breeds across countries. This development stimulated the initiation of specific studies within both the International Dairy Federation (IDF) and EAAP. Visions on the future needs were expressed at about the same time by professors Gravert and Cunningham affiliated with these organizations, and working groups were laying out ideas on how to standardize sire

information for international use (Gaillard et al., 1977). IDF led the further collaborative work supported by the Schaumann Foundation in Germany, primarily by organizing informative international workshops and seminars.

...to formation of Interbull...

In 1983 a formal committee, Interbull, was established by IDF, EAAP and ICRPMA (International Committee for Recording Productivity of Milk Animals, predecessor of ICAR, the International Committee for Animal Recording), and supported by FAO, with a board representing the three founding organizations. Prof. H.O. Gravert became the first chairman of the Interbull committee and the author of this paper became the secretary. Thus, the secretariat was located at SLU, Uppsala, Sweden. The Interbull committee regularly organized meetings for sharing information and experiences of genetic evaluations as practiced in different parts of the world, while also guidelines were produced for improved and harmonized practices. Meanwhile a tremendous growth of the international trade of semen took place. The breeding programs had been truly global and the needs for comparable breeding values of individual bulls across countries had been an acute reality. The methods for conversion of breeding values between countries were extensively practiced, but became by time impractical with the many populations involved. In 1988 it was decided that Interbull should be hosted by ICAR only and become a permanent subcommittee with its own Steering Committee as deciding body. In the following year it was decided to form a Center for demand driven operational activities. These should include R&D in order to develop international genetic evaluation procedures.

..and a Center for international genetic evaluations

The Center was established in Uppsala in 1990/91, i.e. 20 years ago, after a tendering process and the required R&D was financed for five years by Swedish organizations. Finally, in 1994 the first international

evaluations were conducted, and in the following year MACE, assuming genetic correlations less than 1.00 between countries, was applied. In 1996 the EU Commission appointed the Interbull Centre as its official Reference Laboratory for bovine evaluations and later EU provided gradually increasing funds. Then also USDA provided valuable funds for further R&D at the Center. SLU has all the time financially supported the development of methods for practical use by the Center as a result of its contribution to internationally recognized research.

...and the concepts were established

The years of collaboration within the frameworks of both IDF and the Interbull Subcommittee had proven the benefits of cooperation among both importers and exporters of genetics as well as among scientists representing both academia and industry. The importers wanted to know the genetic level of foreign genetics from different sources in comparison with their own stock, whereas the exporters wanted to get access to foreign markets, which became gradually more demanding as regards the comparability of sire proofs (EBVs and PDs expressed in relation to a variety of defined and non-defined genetic bases) of bulls from different countries.

The objectives of Interbull were summarized in four points for international cooperation:

- Sharing of information and experiences regarding genetic evaluation of dairy cattle by organizing open seminars, technical workshops and publications.
- Conducting international genetic evaluations for important traits demanded by stakeholders to facilitate comparable breeding values of bulls across countries, regions or continents

- Supporting countries and organizations in their preparations for participation in international genetic evaluations, and
- Conducting R&D in house as well as in cooperation with a network of scientists and genetic evaluation units across the world.

These objectives were clearly demand driven, and the annually arranged open seminars have always attracted a broad audience of scientists of research organizations as well as of the industry and genetic evaluation units. A unique platform had been created for information sharing and initiation of R&D among scientists and stakeholders. A key to the development of the Interbull concepts to be realized was that the ability to produce international genetic evaluations had been proven during the initial 5-year period. As the benefits of participating were shown it was rather easy to reach a joint decision of financing the future activities by service fees paid by the users of the service provided.

Key publications demonstrating the development of international genetic evaluations and Interbull activities are given in the reference chapter at the end of the paper.

Increasing interest for international evaluations and broadened breeding objectives

Since 1994 the number of traits as well as number of countries participating in international genetic evaluations has gradually increased. Presently about 175,000 AI bulls of six major breeds of more than 30 countries are regularly evaluated three times a year for seven trait groups including 40 sub-traits (see table 1).

Table 1. Number of populations participating in Interbull evaluations by breed and trait group (2011).

Breed	Prod	Conf	Udder health	Longevity	Calving	Fertility	Workability
Start	1994	1999	2001	2004	2005	2007	2009
BSW	10	7	9	9	5	7	5
GUE	6	4	5	5	-	4	-
HOL	28	21	27	18	12	18	6
JER	11	9	8	7	-	7	3
RDC	14	8	12	7	3	8	4
SIM	11	-	9	3	-	2	-
Total	80	49	70	49	20	46	18

The early adoption of MACE with genetic correlations less than 1.00 had enabled each country to receive international breeding values of all bulls of each breed world-wide, comparable on the scale for use of the genetics. Truly functional traits of importance for animal welfare, such as ease of calving, resistance to mastitis and female fertility, has been adopted by a wide number of countries and breeds as a result of pioneering R&D by the Interbull Center and its collaborators in individual countries. This development was clearly driven by Interbull from both farmers' needs and the societal demands of responsible breeding.

With all traits now being considered, total merit indexes may be produced in most countries based on international genetic evaluations for all traits. It leads to the freedom of each country or organization to define its own breeding objectives and allows a level playing field for bulls to be marketed according to the objectives and scales of each

country. It is a win-win situation for both buyers and sellers of semen, provided suitable genetics is available.

Global genetic trends

The build-up of the Interbull data base, to accommodate for both proofs of all traits and pedigrees provides a unique opportunity to monitor the global trends by breed, and also by region, for important production and functional traits as well as for inbreeding rate.

Figures 1 and 2 show the global genetic trends in Relative Breeding Value (RBV) units for Holstein and the Red Dairy Cattle breeds (RDC) for protein yield (pro), somatic cell count (scs), longevity (dlo) and female fertility (int). All results are given on the Nordic scale (DFS). It is obvious that a tremendous genetic increase in production level has occurred, three standard deviation units in RBVs in 20 years

for both breeds. A positive trend is observed for both breed groups also for longevity. Longevity is expressed as productive longevity. Thus, increased production partly explains the increasing trend in longevity. Breeding values for somatic cell score, as indicator of mastitis, show a slightly positive trend for RDC and in later years also for Holstein.

Female fertility has dropped considerably over the years for Holstein, but this decline seems to have stopped since five years, and maybe signs of improvement can now be detected. For RDC female fertility has been largely unchanged over time. This is expected since female fertility has been considered in bull sire selection along with other traits in Total Merit Indexes practiced for 20-30 years in the major (Nordic) RDC populations.

The genetic trend for the Holstein breed split on the results for different regions show the initial superiority of the North-American Holstein population, especially in comparison with the East European population (figure 3). It can also be seen that the "holsteinization" started much later in this region, but also that the genetic differences between the regions are much smaller nowadays, except for the Oceanian population which is producing under different production systems.

For female fertility it is equally obvious that the North-American population initially was inferior to the Friesian populations in the other parts of the world (figure 4). However, the rapid "holsteinization" led to a decline in fertility of all the other populations. The decline in the Oceanian population was reversed into an improvement of the fertility much earlier than in the rest of the world. The developments in national and international genetic evaluations for female fertility in the past five years are extremely important for the Holstein breed to capture in selection programs, as the genetic correlation with production is unfavorable of the order 0.4.

The RDC populations show a more variable picture for protein yield (figure 5). The superiority in production of the West European population has increased by time in relation to the North-American and East European

populations, whereas the rate of gain in the Oceanian population is comparable with the West European population but at a lower level.

As regards female fertility in the RDC populations, no clear trends are observed, while the Oceanian population shows the consistently highest level of fertility (figure 6).

In general, it seems important to closely monitor the genetic trends for all important traits, especially health and reproduction traits, to be able to respond with accurate figures on developments related to animal welfare discussed in the society, and because these traits are of economic importance.

High rates of inbreeding

Figures 7 and 8 show the inbreeding trends among bulls with international proofs. Only bulls with at least 80% complete pedigrees reported to the Interbull data base are included in the calculations. More than 90% of the bulls fulfill this requirement.

Figure 7 shows the global trends for all six breeds, whereas figure 8 shows the development within the Holstein breed split by regions. Striking differences exist among the breeds. Guernsey, Jersey and Holstein have had the largest increases in inbreeding. A slightly lower trend is observed for Brown Swiss and the markedly lowest trends are found with Simmental and RDC. The figures for especially Guernsey, with its small population size, are rather serious. The Jersey figures indicate problems too, as there are large differences between regions. The recent drop is reflecting the use of crossbred bulls in New Zealand, but in North-America the rate of inbreeding of this population is high.

For Holstein a 3%-units increase in 12 years time has been noted and that is a high value, exceeding the 0.5-1.0% per generation that is normally accepted. When looking at the trends for Holstein in different regions, the same drop is seen for the Oceania Holstein population as for Jersey due to use of crossbred bulls, but probably also to some extent depending on less complete pedigrees. The North-American and West European

populations have had about the same trend, whereas the East-European population lately has had the largest increase, 4% in 13 years, when the inbreeding rate started to increase.

Further analyses have revealed the dominance of certain blood-lines that most breeders know of. Certain bulls have been extensively used all over the world and some of these have been very good. But there are also examples where extensively used bulls have transmitted less desirable traits, e.g. low female fertility, or genetic defects. Thus, the importance of accurate testing of bulls and keeping a broad genetic basis for selection are important ingredients of any sustainable breeding program. Introduction of genomic selection introduces new opportunities of managing inbreeding. More accurate measures that reflect the real homozygosity levels could be provided, rather than the expected inbreeding level resulting from statistical pedigree relationships.

The Interbull data base will continuously improve and may be more extensively used in the future for studies of genetic trends in important traits by breed as well as of inbreeding trends for possible consideration by breeding companies and by world and regional breed societies.

Experiences and lessons learnt

Why this historical review? First of all I wanted to show some global trends that the Interbull data base now allows us to produce. Secondly, I believe we always need to analyze past developments to get perspectives on what were the most important achievements in order to better understand what to do in future. It is obvious that genomic selection offers increased opportunities for genetic improvements. But the higher expected rates of genetic change also require higher demands that the direction of breeding and selection is right. Thus, we need always to analyze the effects of past interventions in genetic evaluations and selection to make adjustments where needed.

I may mention two over-arching achievements that I think are of importance when we want to publicly present the profile of our breeding programs.

The initiatives by Interbull to develop and include several animal welfare and reproduction traits into the evaluations did clearly speed up the adoption of these traits in the breeding objectives, recordings and evaluations in a number of countries where they otherwise would have been missing for some time. Today we know that all over the world animal welfare has become an important factor to consider in relation to our societies.

I also think that the collective efforts to generally improve the dairy production efficiency responds well to the societal needs of environment improvements, as the dairy industry globally can prove its ability to continuously produce less green house gases per unit of milk. This is at least partly thanks to increasingly better use of the globally best genetics, an important fact in relation to the common accusation of ruminants for degradation of the air.

Other key factors to consider responsible for the Interbull developments and achievements so far could be summarized in the following points:

- The creation of Interbull as an independent non-commercial body with international status for R&D and rendering of demand driven services to a highly competitive industry.
- The creation of a global platform for sharing new knowledge and experiences in dairy cattle breeding filled a gap that neither the industry nor the scientific community had been able to establish. The success of Interbull meetings, workshops and their following publications, have been recognized in different ways, e.g. by giving Interbull the responsibility to organize the scientific dairy cattle breeding sessions at the last three WCGALP meetings.

- Sharing of R&D resources among Interbull stakeholders to the benefit of all users of the service, not least as there is a global shortage of quantitative geneticists.
- Efficient use of phenotypic information (EBVs) from all over the world to produce accurate EBVs for the most important traits of all available bulls of the major dairy breeds adjusted to the scale of each environment (country) has contributed to opportunities for efficient selection of bulls independent of origin.
- Qualified support to new tentative participants of the service for preparation of data to be used in the Interbull context.

What about the future role of Interbull?

The introduction of genomic selection offers fantastic opportunities for more efficient selection of breeding stock in a species such as dairy cattle, where most important traits are sex-limited. The rapid technological developments in sequencing and producing SNP chips need high competence and flexibility in approaches for genetic evaluations as well as for the design of breeding programs. The past few years of intensive research and simultaneous implementation of new selection strategies has demonstrated a much more complex situation to meet with adequate and reliable methods for genetic evaluation than has been handled previously. This applies to national genetic evaluation centers as well as at the Interbull Center and in the industry. The rapid up-take of the new methodology in the industry has even preceded the scientific validations of the results. At the same time it has been realized that the solutions for implementation of genomic selection is not always as simple as it at a first glance may have been thought of.

Having observed the developments in the last 2-3 years it is obvious that the needs for sharing and discussing new knowledge and exchange of experiences among scientists and industry people have never in the history of Interbull been as large as in this period. Interbull workshops and open seminars with large audiences have on demand been arranged

twice a year. Further meetings by breed groups or regions have taken place at other occasions.

A gradual realization of the needs for cooperation among different parties has taken place. This is not only the case for small breeds but also the bigger ones. The issue of pulling resources together to get enough large reference populations is obvious. Since large-enough reference populations are only achieved through data sharing, countries depend totally on the MACE EBVs to be able to “feed” their genomic evaluations with proper phenotypes for the foreign reference animals. This has increased dramatically Interbull’s responsibility and contribution. More than probably initially expected, there is a continuous need for large volumes of phenotypic data, e.g. milk recording, reproduction and health data to be used for genetic evaluations of all traits included in present and future breeding goals. The necessity of access to accurate phenotypic records must be emphasized in order to both continuously establish reliable prediction equations, and for monitoring the really achieved results at farm level.

Introduction of new methodologies requires validation of these methods to be consistent and effective in delivering both accurate and unbiased predictions of breeding values. This area of work has proven to be an extremely important task for Interbull to undertake. EU has for instance required that Interbull validates the genomic evaluations practiced in different countries in order to allow free trade of semen based on genomically enhanced breeding values of young AI bulls.

The new methodologies raise the questions of several new areas for cooperation beyond international genetic evaluations with and without genotypic information, e.g. information on what animals have been genotyped in order to avoid double work, and keeping repositories for genotypic information.

However, one should not see the requests for new types of R&D and services to be a challenge following only the introduction of genomics as a tool in cattle breeding. Other changes may take place in reproduction technology, markets or regulatory areas that

need attention by geneticists and organizations in the breeding industry.

Whatever happens, I believe Interbull has steadily an important role to play in providing the platform established for science and practice to meet for sharing and exchange of knowledge and experiences. Furthermore, it is obvious that phenotypic information is more than ever needed for international use in order to apply genomic selection, for validation of methodologies and for monitoring the changes realized in the various populations as regards both traits and genetic diversity. New services may as well be developed pending on the needs. The important thing is that the present and future activities of Interbull are demand driven by a majority of the breeding community, realizing that the requests for services may be more diversified among the customers.

A rewarding concept for cooperation

Interbull evaluations have become an internationally accepted standard for evaluation of AI bulls for domestic and global use. But more than that, the Interbull concept has pointed at an interesting and rewarding way of cooperation between science and practice in a very competitive market. And that concept will be important to foster also in the future.

Professional people and generous support

The achievements of Interbull are greatly resulting from a unique international cooperation between scientists and industry representatives around a common goal, to genetically improve domestic dairy cattle populations through global use of the best genetic resources. Wise leadership by the Interbull chairpersons Hans_Otto Gravert, Brian Wickham, Jean-Claude Mocquot and Reinhard Reents, members of the Steering Committee, the Scientific Advisory Committee, the Technical Committee, and professional and dedicated work by the Interbull Centre directors Georgios Banos, Ulf Emanuelson, Freddy Fikse and João Dürr, and

their staff at the Interbull Centre, has been of utmost importance. The financial support, initially only from Sweden, both by the dairy industry and SLU, but later on through generous grants from USDA and EU, has been greatly appreciated. Among the breed societies Interbull has enjoyed a professional cooperation with the US Holstein when outsourcing parts of the conformation evaluations to a North-American consortium. For its size the World Guernsey Cattle Federation has contributed with a very much appreciated support of the Interbull activities.

For providing information to this paper Jette Jakobsen, Valentina Palucci and João Dürr at the Interbull Centre are specifically acknowledged

References

- Boichard, D., Bonaiti, B., Barbat, A. & Mattalia, S. 1995. Three methods to validate the estimation of genetic trend for dairy cattle. *J. Dairy Sci.* 78:2, 431-437.
- Chesnais, J.P. 2010. How is the AI industry using genomic tools in practice? Proceedings of the Interbull International Workshop Paris, France March 4-5, 2010. *Interbull Bulletin* 41, 59-62.
- Ducrocq, V. & Santus, E. 2011. Moving away from progeny test schemes: consequences on conventional (inter)national evaluations. *Interbull Bulletin* 43. Proceedings of the Interbull International Workshop Guelph, Canada February 27-28, 2011, http://www.interbull.org/images/stories/Ducrocq_copy.pdf *Interbull Bulletin* 43, 43-45.
- Dürr, J. & Philipsson, J. 2012. International cooperation: The pathway for cattle genomics. *Animal Frontiers* 2, 16-21. doi:10.2527/af.2011-0026.
- Gaillard, C., Dommerholt, J., Fimland, E., Gjøl-Christensen, L., Lederer, J., McClintock, A.E., Mocquot, J.C. & Philipsson, J. 1977. AI bull evaluation standards for dairy and dual purpose breeds. *Livest. Prod. Sci.* 4, 115-128.
- Goddard, M. 1985. A method of comparing sires evaluated in different countries. *Livest. Prod. Sci.* 13, 321-331.

- Goddard, M.E. & Hayes, B.J. 2007. Genomic selection. *J. Anim. Breed. Genet.* 124, 323-330.
- Gravert, H.O. 1976. Methods for assessing breeding value of bulls in relation to milk yield. Account of the results of Questionnaire 1176/A. *IDF, A-Doc 31*.
- IDF. 1981. IDF recommended procedure for international comparison of genetic merit of dairy cattle. *IDF, A-Doc 64*.
- Interbull. 1990. Recommended procedures for international use of sire proofs. *Interbull Bulletin no. 4*, 17 pp.
- Interbull. 1993. Report of a joint research project between Interbull and COPA/COGECA on the feasibility of a simultaneous genetic evaluation of Black-and-White dairy bulls across the European Community countries. *Interbull Bulletin 9*, 31 pp.
- Liu, Z. 2011. Use of MACE results as input for genomic models. *Interbull Bulletin 43*. Proceedings of the Interbull International Workshop Guelph, Canada February 27-28, 2011, <http://www.interbull.org/images/stories/Liu.pdf> *Interbull Bulletin 43*, 32-35.
- Mäntysaari, E., Liu, Z. & VanRaden, P. 2010. Interbull validation test for genomic evaluations. Proceedings of the Interbull International Workshop Paris, France March 4-5, 2010. *Interbull Bulletin 41*, 17–22.
- Philipsson, J., Danell, B., Schaeffer, L.R., Schneeberger, M., Schulte-Coerne, H. & Wilmink, J.B.M. 1986. Procedures for international comparisons of dairy sires – current practice and evaluation methods. *Interbull Bulletin 1*, 28 pp.
- Reents, R. 2011. Implementation of genomics in dairy cattle breeding schemes and uptake by the farmers: European perspective. Book of abstracts No. 17. *Proceedings of the 62nd Annual Meeting of the EAAP*. Stavanger, Norway August 29- September 2, 2011, 77.
- Schaeffer, L.R. 1985. Model for international evaluation of dairy sires. *Livest. Prod. Sci.* 12, 105-115.
- Schaeffer, L.R. 1994. Multiple-Country comparison of dairy sires. *J. Dairy Sci.* 77, 2671-2678.
- Schaeffer, L.R. 2006. Strategy for applying genome-wide selection in dairy cattle. *J. Anim. Breed. Genet.* 123, 218-223.
- Sigurdsson, A., Banos, G. & Philipsson, J. 1996. Estimation of genetic (co)variance components for international evaluation of dairy bulls. *Acta Agric. Scand., Sect. A, Animal Sci.* 46, 129-136.
- Stolzmann, M., Jasiorowski, H., Reklewski, Z., Zarnecki, A. & Kalinowska, G. 1981. Friesian cattle in Poland. Preliminary results of testing different strains. *World Animal Review*, 38:9.
- VanRaden, P.M. & Sullivan, P.G. 2010. International genomic evaluation methods for dairy cattle. *Gen. Sel. Evol.* 42, 7.
- Wilmink, J.B.M. 1986. Conversion of breeding values for milk from foreign populations. *Livest. Prod. Sci.* 14, 223-229.

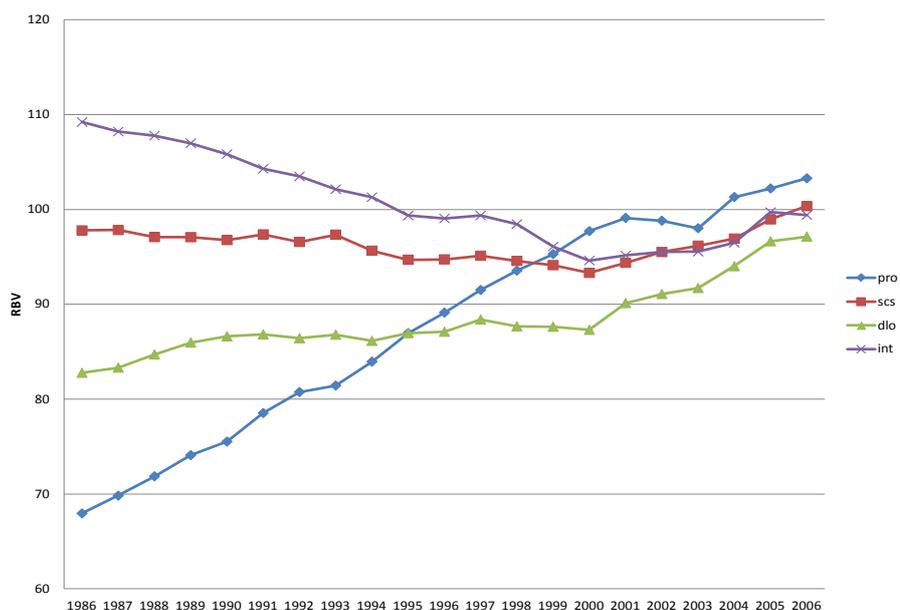


Figure 1. Global genetic trends for Holstein for protein, somatic cell scores, longevity and female fertility on the Nordic (DFS) scale.

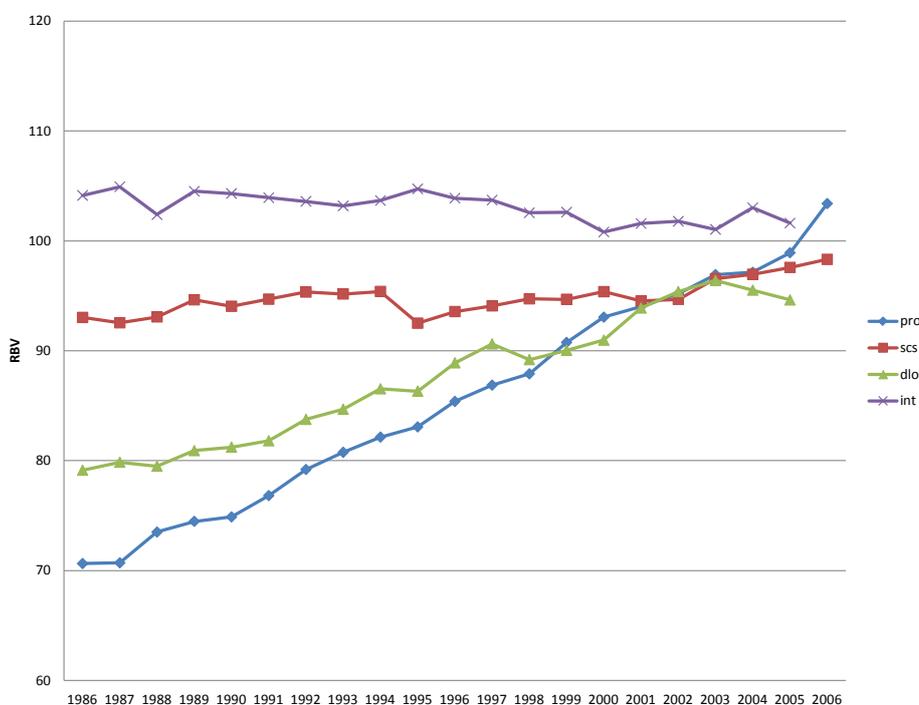


Figure 2. Global genetic trends for Red Dairy Cattle (RDC) for protein, somatic cell scores, longevity and female fertility on the Nordic (DFS) scale.

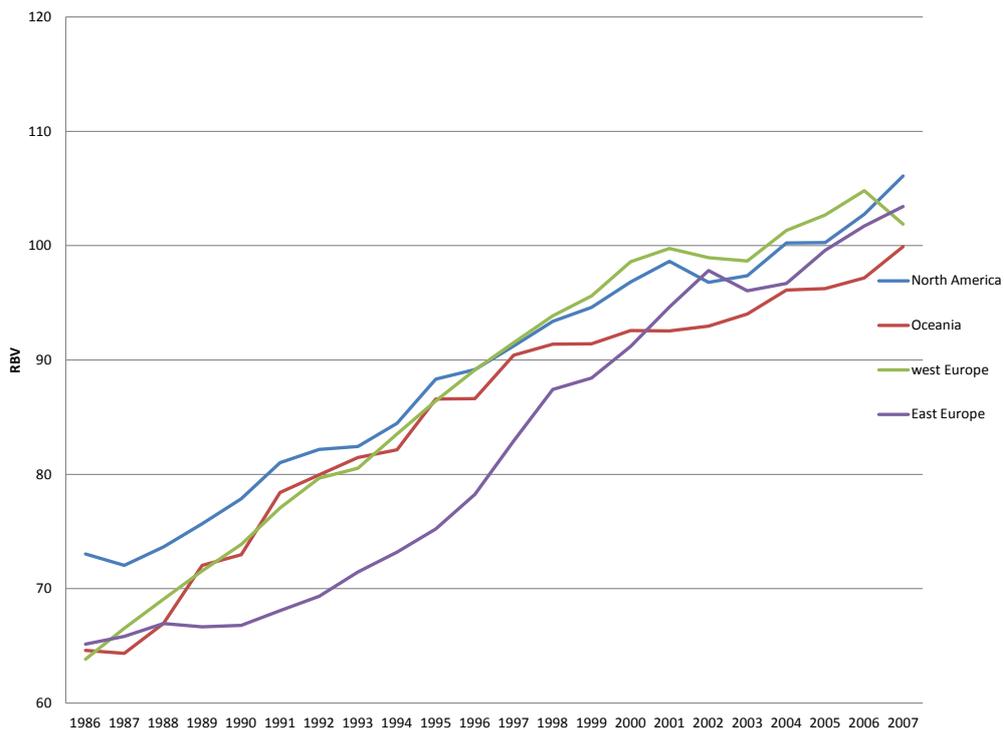


Figure 3. Global genetic trends for protein of Holsteins in different regions of the world (DFS scale).

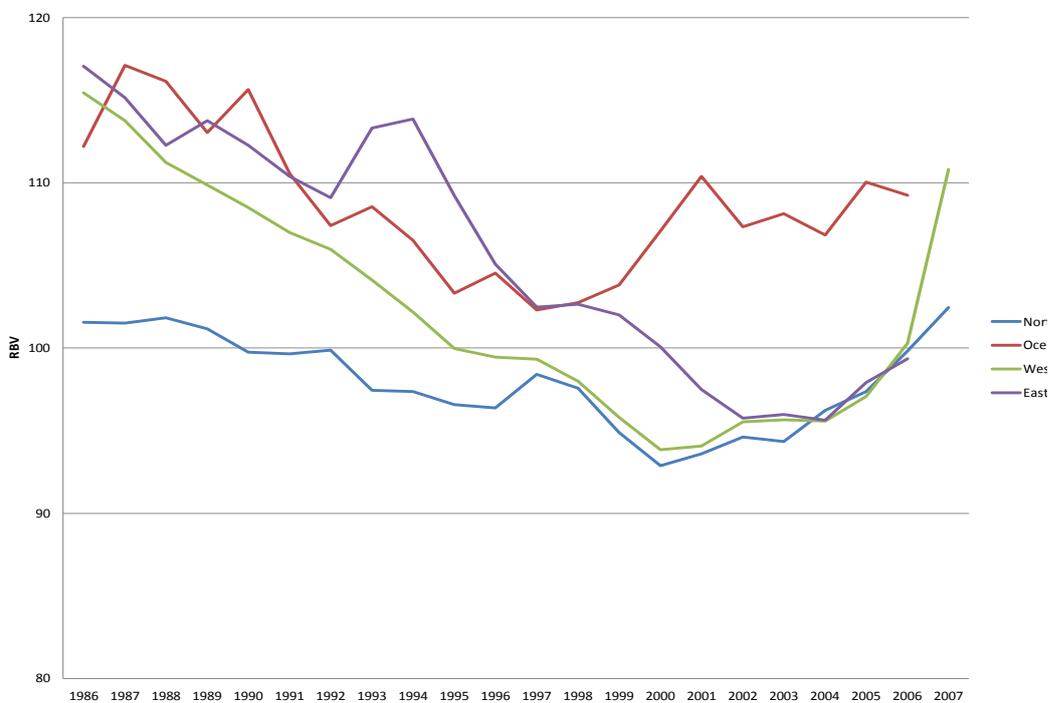


Figure 4. Global genetic trends for female fertility of Holsteins in different regions of the world (DFS scale).

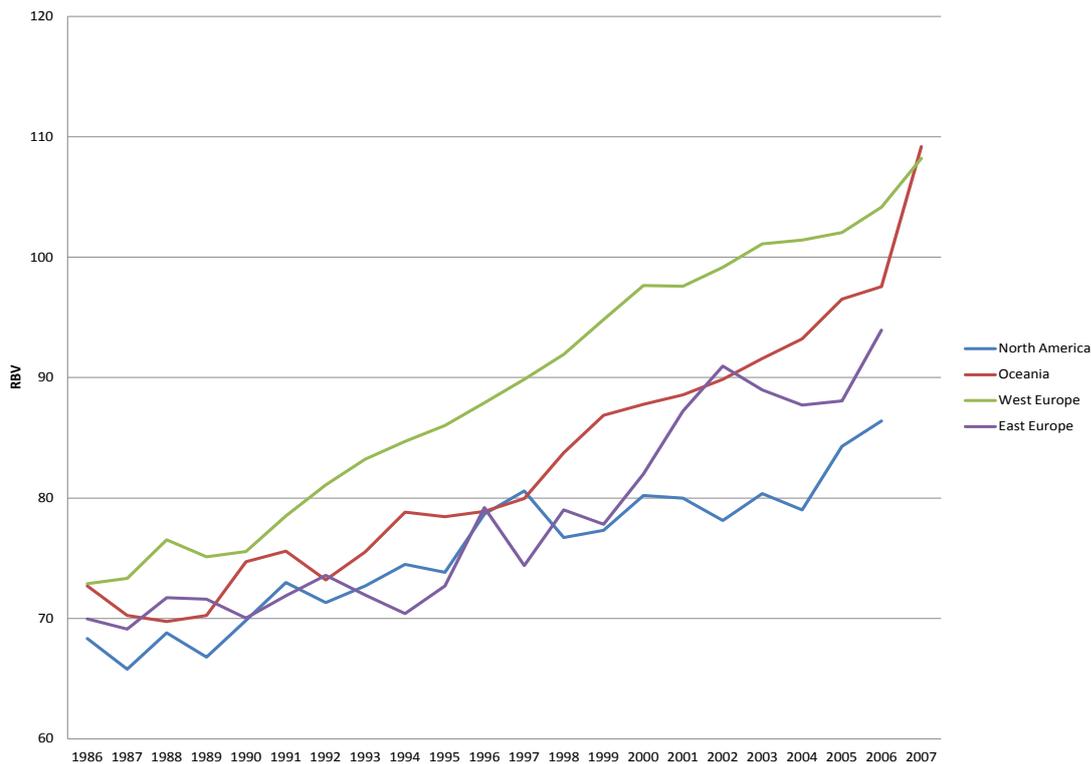


Figure 5. Global genetic trends for protein of Red Dairy Cattle in different regions of the world (DFS scale).

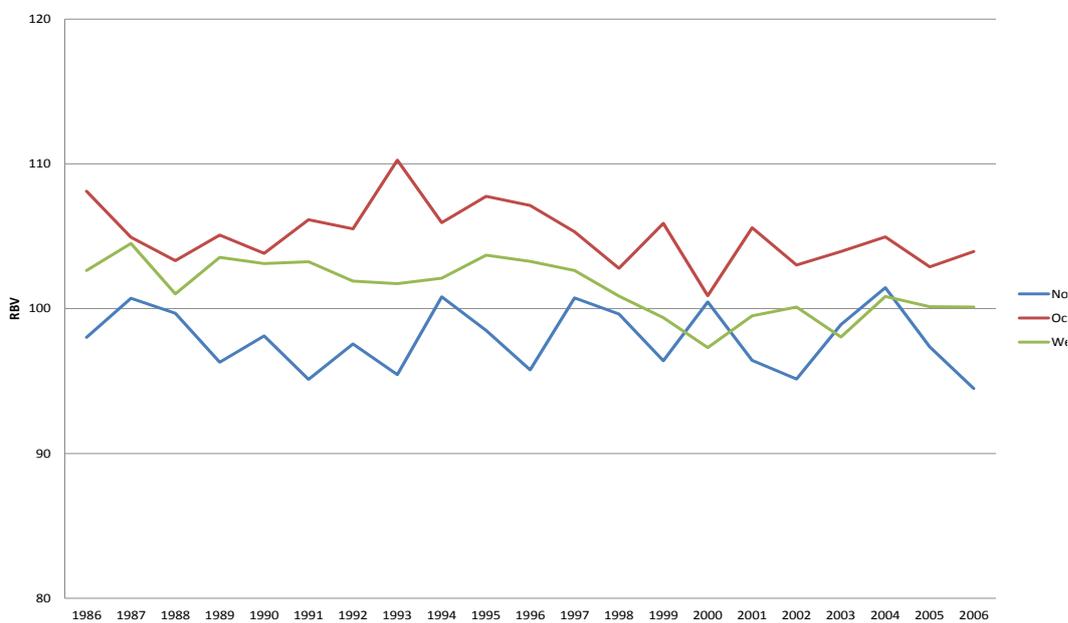


Figure 6. Global genetic trends for female fertility of Red Dairy Cattle in different regions of the world (DFS scale).

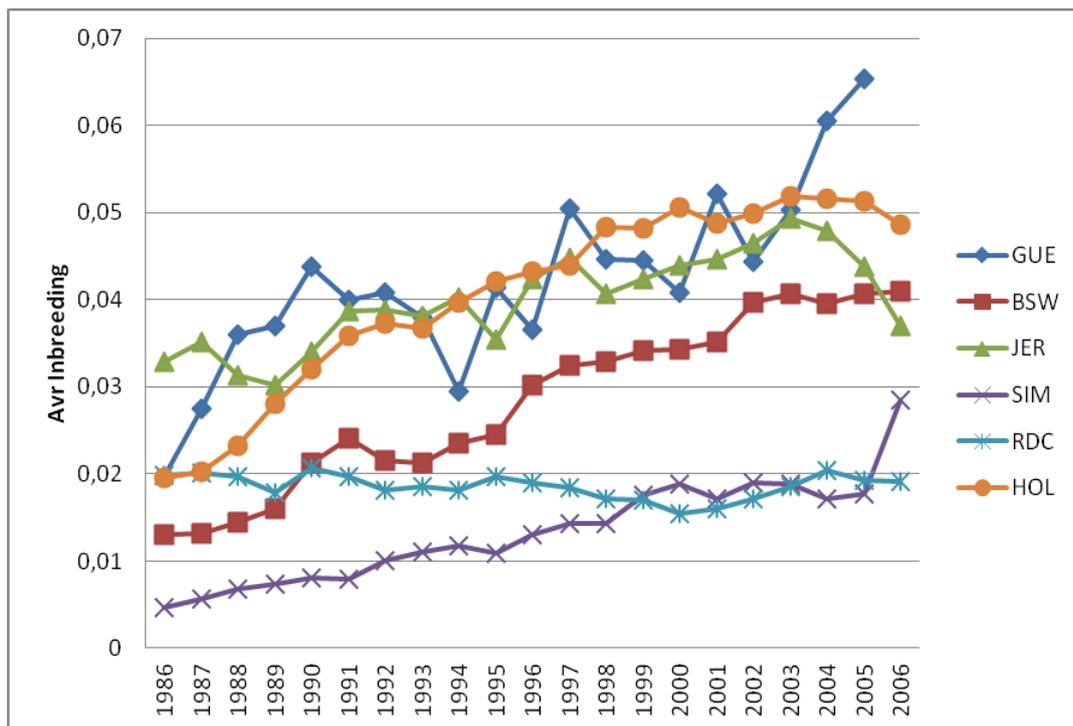


Figure 7. Mean inbreeding level of internationally proven bulls of six breeds by birth year.

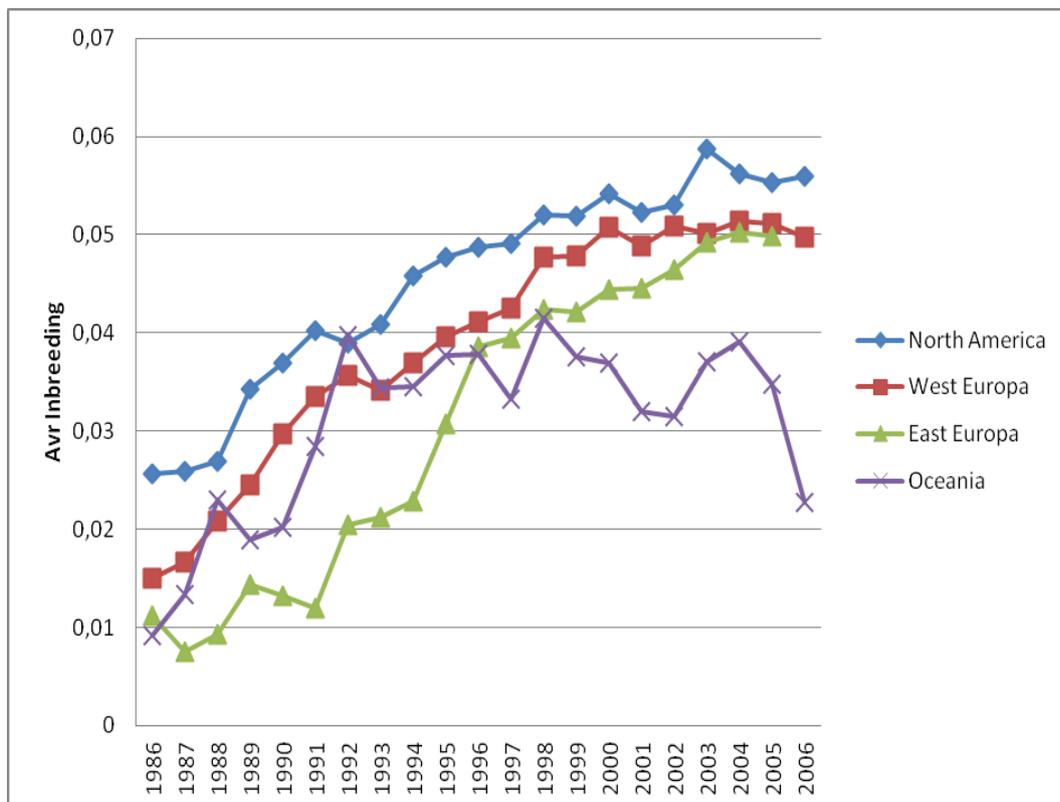


Figure 8. Mean inbreeding level of internationally proven Holstein bulls in different regions of the world.