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Genomic selection for more sustainable livestock production: the French situation

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Introduction

The availability of high throughput genomic technologies over the last decade has allowed the development of genomic selection (GS) programs, i.e. the use of genomic information (i.e. DNA chips or sequence data) to genetically evaluate and select candidates to selection. These new tools are likely to change radically breeding programs in both livestock and plant populations. INRA has put GS as one of its research priorities through one of its metaprograms (acronym SelGen - see <http://www.selgen.inra.fr> for details). Over last years, the INRA animal genetics division has devoted a lot of efforts to both theoretical and practical aspects of the development of GS in livestock populations. This paper reviews major breakthroughs achieved over this period of time. Advances made in cattle, which has been by far the most impacted species, will be described first. Applications to other livestock species and theoretical developments will then be presented.

Genomic selection in cattle

The development of GS in French dairy cattle populations has strongly benefited from the implementation of a large-scale (14 chromosome regions, 45 microsatellites) Marker Assisted Selection (MAS) program in Holstein, Normande and Montbéliarde breeds in the early 2000's. After 7 years of activity, more than 70,000 animals had been genotyped, and the efficiency of the MAS program was close to its expectation (Guillaume et al., 2008). This large reference population, as well as the experience gained from this first-generation program, were very useful for the development of GS. Indeed, as soon as the BovineSNP50TM beadchip (Illumina Inc, San Diego, USA) has become available in late 2007, it has been intensively used to upgrade the MAS program, leading to a first release of genomic breeding values (GEBV) as early as fall 2008 (Boichard et al., 2012b).

GEBV became an official genetic evaluation method in 2009, which allowed genomically evaluated bulls without progeny test to be marketed. An original genetic evaluation model including QTL traced with haplotypes as well as a polygenic residual component was used. QTL were initially detected through GWAS and then by ElasticNet, the latter approach allowing for a larger proportion of genetic variance to be explained (Croiseau et al., 2011).

To increase the reliability of GEBVs, a European collaboration resulted in the creation of the Eurogenomics consortium, which gathered research industry players from France, Netherlands, Germany and Nordic countries (followed later by Poland and Spain). Through this alliance, a large reference population of 16,000 Holstein bulls was assembled in 2009, reaching 30,000 in 2015. The gain in reliability was estimated at about 10% for each trait in all countries (Lund et al., 2011). This initiative then appeared as an excellent platform for common data management and standardization, for shared R&D - e.g. imputation

(Schrooten et al., 2014) or use of sequence data -, and for common chip ordering. In 2013, a similar international cooperation was set up in the Brown Swiss breed, a small population in France but a large one worldwide, leading to an official evaluation in this breed in 2014.

Possibilities to build an across-breed genomic evaluation were investigated in the frame of the GEMBAL project funded by the French National Research Agency (ANR) and the French cattle industry. It was based on the use of the High Density chip (HD, 777k), a device INRA contributed to develop in 2010. The goal was to extend genomic evaluations to all beef and dairy breeds by using as much as possible a common reference population. Over 5,000 bulls from 18 breeds were genotyped with the HD chip. The first step of the project, the imputation from 50k to 777k was found to be highly accurate, provided that at least 200 important bulls were genotyped with the HD chip (Hoze et al., 2013). Imputation accuracy slightly varied according to breed effective size and genetic relationship between individuals. The second step, i.e. genomic prediction, gave less favourable results: in agreement with other initiatives at the international level, prediction accuracy only slightly increased when using across breed information, even with INRA model explicitly taking into account QTL effects (Hoze et al., 2014). Several reasons can be put forward to explain this somewhat disappointing result: a low proportion of shared QTL between breeds, varying QTL effects according to the genetic background, or more likely insufficient linkage disequilibrium. As a consequence, the idea of an across breed evaluation based on a HD chip was abandoned, but should be revisited in the future using sequence data.

Indeed, sequence data include information on causal mutations, and we can assume that including this information in the evaluation will improve the accuracy, and particularly the persistency, of genomic prediction. However, the huge number of polymorphisms included in sequence data generates a lot of noise, so that an efficient marker selection step has to be developed in order to filter out the vast majority of useless information. This question was addressed through the GENSSEQ project funded by INRA SelGen metaprogram. About 300 whole genome sequences were obtained through different projects in a variety of breeds. Most of them are shared or are going to be shared in the “1000 bull genomes” consortium (Daetwyler et al., 2014). In a joint work with Danish colleagues, it was demonstrated that GS accuracy is improved when causative variants or very close polymorphisms (<1kb) are included in the analysis, whereas more distant markers generate noise and are detrimental for the quality of predictions (van den Berg et al., 2014). A large-scale project based on GWAS analysis on imputed sequences to identify many causal variants and use them in predictions is currently being developed.

A large-scale use of GS is highly strategic. It is a profitable innovation for ^[1]farmers with strong consequences on production systems. It is also of major importance for the replacement of reference populations, because the future number of precisely evaluated bulls will be ^[1]limited (Boichard et al., 2015). However, this large-scale use of GS is highly dependent on ^[1]its cost. In order to reduce genotyping costs, INRA developed in 2011-2012, in the frame of an international consortium gathering USDA, DPI Australia and ^[1]Illumina, a low-density chip (7K) optimized for imputation over a large range ^[1]of cattle breeds (Boichard et al., 2012a). This chip is now widely used worldwide. In 2012, an ^[1]automatic procedure was implemented to deliver GEBVs on ^[1]a weekly basis. In 2013, the chip was improved by adding two types of markers: a) generic markers to further improve imputation or predict targeted ^[1]genes, b) candidate mutations (5,000 in its fall 2014 V4 release) for large scale validation and, ultimately, to improve genomic predictions. In early 2015, more than 400,000 animals had been genotyped so far, about 80,000 genotyped females had phenotypes and were included in the genomic predictions.

The impact of GS on dairy cattle breeding schemes has been very strong. As soon as

2009, following INRA recommendations, the progeny test of young bulls was stopped and the market share of genomically evaluated bulls increased from 25% in 2010 to 75% in 2014. To limit the increase in inbreeding due to the reduced generation interval, the use of a large number of young bulls as cow and as bull sires was recommended (Colleau et al., 2009; Colleau et al., 2015) and has been well followed by the breeding companies. The higher efficiency of GS allowed breeding goals to be modified in 2012 towards a higher sustainability by decreasing the weights of production traits and increasing those of functional traits. Several projects are currently developed to implement genomic evaluation for new traits (health, carcass traits, cheese-making properties...) and include them in the breeding goal and to set up genomic evaluations for additional breeds.

Genomic selection in other livestock species

The utility of GS in other livestock species was investigated using a combination of theoretical and practical approaches. In dairy sheep, genomic predictions using Single Step BLUP proved to be more accurate than traditional indices in the Lacaune and in the Basco-Béarnaise breeds (Duchemin et al., 2012; Baloché et al., 2014). When reference populations are small (e.g. in the Saanen and Alpine goat breeds, in French “Manech Tête Noire” and in Spanish “Latxa Cara Negra Navarra” sheep breeds), multiracial approaches based on the two-step GBLUP or Single Step BLUP appeared as very efficient, with gains depending on the trait considered (Carillier et al., 2013; Legarra Albizu et al., 2014).

The UTOPIGE project, financed by ANR and the pig and poultry industries, was launched to assess the utility of GS in pigs and in laying hens, where commercial animals are issued from complex crossbreeding plans between several pure lines, with important environmental differences between nucleus and commercial herds. First results appear as promising, with a noticeable gain in accuracy of GEBV as compared to usual indices in laying hens (Chapuis et al., 2015). In horses, GBLUP and Bayes C methods appeared as only slightly more accurate than classical evaluation procedures (Ricard et al., 2013).

The interest of GS was also investigated through the modelling of selection programmes. In small ruminants, deterministic approaches were developed to compare scenarios including or not genomic information (different populations or genotyped candidates, maintenance or suppression of progeny testing) and to identify necessary changes in the organisation of selection programmes associated with the use of genomic selection (Shumbusho et al., 2013). In pigs, stochastic simulations were used to describe a male line selected for two uncorrelated traits recorded in candidates or their relatives and showed that GS may boost annual genetic trends by 25 to 30% while ensuring a better control of genetic variability (Tribout et al., 2012). In all cases, a large reference population and low genotyping costs are necessary. Profitability analyses of these investments are essential, and will allow economically viable solutions to be proposed (Tribout et al., 2013).

Conclusions

GS has markedly changed (dairy) cattle breeding schemes over the last decade, as it appeared as both less expensive and more efficient than traditional selection methods. The situation is less straightforward in other livestock species, but results obtained so far tend to show the interest of an appropriate use of GS in most livestock species. As in cattle, these new tools should be used to improve the sustainability of future livestock production systems.

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