



# Trajectories of genetics, 150 years after Mendel/Trajectoires de la génétique, 150 ans après Mendel Genomic selection in domestic animals: Principles, applications and perspectives



## *Sélection génomique chez les animaux domestiques : principes, applications et perspectives*

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### ABSTRACT

The principles of genomic selection are described, with the main factors affecting its efficiency and the assumptions underlying the different models proposed. The reasons of its fast adoption in dairy cattle are explained and the conditions of its application to other species are discussed. Perspectives of development include: selection for new traits and new breeding objectives; adoption of more robust approaches based on information on causal variants; predictions of genotype  $\times$  environment interactions.

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### R É S U M É

Cet article décrit les principes de la sélection génomique, avec les principaux facteurs de variation de son efficacité et les hypothèses sous-jacentes aux différents modèles proposés. Il présente ensuite les raisons de son adoption rapide en bovins laitiers et les conditions d'application aux autres espèces pour lesquelles la situation est moins favorable. Les principales perspectives de développement dans les prochaines années concernent la sélection de caractères nouveaux, l'adoption d'approches robustes utilisant l'information des mutations causales et la prédiction des interactions génotype  $\times$  milieu.

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## 1. Introduction

Artificial selection in domestic species has been based for centuries on the own phenotypes of animals. During the 20th century, selection index theory first, then Best Linear Unbiased Prediction (BLUP—a more sophisticated approach

relying on mixed linear models) allowed the use of information on phenotypes of relatives to predict “breeding values” of candidates for selection. This led to the successful selection of easily recorded phenotypic traits with moderate or high heritability. But to be efficient for traits difficult to measure or with low heritability required costly phenotyping investments. During the last 25 years, a number of Quantitative Trait Loci (*i.e.* regions of the genome responsible for a fraction of the genetic variance of a trait) have been mapped with genetic markers, paving

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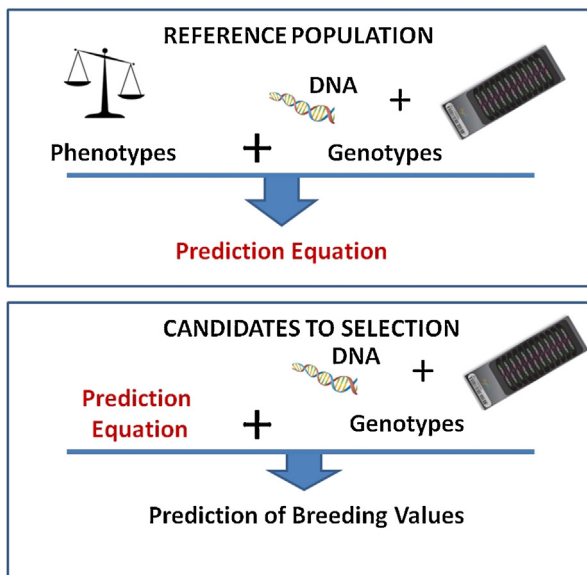


Fig. 1. Principles of genomic selection. Top: a prediction equation is obtained from a reference population with phenotypes and genotypes; bottom: this prediction equation is used on candidates with genotypic information only.

the way to marker-assisted selection (MAS). A genetic marker is a polymorphic sequence, usually without biological effect, but easy to genotype, and, consequently, widely used in genetic studies. The MAS approach was successful for traits with a simple genetic determinism, but provided disappointing results in many more complex situations. The two main reasons for this low efficiency were the limited and always overestimated part of the genetic variance explained by these small numbers of QTL, and also the low association (or linkage disequilibrium) between markers and QTL at the population level. In 2001, Meuwissen et al. [1] proposed a novel approach where the breeding value could be estimated from markers spanning the entire genome. With this approach, genetic effects are estimated for each marker and then summed up to predict the overall breeding value of any animal (Fig. 1). This estimation of marker effects is carried out within a reference population, *i.e.* a large group of individuals with both phenotypes and marker genotypes information. These effects are then applied to candidates for selection with marker genotype information, but without known phenotypes. To be effective, this approach is very demanding in terms of both number of individuals genotyped and number of markers on the genome. Its application was unfeasible until the development of large-scale and cheap genotyping methods.

## 2. The success story of genomic selection in dairy cattle

Before the genomic era, genetic improvement of dairy cattle was relying on a vast phenotype recording system distributed over most French farms. The best bulls were selected after a lengthy progeny test based on the performances of more than 100 daughters spread in many herds. They were used through artificial insemination to

breed the next generation. Each bull was genetically evaluated on about 40 traits relative to milk production and composition, resistance to mastitis (*i.e.* udder infection), fertility, conformation, calving conditions, longevity, etc. In 2007, just after the first draft of the bovine genome was assembled, the Illumina Company together with an international consortium developed a chip to genotype over 54,000 single nucleotide polymorphisms (SNP) simultaneously. These markers represented only a small proportion of all discovered SNP, but they were highly polymorphic in a large range of breeds and evenly spaced over the genome. This chip was immediately used to genotype existing progeny-tested bulls. With these first reference populations, genomic breeding values were accurate enough to replace progeny testing. They were made official in 2009 in different countries, allowing the dissemination of semen of young bulls with genomic evaluation only. This revolutionized selection: progeny testing was no longer necessary, simplifying the selection process and decreasing its cost; due to a strong reduction in generation interval, the yearly genetic trend could be doubled; due to their lower production cost, a much larger number of bulls could be selected and marketed, leading to a better management of genetic resources, limiting inbreeding trends [2], and more easily satisfying a diversity of needs and objectives; selection for more balanced and sustainable objectives was easier, including low heritability traits such as fertility or mastitis resistance. Because good accuracy of breeding values requires large reference populations, international collaborations started between breeding cooperatives, leading to the emergence of large consortia such as Eurogenomics in Holstein (nine European countries). Then, in order to decrease the genotyping costs, a low-density chip was designed, with very good imputation accuracy [3], *i.e.* with excellent prediction of missing markers. A virtuous circle was created: the large number of genotyped animals decreased the cost of genotyping, leading to an increase in volume. At the farm level, this tool is now used to optimize within herd selection, matings and replacement, as each genotyped female is as accurately evaluated as artificial insemination males. In December 2015, the French national database included 400,000 genotyped animals, including 100,000 for 2015 alone. Now, this large number of genotyped cows is the major resource for population reference replacement and updating. In small dairy breeds or in beef breeds with fewer artificial insemination bulls, such reference populations partly consisting of cows with own performances are the only way to implement genomic selection. In 2016, 12 French cattle breeds, including several small ones, use genomic selection in their breeding program. This is a crucial evolution, because initially only the largest breeds were able to benefit from this innovation, creating a technological gap with the smaller ones.

## 3. Factors of variation of genomic selection efficiency

Whatever the domestic species, the yearly genetic gain depends on four parameters: genetic variability of the trait, selection intensity, evaluation accuracy, and generation interval. The three latter can be modified by genomic selection. The main advantage of genomic selection is that

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