

Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery

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The rate of annual yield increases for major staple crops must more than double relative to current levels in order to feed a predicted global population of 9 billion by 2050. Controlled hybridization and selective breeding have been used for centuries to adapt plant and animal species for human use. However, achieving higher, sustainable rates of improvement in yields in various species will require renewed genetic interventions and dramatic improvement of agricultural practices. Genomic prediction of breeding values has the potential to improve selection, reduce costs and provide a platform that unifies breeding approaches, biological discovery, and tools and methods. Here we compare and contrast some animal and plant breeding approaches to make a case for bringing the two together through the application of genomic selection. We propose a strategy for the use of genomic selection as a unifying approach to deliver innovative ‘step changes’ in the rate of genetic gain at scale.

The global food price crisis of 2008 highlighted the necessity for innovation in agriculture to address food insecurity in the context of a changing climate and a growing population. The world population is predicted to reach 9 billion within the next 35 years, which will require a 70–100% increase in food production relative to current levels^{1–4}. A burgeoning world population is not the only threat to global food security. Changing lifestyles, altered population demographics, competition from subsidized biofuels, deterioration of natural resources, climate change and dwindling supplies of water will necessitate considerable financial, intellectual and research investment in agriculture, particularly in the developing world^{1,2,4}. Breeding of livestock and crops is one of the key routes through which increased production, efficiency and sustainability can be delivered.

In this Perspective, we outline both the opportunities and challenges for the deployment of genomics in breeding programs, drawing attention to the fundamental role that quantitative genetics has played as the intellectual cornerstone of plant and animal breeding

for the past century. Access at unprecedented levels to large-scale sequence and phenotypic information will bring opportunities to unify breeding methods, tools and technologies across several plant and animal species, which in turn will catalyze the modernization of breeding programs. Furthermore, we postulate that the adoption of these new technologies and approaches at scale will enable breeding programs to be platforms for both the delivery of new products and biological discovery based on genome-wide association studies (GWAS) with field validation of new alleles.

A brief history of plant and animal breeding

Breeding of livestock and crops is as old as agriculture itself. At the heart of all breeding remain such traditional pursuits as designing and analyzing performance trials to rank selection candidates in order of merit, with the aim of maximizing selection gain per unit of resources expended⁵. The history and development of scientific animal and plant breeding can be traced back to the contributions of many individuals, but there are a few outstanding additions—at least from our current scientific perspectives (Fig. 1). These have been extensively reviewed elsewhere and will only be discussed briefly here.

Despite the conceptual similarities between animal and plant breeding, their theoretical models and breeding methods have diverged. This is mainly because of differences in the development and application of new breeding technologies and methods⁵. Although the divergence between animal and plant breeding is rather nuanced because of species-specific characteristics such as mode of reproduction and number of progeny per reproduction cycle, theoretical concepts as well as tools and methods that are clearly different have developed for the two. For plants, breeding can be regarded as having started with domestication. However, for the vast majority of the past 10,000 years, breeding has consisted of only selection with no enforced crossing; the sexual mechanism in plants and the need for hybridization have only been generally recognized in the last 250 years⁶. In animals, artificial selection had to include sex to create progeny, as this was the only possible means of reproduction, and a more structured approach to breeding was adopted earlier than in plants, with the use of ‘herd books’ to trace the pedigree of selected animals⁷.

Following the rediscovery of Mendel’s laws in the early twentieth century, plant breeders started selecting and crossing superior individuals, moving on (in some species, at least) from developing and maintaining cultivars by (unknowingly) harvesting selfed seed, or vegetative propagation. The highlights of animal breeding developments over the twentieth century have centered on improving

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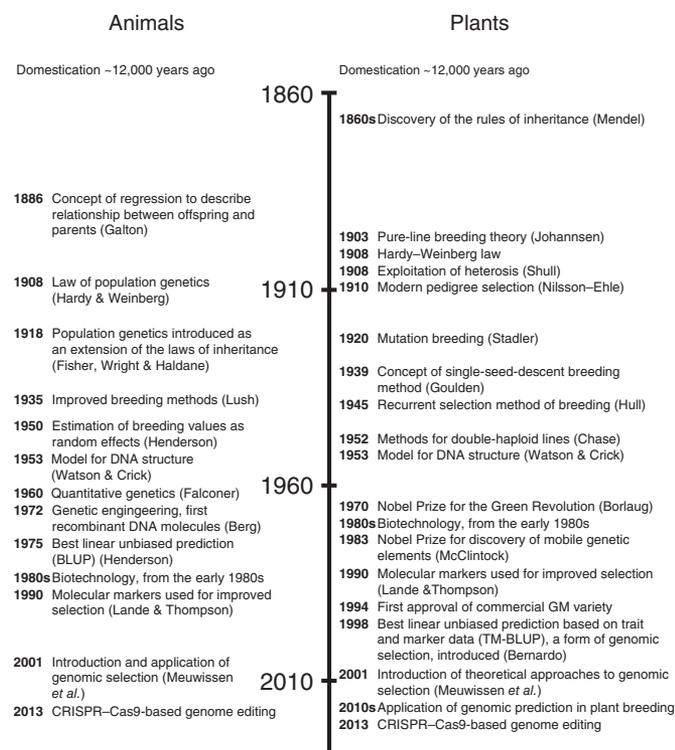


Figure 1 Some key milestones of selective animal and plant breeding.

exploitation of information from relatives through selection indices⁸, estimation of breeding values as random effects⁹ and statistical methods to estimate genetic relationships¹⁰. Galton developed the concept of regression (essentially heritability), from which response of traits to selection can be predicted¹¹, and Fisher developed a theory to demonstrate that the mean trait value for polygenic traits can change markedly under selection with only a small change in allele frequencies at individual loci¹².

Both plant and animal breeders deal with complex traits, but individual mutations with moderate to large effects have been exploited more widely in plant breeding than in animal breeding (for example, resistance to yellow (stripe) rust in wheat¹³ and the dwarfing genes in wheat and rice). Like some important plant traits, such as yield, most traits in animal breeding are polygenic. Additionally, plant breeders can usually generate genetically identical individuals or reproducible cultivars and test them in well-designed trials, whereas animal breeders must usually rely on unbalanced phenotypic data from individual animals in different production units. As a result, animal breeders were naturally forced to use complex statistical methods to estimate breeding value, whereas plant breeders used well-designed trials to measure phenotype as a means to inform their selection.

Animal breeders often have to use information from the relatives of selection candidates because they have to select for traits that cannot be measured in the candidates themselves (for example, milk yield in bulls), that have low heritability or that are measured late in the breeding process. Plant breeders generally do not have the problem of 'sex-limited' traits and can experimentally increase selection accuracy by growing more plants from the same cultivar. As a result, the merit of a cultivar in a plant breeding program can often be measured at any level of precision that the breeder desires. Reproductive rates and expense make this approach harder for animal breeders

to follow. A comparison of typical plant (an inbreeding cereal) and animal breeding approaches is shown in **Figure 2**.

Modern quantitative methods, including computer simulation, are pivotal to and underpin a host of new technologies and approaches that are of critical importance for the future of plant and animal breeding¹⁴. Many plant breeders view selection as a process of accumulating favorable alleles within a single line and use a Mendelian approach to identify and incorporate major beneficial alleles. In contrast, animal breeders have viewed response to selection as a slow increase in the frequency of favorable alleles in a population, predictable from the 'breeder's equation' (ref. 15). Animal breeding has therefore deployed a more classical biometrical approach by combining phenotypic, pedigree and genotypic information from records of individuals to build estimates of breeding values as a means to inform selection decisions. Similar approaches are also deployed in outbreeding crops, such as maize and forages (for example, in hybrid breeding)¹⁶. However, quantitative genetics approaches in plant and animal breeding have developed largely in parallel, with different focuses: for animals, the focus is on the statistical partition of phenotypic variation in a population into genetic and environmental components, whereas for plants it is on the descendants of crosses between two inbred lines¹⁷, with emphasis on identifying 'transgressive segregants', which are individuals with one or more traits better than those of the best parent. Furthermore, since the 1980s, plant breeders have used various biotechnologies, such as transgenics, to a much greater degree than animal breeders and, perhaps consequently, have made much more explicit use of physiology. On the other hand, animal breeders have perhaps more systematically incorporated economics in the definition of their breeding goals to a greater extent than plant breeders. All of this has meant that the fields of plant and animal breeding have diverged somewhat over the decades, leading to inefficiencies, delays in the adoption of technology and a number of missed opportunities.

The advent of genomic selection has led to the re-emergence of quantitative genetics as a framework for incorporating marker and sequence information to supplement and complement standard phenotypic descriptors and pedigree information. Technological changes are now bringing together the biometrical approach of animal breeders and the Mendelian approach of plant breeders. The deployment of modern sequencing methods to identify large numbers of molecular markers and the emergence of cost-effective high-throughput genotyping and phenotyping technologies for crops and animals are not only revolutionizing breeding, but are also offering new incentives for the migration of information and approaches between plant and animal breeding and for the unification of breeding and biological discovery efforts.

Genomic selection is a unifying theme across plant and animal species

In 2001, a landmark paper¹⁸ that followed on earlier work, notably by Lande and Thompson¹⁹, Nejati-Javaremi *et al.*^{20,21}, Lynch and Walsh²², Bernardo²³, Haley and Vischer²⁴ (who coined the term 'genomic selection') and Whittaker *et al.*²¹, anticipated the availability of affordable high-density genomic data and proposed statistical methods that enabled this type of data to be used to increase the accuracy of selection. This method came to be called genomic selection. Subsequent modeling showed that genomic selection could have a large impact on genetic progress²⁵, and the technology was quickly adopted across a range of livestock species. Genomic selection has played different roles depending on the biology and economics of particular species and the breeding and production systems in

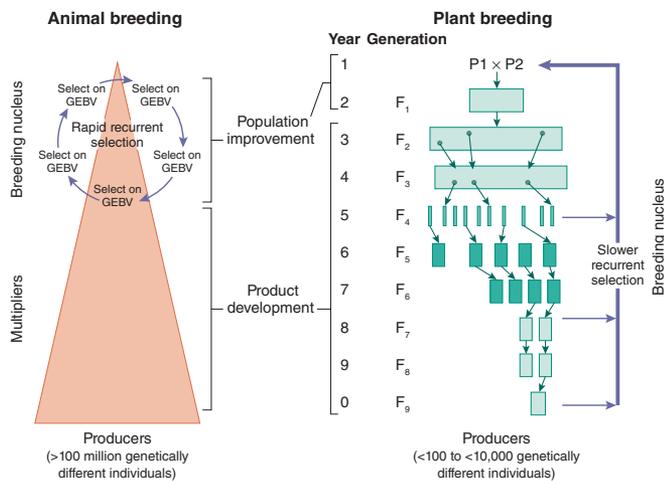


Figure 2 Comparison of animal and plant breeding approaches. In some areas, plant and animal breeders have adopted similar approaches. All breeding programs can be thought of as having two basic components: (i) a recurrent selection component that seeks to increase the frequency of favorable alleles in a population, which in turn increases the mean genetic merit of the population, and (ii) a product development component that seeks to extract genotypes from this improved population for a farmer to produce. A major difference between animal and plant breeding has been that the former places greater emphasis on population improvement, with product development consisting primarily of multiplication of stock that is not recycled into the breeding nucleus, whereas in the latter greater emphasis is placed on selection of an improved product in the form of a recognizable plant variety, which is often also the source of parents for the next breeding cycle. That is, while varieties (often protected by plant breeders' rights) are the focus in plant breeding, this concept is almost irrelevant in animals. GEBV, genomic estimated breeding value.

which they reside. For dairy cattle breeding in advanced economies, genomic selection has largely replaced progeny testing, enabling the generation interval to be shortened from 5 years to 2 years, with consequent increases in rates of genetic gain. For example, in the Netherlands, on-farm production levels increased by 21 index points per year in the 7 years before the adoption of genomic selection in 2008. Since the adoption of genomic selection, on-farm production levels have increased by 34 index points per year, a 60% increase. The generation interval of sires, the key pathway through which genetic gain is achieved in dairy cattle breeding programs, has decreased from ~2,500 days to ~1,250 days²⁶. In pig breeding for commercial production systems, genomic selection has resulted in increased accuracy of selection and better alignment of selection accuracy with the breeding goal; this has driven a 35% increase in the rate of genetic gain in the breeding program that drives genetic improvement in 25% of the commercially raised pigs globally (W. Herring, Pig Improvement Company (PIC) North America, personal communication). In other species, such as beef cattle and sheep, which are often extensively rather than intensively farmed, genomic selection has also provided the technology leap required to enable scientific breeding programs to greatly increase rates of genetic improvement.

While genomic selection was adopted rapidly across the more technologically developed livestock sectors and at a somewhat slower pace in international seed houses, the uptake has lagged in public-sector plant breeding programs and in plant and animal breeding programs in the developing world. Major international seed companies are routinely using genomic selection, and many public-sector breeding programs are exploring this technology or partially using

it, particularly for clonally propagated long-lived perennials²⁶. The explanations for this lag are complex and include the difference between the skills of a typical field-based plant breeder and the skills required to implement genomic selection; the barrier to entry created by the expense of investing in both the computational and recording infrastructure and the genotypic and phenotypic data required to effectively implement genomic selection; the complexity of the genomes of many plant species; and the fact that plant and animal breeding have somewhat diverged over the decades and that it takes some time for advances in one field to be translated to the other. On the other hand, some argue that plant breeders can derive some of the expected benefits of genomic selection through other technologies and methods. For example, the application of doubled-haploid technology²⁷ can reduce generation time substantially, and plant breeders can achieve more reproducible estimates of phenotype by replicating clones and inbreds across generations and sites.

Effective implementation of genomic selection is expensive and requires specialist skills, creating large barriers to entry. However, because many of the skills and resources necessary for genomic selection are broadly applicable, interdisciplinary and collaborative networks that bring together breeding programs for different plant species as well as animal species could enable widespread adoption of genomic selection across the many small-scale breeding programs in the developing world. This is because, despite the differences between species (within and between the plant and animal kingdoms) in terms of genomes, breeding mechanisms, etc., they require similar concepts and tools for genomic prediction. Thus, plant and animal breeders will benefit from working together to address problems that are common to the two disciplines, such as prediction of traits in structured populations⁵. The cross-fertilization of ideas will develop a critical mass around which more can be done per unit of resource and will help to produce a new cadre of scientists with better skills.

Additionally, the skills and resources that would be assembled for genomic selection could serve as powerful platforms for biological discovery, enabling dissection of the true relationship between genomes and traits and increasing the frequency of favorable alleles in breeding programs. For example, the major pig, poultry and cattle breeding programs have assembled data sets with dense genomic and phenotypic information from several hundreds of thousands or even millions of individuals, and results in the public domain suggest that international plant breeding organizations have done the same, at least for maize. With regard to agriculture in the developing world, the Consortium of International Agricultural Research Centers (CGIAR) works on a number of plant and animal species, and it could synergistically combine its resources and expertise (for example, for prebreeding, conventional and molecular breeding, and other research and translational activities) by centrally coordinating activities in genomic selection across its network. This will allow the exchange of knowledge and expertise between programs working on different species to develop deeper and more general insights than what is achievable in the individual programs. We believe that quantitative genetics provides an objective framework for doing this and that four different aspects need to be considered: (i) the breeder's equation; (ii) unification of biotechnology and quantitative genetics; (iii) integration of plant and animal breeding concepts and approaches; and (iv) unification of breeding and biological research.

The breeder's equation—opportunities for more gain

The optimal design of any breeding program involves harnessing multiple disciplines, including genetics, statistics, computer science, physiology, molecular biology, logistics, economics and social

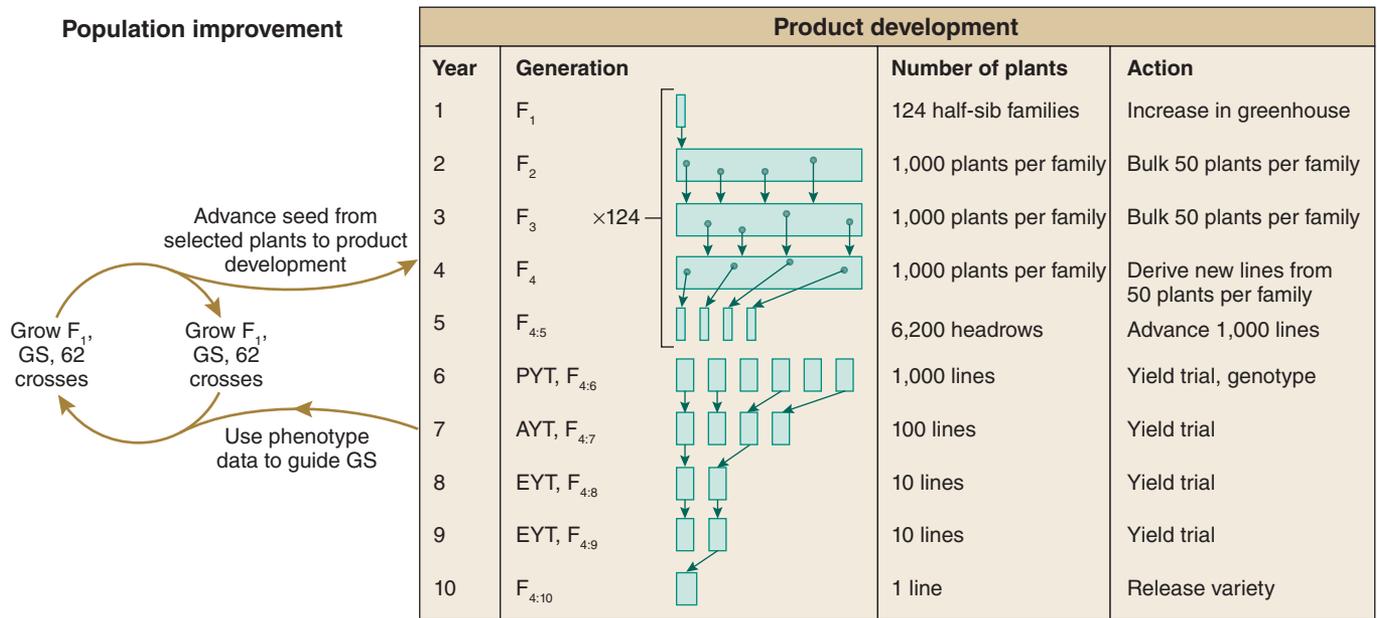


Figure 3 A variant of the two-part breeding program design for plant breeding. GS, genomic selection; PYT, primary yield trials; AYT, advanced yield trials; EYT, elite yield trials.

science. The breeder’s equation, originally introduced by Lush¹⁵, provides a framework through which the impact of each of these disciplines, their underlying technologies and choices about how they are used can be evaluated^{22,28}. The equation models the expected change in a trait in response to selection and can be written as

$$R = \frac{\delta_g \times i \times r}{L}$$

where *R* is the change in trait mean per year, δ_g is the amount of genetic variation within the population, *i* is the selection intensity, *r* is the accuracy of the selection and *L* is the generation interval.

Genomic selection directly addresses the four factors that affect the rate of genetic gain in animal and plant breeding²⁹:

1. Breeding is faster because breeders can recycle individuals more quickly if selection is based on genomic estimated breeding value (GEBV), which is generally more effective than selection based on phenotype.

2. Selection intensity is greater because breeders can select more individuals genotypically than they can phenotypically: the cost of genotyping is typically lower than that of phenotyping, so more candidates for selection can be evaluated. This is particularly important in plant breeding.

3. GEBV can be more accurate than the estimated breeding value based on phenotype and pedigree alone.

4. Genomic selection tools can also make integration of new genetic material much more efficient³⁰ through application of factors 1–3 above in wide crosses and prebreeding programs and the use of optimal contribution theory driven by genomic information.

Unification of biotechnology and quantitative genetics

The application of biotechnology has had a profound effect on plant and animal breeding; in some cases, this has been at the expense of quantitative genetics and selection theory⁵. Genomic selection offers an opportunity to build common ground between biotechnology and quantitative genetics. Quantitative genetics is the study of the genetics of complex traits that are controlled by a large number of loci and

whose regulation often involves nongenetic factors³¹. Sequencing and resequencing of crop and animal genomes provide the opportunity for identification of genome-wide genomic polymorphisms and correlative relationships between variants and complex traits. However, causative variants are more difficult to decipher, particularly in regions of high linkage disequilibrium³². The potential of CRISPR–Cas9 for genome editing in theory will provide new ways of validating causative effects, particularly for traits that exhibit complex modes of inheritance³³. Furthermore, simulation studies³⁴ have recently shown how genome-editing technology can be coupled with genomic selection to double the rate of genetic gain as compared with genomic selection conducted in isolation. This new approach for deploying genome editing in breeding programs, referred to as PAGE (promotion of alleles by genome editing), has considerable potential for acceleration of genetic gain in plant and animal improvement programs. In animal breeding, the cost of genotyping and resequencing has reached a point where producers and multipliers, in addition to members of the breeding nucleus (Fig. 2), can be genotyped and have sequencing information accurately imputed for a modest investment. The population of genotyped or sequenced animals is therefore on the order of millions (for example, in Ireland, more than 1 million beef cattle are being genotyped; in major pig and poultry breeding programs, data sets with similar numbers of individuals have been genotyped and are being imputed to whole-genome sequence data), and on-farm or slaughterhouse phenotype data are also available for these animals. Moreover, this huge resource can also be treated as a genome-wide association-mapping panel, which can be used as part of a cascade of technologies³⁵ to detect causative variants of quite small effect with great power. These variants can then be used as targets for genome editing. Only small numbers of editing events are required to make substantial improvements in genetic gain. In plant breeding, the number of genetically distinct individuals in production is much smaller than in animal breeding (Fig. 2), so a directly comparable approach to PAGE in animals may not be as applicable. However, in many minor and so-called ‘orphan’ crops with less advanced breeding programs, the cultivars released for pro-

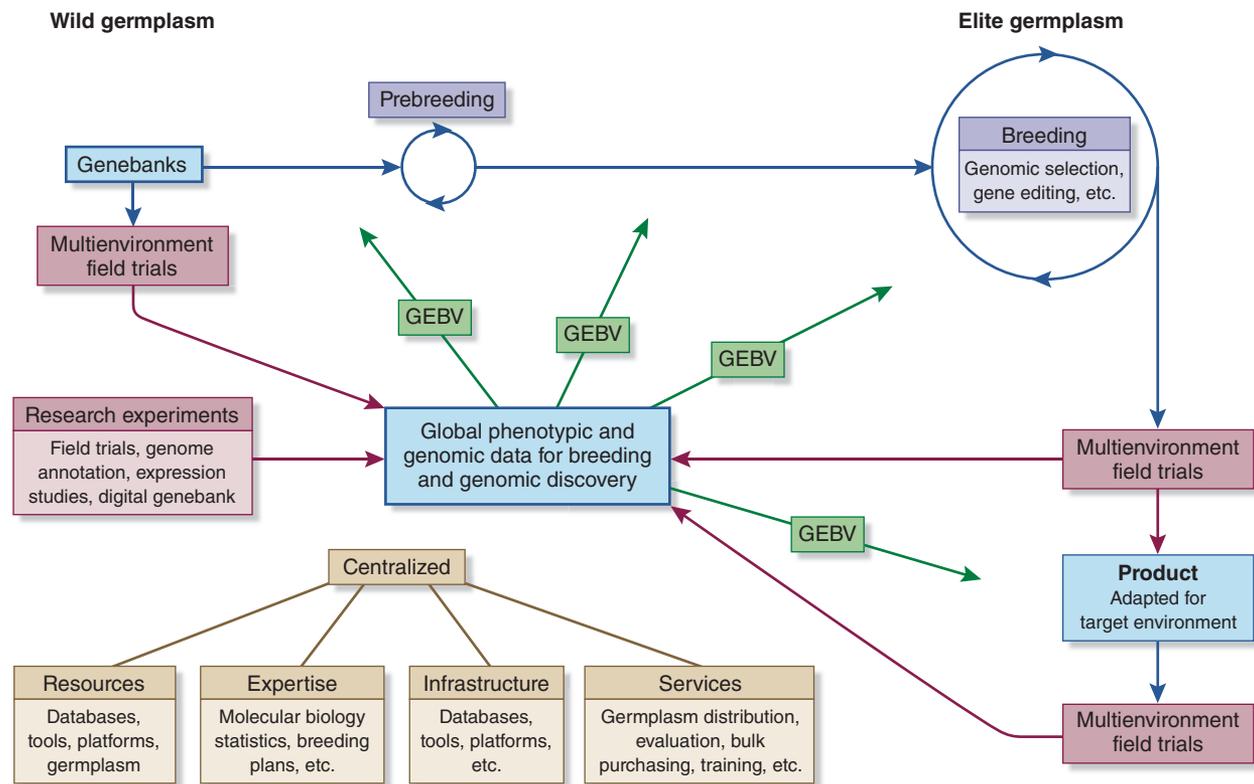


Figure 4 Framework for combining approaches. Capturing new opportunities to accelerate the pace of genetic gain based on efficient and targeted access to genetic diversity, coordinated phenotyping across environments, cost-effective sequencing, genomic prediction and genome editing.

duction can be quite genetically diverse. If relevant phenotypic data can be collected for individuals of these cultivars, there may be an opportunity to introduce PAGE-like methods more rapidly in such cases. This might apply, for example, to some tree species.

Integrating plant and animal breeding approaches

The various plant and animal species used in agriculture have different biological systems and are farmed in different environments or within different economic settings. Thus, they require breeding programs that are specifically tailored. However, the underlying principles of breeding programs are common, and generic approaches could be devised for local deployment and adaptation. Recently, Gaynor *et al.*³⁶ proposed the reorganization of traditional plant breeding programs for inbred or hybrid crops into two distinct parts as a strategy for implementing genomic selection (Fig. 3). The first is a population improvement element that develops improved germplasm. The second is a product development component that identifies new inbred varieties or parents for hybrids. The first part is highly analogous to a classical animal breeding program based on recurrent selection and could make use of all of the tools and techniques that are well established in that domain. These include optimal contribution theory, economic selection indices, short generation intervals, multiple-trait evaluation and selection techniques that are not widely used in plant breeding. The second part is highly analogous to a classical plant breeding program and could similarly make use of all the tools and techniques that are well established in that field, supplemented by careful use of genomic selection. Stochastic simulations showed that program using the two-part strategy generated a rate of genetic gain more than 2.5 times that

of the conventional program and nearly 1.5 times that of the best performing program using an alternative genomic selection strategy based on a standard plant breeding program design for the same cost and in the same amount of time (Fig. 3). The results also illustrate the synergy that can be realized by integrating plant and animal breeding approaches under the umbrella of a common platform.

In plant breeding, there has been a proliferation of powerful high-throughput phenotyping technologies in recent years, which are enabling more accurate characterization of traits and environments along time series³⁷. The expertise in the analysis and utilization of these data and the long-established expertise in the integration of physiological models and quantitative genetics models³⁸ are some examples, of which there are many, of the types of thinking, tools and technology that are common in plant breeding and that could be translated into animal breeding.

Unification of breeding and biological research

Access at unprecedented scales to large-scale sequence and phenotypic information will also provide opportunities to unify discovery biology and breeding. In other words, breeding programs will become test beds for hypotheses, as well as platforms for development and deployment of new varieties and breeds of livestock and fish. The largest impact of such developments will be in the areas of quantitative or complex traits that have been less amenable to reductionist approaches (as breeders now have ways of predicting the effects of causative factors through genomic selection); these developments are likely to deliver major benefits to crop and animal improvement programs. In this way, genomic selection may catalyze a unification of breeding methods, tools and technologies across several

plant and animal species, which in turn can advance the modernization of other aspects of breeding programs. These advances could include the widespread adoption of clearly defined breeding goals, economic selection indices for selection over multiple traits, objective quantification of genetic gains, modeling, new trial design and analyses, and the efficient optimization of resources that underpin both breeding and biological discovery research.

Conclusions

The greatest and most immediate opportunity for the application of genomic selection is in the developing world where the demands and needs are greatest². The recently launched Excellence in Breeding Platform of the CGIAR (see URLs) is designed to create economies of scale and to unify breeding ideas, technology, resources, and demand and capacity across species and systems, which will modernize breeding programs that are focused on meeting the needs of smallholder farmers in the developing world. This approach, summarized in **Figure 4**, embraces many of the concepts outlined in this article and is designed to deliver innovative step changes in the rate of genetic gain for crops, livestock and fish of relevance to the developing world.

The successful implementation of genomic selection for the delivery of public goods to the developed and developing world will require a strategic approach in the design of breeding programs, greater collaboration, new partnerships that span the public and private sectors, and new skills. However, the impact of genomic selection may extend beyond the creation of new crop varieties and improved livestock to include an integrative framework for simultaneous delivery of both scientific discoveries and new products for the developing world. This may represent the biggest incentive for enhanced and global coordination of funding to support modern plant and animal breeding programs.

URLs. CGIAR Excellence in Breeding Platform, <http://excellenceinbreeding.org/>; Genomic bulls in the Netherlands and their impact on the population, http://www.interbull.org/static/web/7_3_deJong.pdf.

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AUTHOR CONTRIBUTIONS

T.C., I.M., J.M.H. and W.P. jointly developed the ideas and wrote the paper.

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