

CAN GRAZING LIVESTOCK IN DEVELOPING COUNTRIES BENEFIT FROM USE OF GENOMIC SELECTION?

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SUMMARY

Genomic selection is transforming animal and plant breeding across developed countries globally, with economic benefits of billions of dollars annually. Despite huge potential for livestock industries in developing countries to achieve similar transformations, to date there has been very limited use of genomic selection in grazing livestock in those countries. This is attributable to several major challenges. This paper discusses those challenges and proposes options to overcome or reduce them. It also identifies priority areas of research that must be undertaken if grazing livestock in developing countries are to benefit from genomic selection. Achieving genetic gains through genomic selection in smallholder cattle herd in Southern Africa and opportunities to extend the concept to other livestock species, and other developing countries, is also briefly examined.

INTRODUCTION

The world's population is predicted to increase from 7 billion in 2011 to 9 or 10 billion by 2050, with most growth occurring in Africa and Asia (Gerland *et al.* 2014). Incomes of many people in these countries are increasing, and with rising incomes, demand for meat and dairy products is also increasing. The increased demand is predicted to continue through to 2050 (Delgado *et al.* 1999). This presents a major opportunity for livestock industries in tropical and sub-tropical environments where ruminant species consume pastures that have few alternative economical uses.

To capture these opportunities, livestock enterprise and industry efficiency must increase by 2.0-2.5% p.a., equivalent to doubling outputs from constant resources over the next 35 years (Mullen 2012). Due to pressures on agriculture in developed countries and the developing world's requirement for high volumes of low-cost food, much of that increased production must occur in the regions of greatest need i.e. Africa and Asia. This increased demand for food is leading to greater competition for inputs such as land, water, fertilizer, grain and labour, driving up costs of livestock production. Climate change is predicted to add to the challenge (Hughes 2003), requiring livestock that are productive under hotter and drier climates and, in the tropics and sub-tropics, requiring animals which tolerate increased ecto- and endo-parasitic burdens and vector-borne diseases.

To double outputs from constant resources by 2050, farmers need to adopt cost-effective, transformational technologies for use in animals that are well adapted to their production environments. Traditional technologies delivering incremental changes will assist in improving productivity, but use of genomic information in proven genetic improvement methods could accelerate the required productivity improvements by increasing the rates of genetic gain for all economically important traits in livestock.

Genomic selection is the use of genome-wide genetic markers to estimate the genetic merit of individual animals (Meuwissen *et al.* 2001). Genome wide markers are required to capture variation

from all the mutations affecting complex traits such as yields and fertility. Recently Meuwissen *et al.* (2016) reported that most economically important traits in livestock are affected by somewhere between 2,000 and 10,000 genes. Single Nucleotide Polymorphisms (SNPs) are the markers most commonly used in genomic selection, owing to low cost of genotyping and ability to genotype tens or hundreds of thousands of SNP in a single assay. Genomic selection therefore estimates the effect of all the SNP on the target trait simultaneously. Genomic selection is now transforming animal and plant breeding across developed countries globally, with enormous economic benefits. However there are no known examples of the successful use of genomic selection in grazing livestock in developing countries. This paper examines the constraints to use of genomic selection in those countries and explores opportunities to overcome them particularly in ruminants (beef and dairy cattle, sheep and goats) grazed at pasture in the tropics and sub-tropics where the greatest opportunities for productivity improvements also exist.

CONSTRAINTS TO USE OF GENOMIC SELECTION IN DEVELOPING COUNTRIES

In this paper we exclude ongoing development of the genomic selection methodology per sé as there are highly-competent research groups around the world undertaking such development. We are confident they will overcome any methodology issues, probably well ahead of development of solutions to other constraints that discourage the use of genomic selection in developing countries. Several of those constraints are also common to extensive livestock production systems in developed countries. The constraints and possible solutions are discussed briefly below.

Lack of phenotypes recorded in accurately-defined contemporary groups. In developed and developing countries, the major constraint to use of genomic (and conventional) selection in livestock is the difficulty and expense of accurately identifying appropriate fixed effects and contemporary groups and measuring the full range of economically important productive and adaptive traits required to achieve a well informed and balanced breeding objective. As discussed by Burrow and Henshall (2014), technology may in future provide a way of measuring animals, but it cannot replace the statistical imperative that, for the measurements to be meaningful, contemporary groups of appropriate structure and sufficient size are required. In extensive production systems and in developing countries, this presents difficulties in both managing and routinely recording large cohort groups. However if the design is inadequate in terms of contemporary group size and structure, the measurements will not provide useful predictions of genetic merit. This is perhaps the greatest constraint for smallholder farmers in developing countries, as often they own only a small number of breeding animals and they generally practice year-round joining.

To overcome this constraint, reference populations which are specifically designed to accurately manage and record animals within contemporary groups and capture data for the traits of interest have been established in some developed countries to exploit the opportunities provided by genomic selection. Examples of these populations in beef cattle are described by Upton *et al.* (2001) for growth, feed efficiency and carcase and beef quality and Burrow *et al.* (2003), Barwick *et al.* (2009) and Johnston *et al.* (2009) for the full range of productive and adaptive traits in the breeding objective. Van der Werf *et al.* (2010) and Swan *et al.* (2012) describe similar populations designed to capture data for a range of productive attributes in meat and wool sheep. A large study in the USA also developed specific populations to record resistance or susceptibility to Bovine Respiratory Disease in both beef and dairy cattle (BRD CAP 2017).

In future, Meuwissen *et al.* (2016) anticipate that accuracy of within-breed genomic selection will be achieved by use of very large within-breed reference populations. Alternately, genomic selection may be applied across-breeds, with accuracy obtained from across-breed reference populations and high-density genomic selection methods focusing on causative genomic regions discovered through programs such as the 1000 bull genome project (Hayes *et al.* 2014). In their

opinion, it is highly likely that future applications will increasingly turn towards across-breed genomic selection (Meuwissen *et al.* 2016). This has considerations for application of genomic selection to developing countries as discussed in a later section of this paper.

Pedigrees and relationships. The benefits from knowledge of pedigree are well understood, allowing progeny test or BLUP-based selection in preference to selection on phenotype. In other than an intensive management system though, the costs are significant. Genomics provides a genuine alternative to the labour-intensive practices of single-sire mating and mothering-up, with the proviso that genotyping is cost-effective. The cost of the cheapest DNA assays on the market are now of the same magnitude as the cost of obtaining a tissue sample and of data management, and the cost of moderate-density SNP assays is not much more. With a thousand-SNP panel, parentage assignment is trivial. With a slightly larger (tens of thousands) SNP panel such as those used for genomic selection, it is not necessary to estimate discrete pedigrees at all, with relationships based solely on genomic similarity (Meuwissen *et al.* 2001).

Creating genetic linkages across livestock populations. Establishing large reference populations where expensive or hard-to-measure traits are routinely measured in accurately-defined contemporary groups requires that genetic linkages be created with the seedstock and commercial livestock populations targeted for genetic improvement. The best way of achieving these genetic linkages is through widespread use of artificial insemination (AI), though there are difficulties with AI programs under both extensive production systems and in developing countries. However as has been shown in the beef industry in northern Australia, where beef producers are prepared to put in the effort, successful AI programs are feasible. Another option for consideration where breeding populations are within relatively close proximity is to rotate sires amongst the breeding herds/flocks so genetic linkages are created through natural mating. Very importantly, the concept of genetic linkage changes with genomic information. When genomic information is available, what is needed is for chromosome segments to be represented across herds and environments, not sires or relatives *per se*. This is one of the advantages of genomic selection: it may be much easier to have chromosome segments, from a common ancestor quite a number of generation ago, represented across herds and environments, rather than progeny of link sires.

Need for consistent trait definitions across livestock populations. When designing resource populations for use in genomic selection programs, consideration must be given to trait definitions, to ensure that animals in multiple populations are recorded for the same trait(s). Alternately the resource populations need to be large enough to allow estimation of genetic correlations with indicator traits, if consistent recording of the same trait(s) cannot be achieved across all populations. Again, estimating these genomic correlations and genotype by environment interactions becomes more straightforward with genomic information, as what is required is observations of the traits/environments on common chromosome segments, rather than sires progeny (Visscher *et al.* 2014; Hayes *et al.* 2016).

Lack of infrastructure and human capacity. Two problems of major significance in developing countries are: a) the lack of infrastructure required to undertake all aspects of a genomic selection program including on-farm management and phenotyping, laboratory testing of animal samples, data capture and storage and lack of computing facilities etc.; and b) lack of human capacity, particularly in areas of technological capability and data analysis and interpretation.

Possibility of Genotype x Environment interactions. Livestock breeders, and particularly those in developing countries in the tropics, need to be cognisant of the possibility of Genotype x Environment (GxE) interactions which could arise from vastly different markets and/or production systems. An earlier review of the literature concluded that GxE interactions were problematic if poorly adapted breeds were compared across temperate and tropical environments, but they were unlikely to be a problem in tropically adapted beef cattle and sheep grazed in either temperate or tropical environments (Burrow 2012). However that review was based on production systems that

aimed to optimise female reproductive performance and achieve premium meat market specifications from sale animals. It did not include consideration of vastly different market endpoints e.g. targeting high-value meat markets in developed countries *cf.* production of high volumes of low-cost meat in the beef, sheep and goat industries of many developing countries. A similar example can be found in the dairy industry, where ‘high-performing’ genetics now used very widely across developed countries globally are often found to be sub-optimal when used in low-input dairy farms in developing countries.

Difficulties of negotiating collaborative research agreements. An important constraint which must be considered during development of any research collaborations is the much greater difficulty and complexity of completing formal research agreements in developing countries (*cf.* those in developed countries). In the authors’ experiences in different developing countries, completion of the formal agreements can sometimes take several years longer than anticipated (which also often means the research needs in the draft agreements have substantially changed in the interim period).

OVERCOMING THE CONSTRAINTS: PHENOTYPING AND GENOTYPING USING BEEF CATTLE EXAMPLES FROM SOUTHERN AFRICA

As flagged by Meuwissen *et al.* (2016), improved accuracy of genomic selection will be achieved in future by use of very large within- or (more likely) across-breed reference populations. The within-breed approach has already proved very successful in dairy and other livestock industries in developed countries. However it is not clear how farmers in developing countries could establish such reference populations due to a lack of both funding for phenotyping and genotyping and technical capacity to design and manage the populations within appropriate contemporary groups. Maiwashe and Banga (2013) suggested that in terms of funding, genotyping and phenotyping should be considered as international and national responsibilities respectively. But livestock farmers in developed countries had already adopted a more commercially-oriented ‘user-pays’ approach. Subsequently though, the South African government (through its Technology Innovation Agency - TIA) initiated a ‘Beef Genomics Program’ (BGP) in 2014 (and a similar program for dairy cattle in 2016 and potentially also for sheep and goats in future) in conjunction with seedstock breeders in South Africa and other Southern African countries, with the aim of developing within-breed reference populations designed to capture the phenotypes and genotypes necessary for genomic selection.

Beef Genomics Program (BGP) in Southern Africa. Currently, seedstock cattle breeders in Southern Africa use different genetic evaluation services and breeders aligned with the different service providers therefore use different approaches to phenotyping and genotyping. Under TIA funding guidelines, each breed society develops its own strategy with respect to use of genomic information. In 2016, 12 cattle breeds (Afrikaner, Beefmaster, Bonsmara, Boran, Brahman, Charolais, Drakensberger, Hereford, Limousin, Santa Gertrudis, Simbra and Simmental) were actively participating in the BGP with Brangus, Nguni and Tuli anticipated to participate from 2017 (Becker, 2016).

Beef cattle breeds aligned with SA Stud Book (26 breeds comprising 60% of registered beef cattle in South Africa, with the Bonsmara being the predominant breed; Stud Book, 2017) are currently focusing on genotyping primarily Bonsmara, Beefmaster and Drakensberger animals which already have Estimated Breeding Values (EBVs) for growth, feed conversion ratio and reproduction traits. Growth and reproduction phenotypes are recorded on the properties of birth of the animals, while feed efficiency is measured on selected bull calves from each on-farm weaning cohort in central bull testing stations. This approach means the phenotyping costs for existing phenotypes are met directly by the seedstock breeders, whereas the genotyping costs are met by the BGP. As a result, proof-of-concept for genomic selection will be demonstrated with the accuracy of available EBVs being marginally increased in these breeds with the inclusion of genomic

information. However phenotypes for other economically important traits such as carcass and meat quality and adaptation are not currently recorded in those breeds, though it is likely they will be included in the anticipated next round of funding in 2018.

The Livestock Registration Foundation (LRF) represents the remaining 40% of registered beef cattle in South Africa, 80% of registered beef cattle in Namibia and 100% of registered beef cattle in Zimbabwe. These breeds have collectively agreed to undertake a 3-year program to collect data in structured contemporary groups using AI or natural mating across designated seedstock herds. All breeds are working at establishing a biobank for storage of DNA samples and genomic reference populations for each participating breed. The LRF breeds are focusing on establishing new phenotypes for traits which are economically important to measure (e.g. feed efficiency, carcass and meat quality and non-traditional measures of reproduction), as well as developing stronger genetic linkages between and within breeds across countries. They also intend to examine the potential for cross-continent genetic evaluations and cross-breed genomic evaluations (Becker 2016).

One genuine opportunity for Southern Africa, to overcome the difficulty of maintaining very large resource populations with accurate phenotypes and matching genotypes for all economically important traits derived from accurately-defined contemporary groups, would be to deliberately create genetic links with existing beef cattle resource populations in developed countries such as Australia. Australian resource populations could include: a) the Beef Information Nucleus (BIN) herds which comprise a nation-wide progeny test program for five cattle breeds, developed collaboratively by seedstock breeders and cattle breed societies in conjunction with Meat and Livestock Australia (MLA; Beef Information Nucleus 2017); and b) the MLA-funded 'Repronomics®' project which is building on the cattle and extensive phenotypic and genotypic databases from the previous Beef CRC herds (Johnston *et al.* 2009) to specifically develop new female reproductive traits using a combination of female and male reproductive traits, novel molecular genetics approaches and innovative application strategies (Johnston 2016). This type of collaboration may also have the added benefit of addressing and at least partially overcoming the lack of laboratory infrastructure that is a common constraint in developing countries.

If it was possible to achieve cross-country collaborations to allow pooling of phenotypes based on common definitions of traits and matching genotypes derived from genetically-linked and accurately-defined contemporary groups, significant benefits would be created for the cattle industries of all partner countries due to a previously unstated constraint that breeders of tropical beef cattle in Australia and Africa have few alternatives to link with other cattle breeds in a similar way that breeders of temperate breeds have done in developed countries to maximise the numbers of animals, thereby sharing the costs of phenotyping and genotyping more broadly, whilst also significantly increasing the accuracy of genomic selection. However significant new research would be needed to benefit the full range of economically important traits and livestock breeds.

OVERCOMING OTHER CONSTRAINTS

Genetic/genomic linkages across livestock populations. Assuming cross-country collaborations can be negotiated as suggested above, there will be a need at the outset to specifically design the extent of genetic and genomic linkages required across the different resource populations.

Use of consistent trait definitions. Generally 'traditional' phenotypes such as weights and weight gains tend to be consistent across different resource populations. However for most economically important traits there will be a need for further research to either estimate genetic correlations between alternative measures of the traits or to re-define measurements using common definitions to allow valid use of genomic selection across the populations. In beef cattle this would require investigation of alternative measures of male and female reproductive traits, bull traits as indicators of male and female reproduction, alternative measures of carcass and meat quality attributes, feed intake and feed efficiency and cost-effective methods of measuring cattle resistance

to environmental stressors such as parasites, diseases and high temperatures and humidity.

Lack of human capacity. As indicated by Maiwashe and Banga (2013), where genomics research has occurred in developing countries, it has tended to focus on ‘low-hanging fruits’ that are also relatively low-cost e.g. use of SNP data to select against genetic defects, breed characterisation, selection for individual heterozygosity to manage inbreeding, parentage verification and individual SNP associations with phenotypes based on relatively small numbers of animals, with the latter primarily being part of PhD-level training. However the technical capacity required to design and fully implement a genomic selection program is now largely lacking amongst livestock researchers in many/most developing countries, primarily because to date there simply has been no need for such expertise. If it was possible to collaborate with developed countries to implement genomic selection across resource populations as suggested above, then the lack of technical expertise would become a critical deficiency. That deficiency could be overcome either by outsourcing the essential services to a developed country with appropriate expertise (not desirable from a developing country perspective) or implementing intensive training programs, ideally with staff from the developing countries visiting international laboratories to undergo the essential training. A particular need identified in Southern Africa is that training in genomic selection and selection indexes needs to occur across all levels from university through to technical and industry levels.

Technical capacity is also required for the development of some phenotypes such as ovarian and carcass ultrasound scanning, measurement of indicators of male reproductive performance, animal body-condition scoring, measurement of meat quality attributes etc. as well as mentoring and quality assurance training for the intermediaries who will ultimately become responsible for training farmers and farm workers.

PRIORITY RESEARCH AREAS

Assuming it is possible to overcome most of the constraints identified above (as we believe to be the case), several priority research areas would need to be addressed to develop and implement a genomic selection program for breeders of grazing livestock across developing and developed countries. The first priority is to establish large reference populations, with animals measured for the target traits and genotyped in appropriate environments. Then priorities include:

Cross-country genetic/genomic evaluations. Estimates of genetic/genomic relationships would need to be developed for the full range of economically important traits included in the pooled phenotypes and genotypes. This would include examining the scope for combining data across countries for multi-trait genetic/genomic evaluations at a trait by country level to inform an understanding of the differences and similarities of traits not recorded identically in different countries. There would also be a need to construct joint G matrices to inform the capacity for joint single-step analysis. Assuming it is feasible, joint single-step analyses could then be undertaken to deliver prototype cross-country joint evaluations. A logical next-step from joint single-step analyses would be the coordinated use of young sires initially within breeds across countries and possibly through shared use of the MateSel program (MateSel 2017). Protocols for the coordinated use of young sires would be informed by the joint G matrix and joint evaluation results.

Use of sequence data in genetic evaluations. A number of research areas could be undertaken to promote the use of genomic selection in developing countries. Specifically with regard to potential collaborative beef research across Australia and Africa described above, this might include:

- Development of a new low-cost SNP chip for use in *Bos taurus*, *Bos indicus* and tropically adapted *Bos taurus* breeds (the southern African Sanga breeds and the West/East African taurine breeds). This would allow an improvement in the accuracy of genomic EBVs across the range of cattle breeds, composites and their crosses used on both continents;
- Development of computationally efficient genomic evaluation algorithms that utilise whole

genome sequence data suitable for multi-breed and crossbred evaluations. As demonstrated by Kemper *et al.* (2015) and Macleod *et al.* (2016), using 50K SNP genotypes and BLUP methodology does not enable genomic estimated breeding values that work across breeds and in crossbreeds/composites (i.e. do not result in increased accuracy in composites when information from the founder breeds are included). Much higher density of markers (up to whole genome sequence) enables multi-breed predictions where breeds not in the reference set, or with only limited numbers in the reference set, can achieve more accurate genomic evaluations;

- Detection of embryonic lethal and other deleterious mutations in the major breeds used in Africa and Australia based on a haplotype analysis to examine if there are regions in the genome where some haplotypes are never observed in a homozygous state, despite the frequencies of these haplotypes being high enough that multiple animals are expected to be homozygous for the haplotypes.

Multi-breed genomic evaluations. Within breeds, accuracy of genomic selection depends on the number of animals in the reference population and strength of linkage disequilibrium (LD) and family relationships between the reference and selection candidates. Across breeds, factors such as differences in LD, allele frequencies and SNP effects between breeds also impact on the accuracy. Pooling reference populations across breeds appears to be a promising method to increase the size of the reference population, particularly in numerically smaller populations, with the proviso the populations being pooled are not genetically distant (Kizilkaya *et al.* 2010). This component of the research would: i) use deterministic methods to determine the prediction accuracy with smaller numbers of genotyped animals before incurring high costs of large-scale genotyping; and ii) undertake a formal breeding program design to determine the feasibility of pooling data across multi-breed populations across continents. Assuming it is feasible to pool data across breeds, the research would also examine options to implement a single-step, multi-breed genomic evaluation.

Selection indexes and GxE interactions. This would involve two elements: i) definition of production system x target market examples on a breed x country basis to determine the extent of differences/similarities between and across objectives in the different regions; and ii) if appropriate, extension of the selection index modelling to include new traits relevant to the production marketing systems for the particular grazing livestock.

APPLICATION OF RESULTS TO SMALLHOLDER FARMERS IN SOUTHERN AFRICA

Once genomic selection is implemented in southern African commercial herds, it will then be relatively straightforward to transfer the benefits of improved genetic gain to smallholder farmers using bulls and semen from superior sires in schemes similar to the ARC's 'Kaonafatso ya Dikgomo' (KyD – animal recording; KyD 2017) scheme in South Africa. Currently the KyD scheme is assisting smallholder farmers across all provinces in South Africa to continually improve their cattle production through recording and monitoring productivity and profitability and providing advice on production, animal health and marketing.

OPPORTUNITIES TO EXTEND THE COLLABORATIONS TO OTHER DEVELOPING COUNTRIES AND OTHER LIVESTOCK SPECIES

Assuming results from the multi-breed genomic evaluations mentioned in the research section above indicate feasibility, there is good potential to extend the BGP concept to other African countries such as Kenya and West Africa in partnership with the International Livestock Research Institute. However the cattle breeds commonly used in East and West Africa are not the same as those participating in the BGP across Northern Australia and Southern Africa, so achieving an expansion in tropically adapted beef resource populations to other countries will also depend on the development of the proposed SNP panel for African and other cattle breeds as described above.

Plenary IV

Opportunities also exist to expand the concept to other livestock species, including planning already underway to establish sheep resource populations across Australia and South Africa.

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