



Genetic improvement of beef cattle through opportunities in genomics

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ABSTRACT - Genomics will improve the efficiency of beef cattle genetic improvement programs through the incorporation of genomic predictions into traditional genetic evaluations. The global dairy cattle breeding industry has been changed considerably in the last year through the implementation of genomic selection. Now proven to work in dairy cattle breeding, the challenge remains for the beef industry to successfully implement this technology. The primary challenge in beef cattle is the required resource population that relates genomic profile to phenotypic performance, which is quite large and its establishment will require collaboration or a significant investment by any one enterprise. Another challenge in beef cattle is the requirement for genomic predictions to function across breeds, which will require denser marker panels. Opportunities to increase genetic progress include increased accuracy of selection, reduced generation interval, increased selection intensity and better utilization of limited recording capacity, such as individual feed intake, along with opportunities to genetically change novel traits. Implementation of a low density panel at the commercial level will allow informative decisions based on genetic potential at all levels of the production chain. This reduced panel will include predictive SNP based on fine QTL mapping efforts, combined with additional SNP to enable imputation of genotypes from a high density SNP panel, when combined with high density genotypes of key ancestors, such as sires. With electronic recording in cattle, a single genotyping event on each animal would provide information throughout the beef production chain, which will create the incentive for genetic change. Genomics will create new opportunities for reproductive technologies such as embryo transfer as elite females will be identified with increased accuracy. Potential changes to the structure of the breeding industry are discussed including changes to recording strategies and the development of novel beef products.

Key Words: breeding strategies, DNA, genomic selection, phenotype, recording, single nucleotide polymorphisms

Melhoramento genético de bovinos de corte utilizando informações da genômica

RESUMO - A genômica oferece um caminho para melhorar a eficiência dos programas de melhoramento genético de gado de corte por meio da incorporação de predições genômicas do mérito genético nas avaliações genéticas tradicionais. A indústria global de melhoramento de gado leiteiro mudou consideravelmente no último ano pela implementação da seleção genômica. Com a confirmação de que ela funciona no melhoramento de gado leiteiro, o desafio continua para a indústria de gado de corte a fim de implementar com sucesso esta tecnologia. O maior desafio para a implementação em gado de corte é a população-referência, que relaciona o perfil genômico com o desempenho produtivo. A população-referência necessária é bastante grande e o seu estabelecimento requer colaboração ou investimento significativo de qualquer entidade. Outro desafio no gado de corte é a necessidade de que as predições genômicas funcionem entre as diversas raças, o que exigirá painéis mais densos de marcadores genéticos. As oportunidades de incrementar o progresso genético incluem o aumento da acurácia de seleção, a redução do intervalo de gerações e o aumento da intensidade de seleção, além de melhor capacidade limitada de medição de certas características, como consumo alimentar individual e criação de oportunidades de mudança genética em novas características. A implementação de um painel de baixa densidade em nível comercial permitirá decisões mais informadas, baseadas no potencial genético em todos os níveis da cadeia de produção. Este painel reduzido incluirá SNP preditivas, baseadas em esforços de mapeamento fino de QTL, combinadas com SNP adicionais para permitir a imputação de genótipos de um painel de SNP de alta densidade, quando combinado com os genótipos do painel de alta densidade de ancestrais importantes, tais como touros. Com a medição eletrônica em gado de corte, uma simples genotipagem de cada animal fornecerá informação através de toda a cadeia de produção, o que, em contrapartida, criará um incentivo para mudança genética. A genômica criará novas oportunidades para tecnologias reprodutivas, como a transferência de embriões, pois as fêmeas elite serão indetificadas com mais acurácia. Mudanças potenciais na estrutura da indústria de melhoramento animal são discutidas, incluindo oportunidades para reduzir custos de obtenção de touros superiores, mudanças nas estratégias de medição fenotípica e desenvolvimento de novos produtos cárneos.

Palavras-chave: DNA, estratégias de melhoramento, fenótipo, gravação, polimorfismos de nucleotídeo único, seleção genômica

Introduction

The genetic improvement of beef cattle has been sought as a means to improve production efficiency for many decades. These efforts have been successful, as published genetic trends attest to. These gains in genetic progress are in traits that comprise the recording and evaluation program. Such traits are those that are obtained relatively easily, at low cost and are useful for cattle management. These traits include weight traits such as birth weight, weaning weight, yearling weight and mature cow weight. In addition, traits related to calving ease, birth dates and breeding dates can form the basis of fertility evaluations. Through large scale recording programs, genetic improvement supported with genetic evaluation programs implementing the animal model have made genetic improvement of these traits possible.

In addition to these traits that are a part of mainstream recording programs, improvement of additional traits such as carcass traits has also been made possible with more dedicated recording efforts. Sire evaluations are of primary interest due to the impact sires can have through many progeny. Effective sire evaluations have been enabled through structured progeny tests. Subsequently, ultrasound has been employed as a predictor of carcass merit. Since its implementation in the 1990's ultrasound has become the primary source of information related to carcass traits. Multiple trait models now allow ultrasound and carcass traits to be combined into multiple trait predictions of carcass merit.

Beyond traits that are measurable in either structured progeny tests or through routine herd recording are a set of traits that are potentially very important, but inherently difficult or expensive to measure. Two excellent examples of these are feed efficiency and beef tenderness. Beef tenderness is the single most important palatability trait (Miller et al., 1995; Smith et al., 1995). Beef tenderness has a significant genetic component with approximately 30% of the variation in tenderness being explained by additive gene effects within a single breed (Koch et al., 1982), which is greater than variation found among breeds (Wheeler et al., 1996). Heritability of beef tenderness found within the University of Guelph population has been estimated at 0.19 (Zwambag, 2007). Feed efficiency is also a trait that is economically very important with genetic variation reported in many studies indicating improvement is possible if measurements are available (Arthur et al., 2001; Schenkel et al., 2004). However, efficient selection programs are limited, as both feed intake and beef tenderness are expensive to measure on an industry-wide basis.

Genetic improvement programs as described above have been effective. A study by Devitt (2003) has identified an improvement of \$5/steer/year considering the genetic change in each trait and the economic value of that trait in a genetic improvement program. Although this improvement is significant it is far from that seen in other species such as poultry (Havenstein, 2003). This paper presents opportunities enabled through genomics to facilitate improved rates of genetic progress, as well as genetic change for the inherently difficult traits such as feed efficiency, in the beef cattle industry.

From candidate SNP to genomic selection

The last decade has seen exponential growth in the development of genomic tests for economically important traits in beef cattle improvement. What started as a few SNP markers for beef quality traits has developed into a number of panels of SNPs for a range of traits in the last half decade. Much of this increased development output can be attributed to rapidly changing technology and the sequencing of the bovine genome (Elsik et al., 2009) resulting in dramatic reductions in genotyping costs. In 2005 research took a major leap forward with the first large SNP panel for cattle, the ParAllele 10K chip (Barendse et al., 2007; Sargolzaei et al., 2008). Following this the Illumina Bovine SNP50 bead chip was released, greatly reducing the cost per genotype and replacing the 10K chip in practice (Matukumalli et al., 2009).

The first DNA tests to be commercialized were based on the discovery of SNP based on a candidate gene approach. This approach has been very successful in finding SNP associated with tenderness, for example. Two competing companies are currently marketing genetic tests with predictive properties for beef tenderness (www.igenity.com and www.pfizeranimalgenetics.com). These tests involve primarily 2 major genes related to beef tenderness, Calpain and Calpastatin, although the tests are being improved with additional SNP being added. The best public source of information for development of these commercial tests is the National Beef Cattle Evaluation Consortium (www.ansci.cornell.edu/nbcec). Studies of the candidate genes involved in the calpain and calpastatin pathway have resulted in the discovery of a number of additional SNP linked to both calpain and calpastatin (Page et al., 2002; Page et al., 2004; Casas et al., 2005; White et al., 2005; Casas et al., 2006; Schenkel et al., 2006). Further work has identified that calpastatin has many SNP and additional SNP will help explain more genetic variation in tenderness (Casas et al., 2009). Despite the extensive work on the calpain-calpastatin system, it is clear that there are many additional genomic

regions with a significant association with beef tenderness, indicating that a few SNP in major genes will not explain all of the variation in a trait under selection.

Following these early developments with a few candidate SNP affecting primarily carcass traits, the implementation of the Illumina Bovine SNP50 Beadchip has enabled the application of genome wide Marker Assisted Selection (MAS). The genomic regions which influence the traits are termed Quantitative Trait Loci (QTL). Selection for these QTL are possible by having a test for a causative mutation in a gene (QTN, Gene Assisted Selection, GAS such as the CAST and CAPN1 described above for beef tenderness) or in a genetic marker in linkage with the QTL, Marker Assisted Selection (MAS). This genetic linkage is known as Linkage Disequilibrium (LD) and occurs when two loci are sufficiently close on the genome that recombination during meiosis between them is rare, and segments of chromosome are conserved from parent to offspring. Selection on the linked marker results in a correlated response in the trait of interest. The use of LD in selection is discussed in more detail in Goddard and Meuwissen (2005). These large panels of SNP at reduced cost have allowed the establishment of “Genomic Selection” strategies which are described in Goddard & Hayes (2007) and different approaches are being researched to determine how to directly utilize these dense SNP sets for “genomic selection” (Schaeffer, 2006, for dairy cattle).

Genomic selection in dairy cattle

Results from the bovine SNP50 array have been quite promising in dairy cattle and it is clear that genomic selection is indeed working with excellent results within breed (Cole et al. 2009; Hayes et al. 2009; Schenkel et al., 2009). Countries have officially been adopting genomic evaluations around the world, with the implementation of this technology being called the largest single technological change to influence the dairy breeding industry since frozen semen made widespread AI and progeny testing possible a half century ago. The dairy breeding industry has experienced a revolutionary change. The dairy industry was able to make such massive gains due to their readily available source of DNA (semen) and highly accurate estimates of breeding value based on daughter performance. Canadian results are demonstrating a 32% improvement in accuracy due to genomics over parental average breeding values that would be available on a bull at birth (Schenkel et al., 2009). Similar results were found for type traits with a reduced advantage for traits of lower heritability such as fertility and calving ease. The beef breeding industry has the advantage of learning from the dairy industry’s experience. The question

is no longer “does it work?”, but “how are we going to make it work in beef cattle”?

With the implementation of genomic selection in dairy cattle there has also been a significant change in breeding program design and structure. Firstly, highly proven sires were affected very little through the inclusion of genomics into breeding value prediction as their proofs were already highly accurate. However, genomics had a significant impact on the ranking of cows and in Canada to be ranked on the Lifetime Profit Index (LPI), cows need to be genotyped. These evaluations are available online at the Canadian Dairy Network (www.cdn.ca/files_ge_articles.php). Unlike sires that have very accurate proofs based on many daughters evaluated across a number of different herds, cow evaluations are based on a limited number of lactation records that can be influenced by environmental factors such as preferential treatment of targeted cow families. When selecting dams or sires, genomics has elucidated more clearly the true genetic difference between selection candidates. The implementation of genomics has changed the top LPI list of cows, highlighting additional selection candidates outside of those previously considered. Since the implementation of genomic selection, AI companies have started to market teams of 5-10 young bulls with no progeny records. These young sires are selected based on their genomic enhanced proof. The effective accuracy of these teams approaches that with proven sires reducing the risk associated with an individual young bull (Chesnaix 2010). These changes to how elite cows are identified and young sires are marketed are dramatic. Changes to the structure of the beef breeding industry as a result of the implementation of genomics will surely be dramatic as well. Some of these potential changes are described in more detail later in this paper.

Genomic selection in beef cattle

The very promising results in dairy cattle are based on within breed predictions. However, when the interest is to predict across breeds, a modified approach is required as prediction equations developed in one breed have been shown not to work in other breeds (Spellman et al., 2007). In beef cattle, comparisons across breeds will be more important as crossbreeding at the commercial and seedstock levels is common and genetic evaluation systems allow the genetic evaluation of hybrid and purebred seedstock together (Sullivan et al., 1999). A genetic prediction based on genetic markers will then have the greatest utility in beef cattle breeding when it can be used across breeds.

The challenge with across breed predictions is that the number of markers currently available as part of the Illumina

Bovine SNP50 array are not going to be of sufficient density for effective selection. It has been estimated that 30,000 SNP are required for within breed selection, whereas >300,000 will be required for a similar accuracy of selection across breeds (Goddard, 2009). The requirement for additional density is a function of Linkage Disequilibrium (LD), where LD is sufficiently high over longer distances within Holsteins (Sargolzaei et al., 2008) then when beef cattle of multiple breeds are considered (Kelly et al., 2008; Lu et al., 2010). In 2010 a new High Density SNP panel for bovine has been released (<http://investor.illumina.com/phoenix.zhtml?c=121127&p=ir-1-newsArticle&ID=1372234&highlight=>) which will provide over 10 times as many SNP as that available from the Bovine SNP50 assay. This panel is expected to have the coverage required for effective selection across breeds.

Typically genomic selection establishes the relationship of each SNP or region of the genome to important traits with a "Discovery" or "Prediction" dataset that is then validated with an independent dataset. The size of the population for prediction continues to be a problem for effective genomic selection in beef cattle. Due to the structure, large numbers of highly proven bulls are not available as exists for dairy cattle. In the Canadian dairy study by Schenkel et al. (2009) more than 11,000 genotyped sires were used. In beef cattle many of the populations used for discovery include animals with their own performance information. It is clear that >10,000 records could be justified to maximize accuracy of the genomic predictions in beef cattle. Goddard (2009) indicated that for a trait with a heritability of 0.3, 4000 records will be required to develop a prediction equation with an accuracy of 0.5. More records would be required for a trait of lower heritability and accuracy would improve with the higher density panel. It is generally accepted that the number of records required in the validation data set can be less than that in the discovery set. The validation set needs to be large enough to be able to determine the accuracy of the prediction equation and should represent as closely as possible (breed and genetic background) the population where selection will take place. In the dairy study of Schenkel et al. (2009) ~500 young bulls were used to determine the accuracy of prediction from the >11,000 older bulls.

It is clear that the size of the populations required for effective implementation of genomic selection soon overwhelms the available resources of any one research institution. For this reason the Universities of Guelph and Alberta in Canada joined into an International collaborative effort with the USDA, Meat Animal Research Centre and the

Cooperative Research Centre for beef genomics technologies in Australia. This international collaboration has allowed resources from association studies primarily with growth, efficiency and carcass traits in beef cattle to be effectively combined for comparison and meta-analysis purposes (Snelling et al., 2010; Bennett et al., 2010). The Canadian contribution to the analyses was ~1000 animals, and the relative population sizes was approximately 2:1:1 for USDA, Australia and Canada, respectively. The result of this collaboration has been the development of a prediction equation that combines the results from all 3 studies. Work is now underway to determine the accuracy of that prediction equation in independent populations of cattle in 2010.

High density genotyping, sequencing and imputation

In addition to large SNP panels, the cost of sequencing has been greatly reduced recently, with whole genome sequence becoming possible for key animals. One immediate outcome of the sequencing efforts is the abundance of SNP discovered to aid in fine mapping efforts. With the possibility of both HD genotyping and sequencing, there will be targeted animals with a large amount of genotype information. However, due to the cost it is not feasible that such high density genotyping will be feasible on all selection candidates. However, there is the potential to combine low density genotyping with a panel of <10,000 SNP to infer the genotypes of the much larger panel (500K or even full sequence where available). With effective imputation algorithms, reduced SNP panels can be implemented within populations to infer higher density genotypes. In beef cattle, this could mean genotyping all sires with the high density panel and then the progeny could all have their HD genotypes imputed from a lower density more cost-effective panel. This prospect of imputing genotypes is very promising, with recent results from Canadian Holstein's presented by Sargolzaei et al. (2010) indicating that when the LD panel had SNP density of >3000, imputation was very successful with accuracy > 0.99.

For practical commercial application it is envisioned that the low density panel will have 2 primary purposes. The first purpose will be direct prediction, where SNP identified as informative and validated through independent studies involving Whole Genome Association Studies (WGAS) with available HD panels will be combined with panels of SNP through causative and fine mapping studies. The second purpose of the developed low density panel will be genotype imputation where additional genotypes could be imputed depending on the density of low density and HD genotypes in the pedigree. Additional SNP equally spaced

across the genome with intermediate allele frequency will then further enable imputation of HD genotypes and allow more accurate prediction.

Breeding program implementation

The implementation of genomic information into selection tools will be different between beef and dairy for many reasons, one being that dairy breeding is dominated through AI where live bulls are still required to service cows in the more extensive environment in beef cattle production. As a result, many more bulls are required in beef cattle production and as a result many more candidates need to be genotyped to determine their genetic merit. The cost of genotyping then becomes an important factor in beef cattle breeding. Where it is very cost effective to genotype all potential dairy sires for the high density chip, this may not be cost effective in beef cattle. This structure is changing as costs of genotyping continue to be reduced. The cost of the Bovine SNP50 assay has been reduced by 40% since it was released 2.5 years earlier and the anticipated cost of the new HD panel with >500,000 SNP is anticipated to be similar to the cost of the Bovine SNP50 array when it was first released.

It is now well accepted that the best way to implement genomic information into genetic improvement programs is simply to allow the genomic information to contribute to the animals genetic evaluation (EPD or EBV). Technically there are a number of ways that this can be done. The simplest approach and the one that has been adopted in some instances is a blending approach. In this approach the animals traditional EBV based on phenotype and pedigree is combined with the genomic EBV or genetic prediction based solely on the markers. This approach considers the weighting of the 2 sources of information which is a function of the accuracy of the 2 predictions. This approach has been implemented by the American Angus Association for example (MacNeil et al., 2010) where a panel of markers is used to predict carcass traits and is combined with the animals traditional EPD. Another approach is to include the two sources of information into a multiple trait genetic evaluation model. This approach has been applied in Australia through Breedplan to generate a tenderness EPD in Brahman. As expected the increase in accuracy was highest for bulls with little information, such as a young sire with just a measure on flight time, which in the analyses was a trait correlated to shearforce, saw an increase in accuracy from 0.13 to 0.29 with the addition of the information on the 4 markers. However, when the information available on a sire is high, such as when progeny information is available, then the 4 marker genotypes added very little to the sire's

accuracy. Research is continuing to develop the best methods to incorporate genomic information into traditional genetic evaluation programs (Kachman et al., 2008).

Genomic information does not change how cattle will be selected, as selection will still be based on genetic evaluations such as EPD or EBV. Similarly, multiple trait selection will also not change with genomic information but will only be enhanced. Multiple trait selection combines all of the genetic evaluations and considers the economic importance of each trait and applies the appropriate weight to determine an overall index value on an animal that can be used for selection. Now with genomic information the process will be the same, but now the EPD or EBV used will include the genomic information and the trait accuracy will be increased. Also genomics will allow EPD for traits that were previously unavailable through traditional genetic evaluation systems such as feed efficiency and meat quality as previously mentioned. Considering this multiple trait approach to selection highlights the importance to use the DNA markers to predict all of the traits. For example, consider an SNP that may have been placed on the panel to increase marbling but the same SNP also decreased feed efficiency. It is important to run the association with the marker panel across all of the traits and adjust all of the traits appropriately so the full impact of the markers can be properly accounted for in multiple trait selection programs.

Combining the low density panel as indicated with HD genotyping of key parents, will provide the beef industry with predictive ability in commercial animals far superior to those previously available. Ideally the accuracy of the low density panel will be 0.5-0.7, similar to that of the HD panel, at a much reduced cost. Implementation of widespread genotyping could have a profound impact on genetic improvement programs. One of the primary impediments to improvement has been the inherent structure of the industry with many independent producers across multiple sectors (Miller, 2002). This segmentation results in little information flow between sectors resulting in little incentive for genetic improvement beyond the cow herd that purchases the genetics. However, with RFID tags, genotyping an animal once enables this information to be available to all sectors, providing informative genetic predictions of important traits at specific points in the production chain. For example, information regarding calving ease, growth and daughter fertility could be made available to the cow-calf producer, feedlot efficiency could be made available to the feedlot, carcass yield and quality

made available to the processor and meat quality to the purveyor. Cost of the genotyping would then be spread across all of these sectors who extract value from the information.

This chain of information will expedite genetic progress through a process of rewarding value. For example, take an attribute such as beef tenderness, which is arguably valuable only to the meat purveyor that sells beef to the consumer. However, this purveyor will send economic signals to the processor that indicates that animals of the favourable tenderness rating are more valuable. This creates demand for those carcasses with the favourable genetic profile for beef tenderness and the processor will then pursue these same genotypes from the feedlot, again creating a price premium by increasing demand. Similarly, the feedlot operator will pursue these calves from the cow-calf producer and finally the cow-calf producer, wanting to capture these calf premiums will seek bulls from the seedstock producer that will produce the calves with the favourable genetic profile. The end result will be the seedstock producer changing his selection practices to produce the bulls with desired genomic profile in demand from the cow/calf sector. This “market pull” approach is one that has not existed to a clear extent in the beef industry and it is proposed here that genomics will provide the mechanism to create that pull as it provides useful information at all segments of the chain.

Accelerating genetic improvement

Genomics will be able to add value to existing technologies that are impeded currently due to cost restrictions. An example of this is the measurement of feed intake to improve feed efficiency. Although the technology exists to measure intake on-farm the cost makes widespread measurement unpractical. However, with the use of genomic prediction based on a panel of markers, the best candidates for measurement for feed efficiency could be preselected based on genotype. As a result, only the best animals are measured with the limited feed intake capacity. This approach increases the probability of identifying the elite animals to be capitalized on further through AI in the breeding program.

As indicated, increased accuracy of multiple trait prediction will be one area where genomics will enable increased genetic progress. Increased accuracy will also be obtained as the genomic predictions are for the direct trait of interest, such as marbling score in steers in the feedlot. This is in contrast to the collection of data on a related trait such as ultrasound intramuscular fat estimated in yearling replacement heifers. By developing prediction equations

directly for the trait of interest, accuracy of selection is ultimately increased. There are other important ways in which genomics will allow increased genetic progress. Firstly, since the DNA sample can be collected at birth, selection candidates can be identified at a much younger age, shortening the generation interval. Although there is a trade off between accuracy and generation interval, generally the reduction in generation interval out-weighs the increased accuracy at later ages. In addition to increased accuracy of breeding value estimates and decreased generation interval, genetic improvement will be further enhanced through increased selection intensity. This increased selection intensity is possible when more animals are genotyped than can be phenotyped. Consider a trait like feed efficiency where there is only limited capacity to measure feed intake. In a scenario where 100 bulls are required for breeding and feed intake measurement capacity is limited at 500, the proportion selected is 1/5. However with a genomic test at low cost, thousands of selection candidates can be genotyped, greatly increasing the selection intensity.

As described above one of the greatest changes in the dairy breeding sector was around the evaluation of cows. A similar change can be expected in the beef sector as well. Generally, females, either as herd replacements or bull dams are selected with lower accuracy information than their bull counterparts. For example, bulls may be part of a post-weaning growth test with feed efficiency and ultrasound measures where females may be limited to weight traits only. Females are similarly disadvantaged in terms of progeny numbers where a 3-year old female will have one progeny record, where a 3-year old bull can have 20 or more. Although some females can have many records, this generally coincides with older cows and longer generation intervals, which can be counterproductive. Genomics will greatly increase the accuracy of selection in cows and will contribute to improved progress through this selection pathway.

As genomics will allow the identification of elite females that was not possible previously, reproductive technologies can be exploited to capitalize on these females. In general genomics will bring new life and opportunities for improvements in reproductive technologies. Such technologies as embryo transfer and in-vitro embryo production, although available for sometime have been underutilized due to the problems of identifying the elite females as illustrated above. Now with increased accuracy of selection in females, the genetic merit of the resulting embryos is increased and as such the breakeven cost of

embryo production is changed and more embryo transfer will be justified. Embryo transfer can also be combined with sexed semen technology that is now available to change the way bulls are developed and sold.

Changing industry structure

If the genetic prediction technology including genomics is capable of identifying elite cows, these cows could be flushed to male semen to produce candidate bulls for customers. These bull embryos could then be sold directly to bull customers to implant into their own recipients, which will decrease costs associated with bull performance testing, trucking, marketing etc. The bull will be acclimatized to the environment where he is raised, which could increase longevity. This approach could reduce the cost of seedstock for the commercial sector. Subsequent genotyping of the bulls born would allow some secondary culling based on Mendelian sampling to increase the average genetic merit of the group of bulls retained. This same approach is not possible without genomic testing as elite females cannot be identified with current systems and as a result performance testing bulls is required to ensure their genetic merit.

This approach of targeted seedstock, generated through embryo transfer could be expanded to include specialized lines for specific markets. For example, a commercial producer as part of a value chain may have a specific market for beef with enhanced tenderness attributes. The possibility of specific value attributes in beef cattle genetics has not been exploited in the past. Genomics will enable the identification of genetics to match specific market opportunities. Beef with more marbling or with exceptional lean characteristics is not a new opportunity but one that will be further enabled with genomics. Genomics will also enable development of specific attributes such as profile of fatty acids or iron content with a goal of producing a more healthy beef product (Reecy, 2008). Such an approach is possible if a discovery population is established with the appropriate measures to determine prediction equations based on the SNP. Given the large estimates of the size of the discovery population required, success will require a significant investment in this area as these measures can have significant costs. The marketplace will determine the potential return from this investment which will determine the feasibility.

The success in the dairy industry in the implementation of genomic selection is based entirely on their existing database of phenotypes through industry recording programs. The recording of the milk production and type

traits along with pedigree has been supported by the dairy breeders and producers. The question going forward is what will happen to recording programs with the implementation of genomics? As teams of young sires with genomic proofs have similar effective accuracy to proven bulls, there will be little incentive for producers to use unproven young sires in a traditional progeny test program. Similarly as genomic information becomes more powerful, individual records on females become less important. These forces combined could lead to a reduction in recording. This would be ironic as it is this very recording that has enabled genomics to advance. Recording programs will still be required as it is important to continue to regenerate the prediction equations relating genomics to performance with advancing generations. The implementation of genomics may change the structure of recording programs from a more public model where breed societies and producers contribute to a national database for example, to a more corporate model where companies interested in developing the genomic tests, or selling the seedstock as a result of the genomic tests, will develop the phenotypic resource populations required. Competition between companies selling bull semen will then be expanded to include their phenotypic resource as well. This model would also enable the investment in more novel trait recording, which could enhance the competitive position of one company over another. For example if one company invested heavily in performance recording for feed efficiency, their genomic prediction equations would be more accurate for this trait and in turn their genetic product (bulls, embryo, semen etc) will become superior to competitors overtime. As described, genomics could encourage some adoption of a nucleus breeding scenario as originally envisioned by Nicholas & Smith (1983).

Conclusions

The implementation of genomics creates many opportunities for beef cattle production through increased genetic progress and the inclusion of new traits of economic importance in the selection program. Enhanced genetic progress will be enabled through increased selection accuracy, decreased generation interval and increased selection intensity. It is clear from success in the dairy industry that genomic selection can work. The challenge for implementation in beef cattle remains the establishment of the required resource population to match genotypic information with phenotypes. These populations' requirements are large and will require a collaborative

effort to establish or a significant investment by any one company. The opportunity for change is great enough with genomics that these obstacles will be overcome and rates of genetic improvement will significantly increase in the next decade as a result.

References

- ARTHUR, P.F.; ARCHER, J.A.; JOHNSTON, D.J. et al. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. **Journal of Animal Science**, v.79, p.2805-2811, 2001.
- BENNETT, G.L.; GODDARD, M.E.; LU, D. et al. Meta-analysis of high-density SNP associations for beef cattle production traits from three countries. In: CANADIAN LIVESTOCK GENTEC ANNUAL RESEARCH SYMPOSIUM, 2010, Calgary Alberta, Canada. **Proceeding...** Calgary Alberta: 2010 (Abstract).
- ELSIK, C.G.; TELLAM, R.L.; WORLEY, K.C. The genome sequence of taurine cattle: a window to ruminant biology and evolution. **Science**, v.324, p.522, 2009.
- CASAS, E.; WHITE, S.N.; RILEY, D.G. et al. Assessment of single nucleotide polymorphisms in genes residing on chromosomes 14 and 29 for association with carcass composition traits in *Bos indicus* cattle. **Journal of Animal Science**, v.83, n.1, p.13-19, 2005.
- CASAS, E.; WHITE, S.N.; WHEELER, T.L. et al. Effects of calpastatin and micro-calpain markers in beef cattle on tenderness traits. **Journal of Animal Science**, v.84, n.3, p.520-525, 2006.
- CASAS, E.; WHEELER, T.L.; SHACKELFORD, S.D. et al. Association of single nucleotide polymorphisms in the cast gene associated with longissimus tenderness in beef cattle. **Journal of Animal Science**, v.87(E-Suppl. 2), p.533, 2009. (Abstract #628).
- CHESNAIS, J.P. [2010]. **Semex's genomic program genomax brochure**. Available at <http://www.semex.com>
- COLE, J.B.; VANRADEN, P.M.; O'CONNELL, J.R. et al. Distribution and location of genetic effects for dairy traits. **Journal of Dairy Science**, v.92, p.2931-2946, 2009.
- GODDARD, M.E.; HAYES, B.J. Genomic selection. **Journal of Animal Breeding Genetic**, v.124, p.323-330, 2007.
- GODDARD, M.E.; MEUWISSEN, T.H.E. The use of linkage disequilibrium to map quantitative trait loci. **Australian Journal Experimental Agriculture**, v.45, p.837-845, 2005.
- GODDARD, M.E. How can we best use DNA data in the selection of cattle? In: BEEF IMPROVEMENT FEDERATION ANNUAL RESEARCH SYMPOSIUM, 41., 2009, Sacramento, California. **Proceedings...** Sacramento, 2009.
- HAVENSTEIN, G.B.; FERKET, P.R.; QURESHI, M.A. Growth, liveability and feed conversion of 1957 vs 2001 broilers when fed representative 1957 and 2001 broiler diets. **Poultry Science**, v.82, p.1500-1508, 2003.
- HAYES, B.J.; BOWMAN, P.J.; CHAMBERLAIN, A.J. et al. Invited review: genomic selection in dairy cattle: progress and challenges. **Journal of Dairy Science**, v.92, p.433-443, 2009.
- JOHNSTON, D.; GRASER, H.; TIER, B. Integration of DNA markers into a BREEDPLAN tenderness EBV. In: GENETIC PREDICTION WORKSHOP OF THE BEEF IMPROVEMENT FEDERATION, PREDICTION OF GENETIC MERIT OF ANIMALS FOR SELECTION, 9., 2008, Kansas City. **Proceedings...** Kansas City, 2008.
- KACHMAN, S. Incorporation of marker scores into national genetic evaluations. In: GENETIC PREDICTION WORKSHOP OF THE BEEF IMPROVEMENT FEDERATION, PREDICTION OF GENETIC MERIT OF ANIMALS FOR SELECTION, 9., 2008, Kansas City. **Proceedings...** Kansas City, 2008.
- KELLY, M.J.; SARGOLZAEI, M.; SCHENKEL, F.S. et al. Comparison of linkage disequilibrium decay between a multi-breed beef herd and purebred Angus, Piedmontese and Holstein cattle. In: CSAS ANNUAL MEETING/KENNEDY CONFERENCE, 2008, Guelph. **Proceedings...** Guelph: 2008. (CD-ROM).
- KOCH, R.M.; CUNDIFF, L.V.; GREGORY, K.E. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. **Journal of Animal Science**, v.55, p.1319-1329, 1982.
- LU, D.T.; SARGOLZAEI, M.; KELLY, M. et al. Linkage disequilibrium in Angus, Piedmontese and Crossbred beef cattle. **BMC Genomics**, 2010. (Submitted)
- MACNEIL, M.D.; NKRUMAH, J.D.; WOODWARD, B.W. et al. Genetic evaluation of Angus cattle for carcass marbling using ultrasound and genomic indicators. **Journal of Animal Science**, v.88, p.517-522, 2010.
- MATUKUMALLI, L.K.; LAWLEY, C.T.; SCHNABEL, R.D. et al. Development and characterization of a high density SNP genotyping assay for cattle. **PLoS One**, v.4, p.e5350, 2009.
- MILLER, M.F.; HUFFMAN, K.L.; GILBERT, S.Y. et al. Retail consumer acceptance of beef tenderized with calcium chloride. **Journal of Animal Science**, v.73, n.8, p.2308-2314, 1995.
- MILLER, S.P. Beef cattle breeding programmes : progress and prospects. In: WORLD CONGRESS GENETIC APPLIED LIVESTOCK PRODUCTION, 7., 2002, s.l. **Proceeding...** s.l.: 2002. (CD-ROM).
- NICHOLAS, F.W.; SMITH, C. Increased rates of genetic change in dairy cattle by embryo transfer and splitting. **Animal Production**, v.36, p.341-353, 1983.
- PAGE, B.T.; CASAS, E.; HEATON, M.P. et al. Evaluation of single-nucleotide polymorphisms in CAPN1 for association with meat tenderness in cattle. **Journal of Animal Science**, v.80, n.12, p.3077-3085, 2002.
- PAGE, B.T.; CASAS, E.; QUAAS, R.L. et al. Association of markers in the bovine CAPN1 gene with meat tenderness in large crossbred populations that sample influential industry sires. **Journal of Animal Science**, v.82, n.12, p.3474-3481, 2004.
- REECY, J. Overview of healthfulness project. In: GENETIC PREDICTION WORKSHOP OF THE BEEF IMPROVEMENT FEDERATION, PREDICTION OF GENETIC MERIT OF ANIMALS FOR SELECTION, 9., 2008, Kansas City. **Proceedings...** Kansas City, 2008.
- SARGOLZAEI, M.; SCHENKEL, F.S.; JANSEN, G.B. et al. Extent of linkage disequilibrium in Holstein cattle in North America. **Journal of Dairy Science**, v.91, p.2106-2117, 2008.
- SARGOLZAEI, M.; CHESNAIS, J.P.; SCHENKEL, F.S. Accuracy of a family-based genotype imputation algorithm. **GEB Open Industry Session**. Saint-Hyacinthe Quebec, Canada, 2010.
- SCHAEFFER L.R. Strategy for applying genome-wide selection in dairy cattle. **Journal of Animal Breeding Genetic**, v.123, p.218-223, 2006.
- SCHENKEL, F.S.; MILLER, S.P.; WILTON, J.W. Genetic parameters and breed differences for feed efficiency, growth and body composition traits of young beef bulls. **Canadian Journal of Animal Science**, v.84, p.177-185, 2004.
- SCHENKEL, F.S.; MILLER, S.P.; JIANG, Z. et al. Association of a single nucleotide polymorphism in the calpastatin gene with carcass and meat quality traits of beef cattle. **Journal of Animal Science**, v.84, n.2, p.291-299, 2006.
- SCHENKEL, F.S.; SARGOLZAEI, M.; KISTEMAKER, G. et al. Reliability of genomic evaluation of Holstein cattle in Canada. In: INTERBULL INTERNATIONAL WORKSHOP:

- Genomic Information in Genetic Evaluations, Uppsala, Sweden, 2009. **Proceedings...** Uppsala, 2009.
- SMITH, G.C.; SAVELL, J.W.; DOLEZAL, H.G. et al. **The final report of the national beef quality audit - 1995**. Fort Collins: Colorado State University, Stillwater: Oklahoma State University, College Station: Texas A&M University, 1995.
- SNELLING, W.M.; ALLAN, M.F.; KEELE, J.W. et al. Genome-wide association study of growth in crossbred beef cattle. **Journal of Animal Science**, v.88, p.837-848, 2010.
- SPELMAN, R.J.; KEEHAN, M.; OBOLONKIN, V. et al. Application of genomic information in a dairy cattle breeding scheme. **Proceeding Association Advmt. Animal Breeding Genetic**, v.17, p.471-478, 2007.
- SULLIVAN, P.G.; WILTON, J.W.; MILLER, S.P. et al. Genetic trends and breed overlap derived from multiple breed genetic evaluations of beef cattle for growth traits. **Journal of Animal Science**, v.77, p.2019-2027, 1999.
- WHEELER, T.L.; CUNDIFF, L.V.; KOCH, R.M. et al. Characterization of biological types of cattle (cycle IV): carcass traits and *longissimus* palatability. **Journal of Animal Science**, v.74, p.1023-1035, 1996.
- WHITE, S.N.; CASAS, E.; WHEELER, T.L. et al. A new single nucleotide polymorphism in CAPN1 extends the current tenderness marker test to include cattle of bos indicus, bos taurus, and crossbred descent. **Journal of Animal Science**, v.83, n.9, p.2001-2008, 2005.
- ZWAMBAG, A.W. **Genetic improvement of beef tenderness in a multi-breed beef population utilizing genetic markers**. 2007. M.Sc. Thesis - University of Guelph, Guelph, Ontario.