The nature and scope of some whole genome analyses in US beef cattle

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Abstract

The production of EPDs from statistical analysis of pedigree and performance records is a tried and true method for characterizing the genetic merit of animals. However, response to selection on such EPDs is suboptimal because there are no EPDs for some economically-relevant traits and for those that are available the accuracies are typically low at the ideal selection ages around puberty, especially for traits with low heritabilities, or those that can be measured in only one sex or late in life. In theory, more accurate genomic enhanced EPDs could be obtained in target populations of selection candidates from prior knowledge of EPD associated with various chromosome fragments. This prior knowledge is typically obtained from Bayesian analyses in a so-called training or discovery population. Three critical issues arise in relation to this process. First, what is the upper limit for accuracy or predictive ability using a high-density 50k genomic panel? Second, how is predictive ability influenced by genetic distance between the training and target population? A close distance would involve training in widely used sires for prediction in their offspring, whereas a long distance would involve prediction in another breed or cross. Third, can a much smaller and cheaper subsample of no more than a few hundred markers be used without substantially eroding predictive ability? All three of these issues are the current focus of whole genome analyses in US beef cattle based on the Illumina 50k panel. Available training resources include populations of AI bulls with published EPD, such as the Angus and Limousin datasets developed by University of Missouri and the multi-breed 2,000 bulls project being undertaken by US MARC. The real power of genomic selection will be achieved when results can be extended beyond the basic suite of EPD traits, and for these purposes dedicated populations need to be collected with specific phenotypes. A study over several generations of F2 Nellore-Angus at Texas A&M University includes temperament and docility measures in addition to feed intake, reproductive and carcass attributes. Several other populations with individual feed intake data have been collected, including those at University of Alberta, Guelph University, University of Missouri and US MARC. Pfizer Animal Genetics has funded projects, principally in Angus cattle, to collect data on carcass and meat attributes including beef healthfulness, and feedlot health and performance data in collective projects that have involved the National Beef Cattle Evaluation Consortium, Iowa State University, Colorado State University, University of California at Davis and Oklahoma State University. Competitive funding through USDA-NRI has been used for projects led by New Mexico State University involving female fertility in Brangus animals, Cornell University to build ongoing and future resource populations, and Iowa State University, Cal Poly San Luis Obispo and US MARC to develop web-accessible publicly available Bayesian analytical tools for genomic selection. A project led by University of California at Davis is considering the integration of DNA information into beef production systems and includes a ranch and rancher focus with comprehensive outreach component.

Collectively, these projects represent major intellectual and economic investments in beef cattle improvement through funding by Pfizer Animal Genetics, Merial, land-grant Universities, USDA-ARS and USDA-NRI that will, over the next 12 months, provide some concrete answers to the three critical issues and deliver improved selection tools to the US beef industry.

Introduction

Conventional beef cattle breed improvement programs have relied on pedigree and performance recording in order to estimate Expected Progeny Differences (EPD). Traits with moderate heritability that can be observed on the selection candidates prior to selection age can be effectively improved. However, beef cattle production systems are influenced by many traits that can only be observed in one sex (eg female reproduction), or late in life (eg stayability, carcass attributes). In these circumstances, information on the selection candidate is typically limited to knowledge of its parent average genetic merit. Since bulls are used more widely than cows, their selection can be more intense and contributes to genetic improvement to a greater extent than female selection, even though both sexes contribute half of the genetic material to their offspring. Ongoing improvement requires that superior sons replace elite sires but such sons cannot be identified until performance observations can be observed on offspring of the son. The time delay required to identify elite sons before they can be widely used is the major limitation to improving current rates of genetic improvement.

Knowledge of the genes that are responsible for variation in performance would allow candidates to be ranked at a young age on the basis of knowledge of the particular genes they inherited from their parents, in addition to using pedigree and performance records. However, although the role of many genes in particular production processes is reasonably characterized, surprisingly little is known about the nature and identity of the genes that contribute to the variation in performance – such as those that distinguish an average from an above-average animal. Fortunately, many genomic regions that exhibit variation in DNA sequence known as polymorphisms are now known, and these can be used as surrogates or markers to try and identify genomic regions, if not genes, contributing to variation in performance.

A polymorphic marker allows the inheritance of a particular fragment of the genome to be readily traced across generations. This in itself is not particularly valuable in helping us find causal genes because one version of the marker may be associated with a favorable gene in some families and associated with the unfavorable form in other families. In order for a marker to be really useful, it needs to be in strong linkage disequilibrium (LD) with the causal gene, the stronger the LD the better. The extent of LD provides a measure of how well the marker variants provide knowledge of the unknown causal gene variants. A marker with a very different allele frequency from a causal gene cannot be in high LD with the causal gene, so ideally a wide range of markers of varying allele frequency would need to be available.

The development of marker tests that are currently available in beef cattle panels marketed by Merial Igenity (http://www.igenity.com) and Pfizer Animal Genetics (http://www.pfizeranimalgenetics.com) have been discovered by creating LD between markers and causal genes using linkage, most commonly be crossing disparate breeds such as Jersey and Limousin, Wagyu and Limousin or Brahman and Angus. The first-cross or F1 animals will have one chromosome in each pair that has originated from each of the two foundation breeds. When inter se mated to produce F2 progeny, the typical chromosome will have had one crossover event, so that part of the chromosome originated from one foundation breed and part from the other. Using as few as ten markers on each chromosome allowed testing for the presence of major gene fragments known as quantitative trait loci (QTL) in each chromosome region. Many such regions have been found for a vast array of traits, but the discoveries have been problematic. First, the experiments were expensive as a result of the genotyping costs. Accordingly the experiments tended to be smaller than they should have been, with the results that they lacked power and tended to only find regions that by chance looked bigger in the discovery experiment than they really were. This resulted in the effect size tending to shrink in subsequent validation studies. Second, the assumption that a few regions accounted for large genomic effects may have been simply untrue, and the real state of nature may have been characterized by many gene regions of small effects.

The sequencing of the bovine genome and the development of technologies to allow the simultaneous characterization of tens of thousands of genetic markers has opened up opportunities to exploit ancestral LD, rather than having to create LD by linkage. The extent of LD increases on average if the marker is physically closer to the unknown causal gene, and as the level of inbreeding increases (or effective population decreases). Since breeds exist as a result of mild inbreeding, some markers will exhibit significant LD if enough are available to saturate every genomic region and to cover a wide range of allele frequencies. Simulation studies had suggested that 50,000 single nucleotide polymorphism (SNP) markers would be adequate in purebreds to allow the characterization of every genomic region in a sufficiently large training population (Meuwissen et al., 2001).

Characterization of a genomic region can be thought of as effectively equivalent to estimating an EPD for every chromosome fragment, rather than every animal. Some chromosome fragments may contribute little or no information, as they do not contain genes explaining variation, whereas other chromosome regions might be highly informative. Knowledge of the effects of chromosome regions allows one to directly infer the EPD of any animal not in the training population based simply on knowledge of the chromosome fragments it inherited, a process known as genomic prediction (Meuwissen et al., 2001).

A high-density bovine panel containing about 50,000 SNP markers was developed using federal funds and made commercially available by Illumina in January 2008. This heralded the beginning of widespread and systematic whole genome analyses of both beef and dairy cattle, in the US and elsewhere in the world. Prior to this release, a proprietary set of SNP markers had been developed by MetaMorphix

(http://www.metamorphixinc.com/16858-trubreed_marketingmaterials.pdf) and used for product development in conjunction with Cargill (Kolath, 2009), but their marker technology was not made available to publicly funded researchers and few details have ever been publicly communicated prior to this BIF conference. The remainder of this paper is limited to describing the nature and scope of publicized whole genome analyses based on the Illumina 50k product.

Industry/seedstock populations

An immediately appealing dataset for genomic analyses comprises widely-used AI sires that are represented in each breed. The advantages of such a dataset, once gathered together is: that investment is only required in the genotyping phase, as deregressed EPDs can be used in place of phenotypic data; and the individuals themselves have, by definition, made major contributions to the modern population for that breed. The disadvantages are that: it can be costly and time-consuming to gather together DNA samples from legacy bulls, particularly those that date back several generations; discovery is limited to traits for which EPD are available, which for many breeds is little more than birth, weaning and yearling weights; there are only a finite number of such animals in each breed, perhaps too few for reliable estimation; and the close relationships and inbreeding of these animals result in LD extending some distance along the chromosome, perhaps being overwhelmed by LD due to recent linkage rather than ancestral genomic proximity.

An Angus resource population now numbering some 2,000 bulls and a smaller Limousin resource population have been developed by Merial and Jerry Taylor at the University of Missouri, in collaboration with the relevant breed associations. Routine national cattle evaluations allow these datasets to be used for training, the process of estimating EPDs for chromosome fragments on birth, weaning and yearling weight direct effects, milk, calving ease direct and maternal, scrotal circumference, carcass weight, ribeye area, yield grade and marbling score. The North American Limousin Foundation also has docility and stayability, whereas American Angus Association includes backfat, mature height, mature weight and prototype heifer pregnancy EPDs.

In a project involving some 2,000 bulls from a range of different breeds, relevant breed associations and the US Meat Animal Research Center (USMARC) has collected together DNA samples from bulls from Angus, Beefmaster, Brahman, Brangus, Braunvieh, Charolais, Chiangus, Gelbvieh, Hereford, Limousin, Maine Anjou, Red Angus, Salers, Santa Gertrudis, Shorthorn, and Simmental breeds (Thallman, 2009). The number of sires sampled in each breed has taken account of their contribution to the US population. These populations are probably individually inadequate for reliable genomic training, but will be useful for validation or as a pooled resource for training/discovery.

Commercial/non seedstock/research populations

An alternative approach to training is to use individual phenotypes rather than EPDs. This has the disadvantage that most individual phenotypes are less informative than the deregressed data that can be obtained from EPDs. Accordingly, more animals would be required to obtain the same level of power in training than would be the case when using sires with progeny information. The main advantage with commercial populations is that they can be simultaneously deeply phenotyped for many traits, including traits that are difficult or impossible to measure on breeding animals. Traits of particular interest might include: feed intake; carcass and meat characteristics; disease resistance; and reproductive performance.

The most difficult traits to get reliable information are those associated with female reproduction. This is the case because lifetime female reproductive performance requires a long-term experiment, is typically characterized by low heritability traits, and the value of individual performance records is further eroded by the diminishing contemporary groups that occur over successive parities. Dr Milt Thomas from New Mexico State University has a project concentrating on female fertility traits including first-calving success from some 800 Brangus females from Camp Cooley. Further, in collaboration with Cornell University, he has collected DNA samples from heifers and their subsequent fertility records over successive parities from large cohorts born and managed on the Rex Ranch in Nebraska.

A trial involving the collection of phenotypic records at harvest on near 2,200 Angus animals from several sources is near completion. The principal focus of this Pfizer-funded trial is on meat quality including aspects of human healthfulness, but the trial (Reecy, 2008) includes: growth traits (birth, weaning, yearling and slaughter weights); carcass attributes (dressing %, ribeye area, backfat thickness, yield grade, quality grade, kidney, pelvic and heart fat); meat traits (shear force, taste test panel, and detailed nutrient components of interest from a human nutrition perspective - fatty acids, sphingolipids, cholesterol, minerals, creatine, creatinine, vitamins and carnitine). The data collection is a collaborative venture involving producers Jack Cowley and Don Smith with a large team of researchers from Oklahoma State, University of California-Davis, Cornell University and Iowa State University.

A study using some 2,900 Angus steers sourced from the Rex Ranch over two years, and fed out at the Southeast Colorado Research Station is being funded by Pfizer Animal Genetics to collect information for genomic studies on feedlot health. In addition to weights and carcass traits, the trial has attempted to measure indicators of temperament (flight speed and chute score) (Weaber, 2008), stress indicators, body temperatures, immune response, visual indicators of sickness (including nasal discharges, coughing, rapid breathing, number of treatments, time to recovery), necropsy results, BVD and observable lung lesions at harvest (Enns, 2008). The trial is being led by Colorado State University, with input from West Texas A&M, University of Missouri, South Dakota State, University of Illinois, and Cornell University.

The largest trial from a single location involves the Cycle VII cattle from USMARC and this involves a large portfolio of traits, including growth, carcass, fertility and feed intake.

This trial involves offspring of Angus, Hereford and composite cows sired by Angus, Charolais, Gelbvieh, Hereford, Limousin, Red Angus, and Simmental sires (Thallman et al., 2009).

The longest running trial involves the inbred Line 1 Hereford herd from Fort Keogh, and involves 250 individuals representing available sires since 1953 and a sample of the current generation of calves (MacNeil, pers. Comm.).

Several previous studies have focused on the collection of feed intake data for the study of residual feed intake (RFI) and these populations at University of Alberta, University of Guelph, and Circle A Ranch in Missouri are being used for studies of efficiency related traits as is a study of F2 Nellore-Angus animals being undertaken at Texas A&M by Dr Clare Gill (http://indicus.tamu.edu/mcgregor/project.cgi) that also includes a substantial focus on various aspects of temperament.

Critical Issues

There are three critical issues relating to the performance of genomic prediction. These are: the proportion of genetic variation in Angus animals that can be predicted from knowledge of the 50k SNP genotypes; the extent to which the predictive ability of the 50k panel erodes when the training knowledge is applied to animals of different breeds; and the ability of a reduced panel to reliably predict performance. Practically no information has been published on these issues except for results based on simulated data. In a USDA-NRI funded project, Iowa State University, Cal Poly San Luis Obispo and USMARC have been developing a web-based bioinformatics platform that includes Bayesian software (Fernando and Garrick, 2008) for the training analyses of populations with high-density SNP data. The Bayesian software for developing prediction equations is currently being applied to many of the datasets described in the previous section, generating some indicative information as to the performance of genomic predictions. Web access to this software can be provided to other parties with relevant data.

Within-breed predictions from 50k panels. The most extensively analyzed dataset has been the Angus AI bull population. The discovery or training process generates an estimate, somewhat like heritability, of the proportion of phenotypic variation that can be accounted for using the SNP markers. Low estimated values for this parameter indicate that the marker predictions will not be very good, but high values only indicate that the markers are predictive in the training population. Confidence in the genomic predictions can only be provided by validation in a group of animals that were not included in the training population (Goddard, 2009). Accordingly, our approach to training typically involves subdividing the data, say into thirds, and training in two-thirds of the data followed by validation in the other third. The subsets are chosen so that the same sires do not have sons in both the training and validation datasets. This training can be done three times for different dataset combinations, so that each bull is represented in one validation set. The results vary according to trait and data subset (Table 1), but the general conclusion is that correlations between

genomic predictions from 50k markers and realized performance in an independent dataset is in to the order of 0.5-0.7. This is equivalent to genomic predictions that are accounting for between 25% and 50% genetic variance. Put in perspective, the 50k genomic prediction is equivalent to about 6-16 offspring in a progeny test if the trait had a heritability of 25%. These correlations are as good as those being achieved in dairy populations before the genomic predictions are blended with national evaluation information on parent average.

Table 1: Correlations between 50k genomic prediction and realized performance for validation of Angus sires in independent Angus datasets for backfat (BFat), calving ease direct (CED) and maternal (CEM), carcass marbling (Marb), carcass ribeye area (REA), scrotal circumference (SC), weaning weight direct (WWD) and yearling weight (YWT).

Trait	Train 2 & 3 Predict 1	Train 1 & 3 Predict 2	Train 2 & 3 Predict 3	Overall[1]
BFat	0.71	0.64	0.73	0.69
CED	0.65	0.47	0.65	0.59
CEM	0.58	0.56	0.62	0.53
Marb	0.72	0.73	0.64	0.70
REA	0.63	0.63	0.60	0.62
SC	0.60	0.57	0.50	0.55
WWD	0.65	0.44	0.66	0.52
YWT	0.69	0.51	0.72	0.56

[1]Overall correlation estimated by pooling the estimated variances and covariances from each separate validation

Across-breed predictions from 50k panels. The prospect of using training results obtained in one breed to predict performance in another is particularly appealing. However, there are several reasons why this may not work. First, the gene effects may exhibit dominance, and the allele frequency may vary between populations. Second, the gene effects may exhibit epistasis, so their effects depend upon the allele frequency of other genes. Third, there may be estimation errors in the prediction equation that lead to spurious results in any validation dataset. Finally, there may be differences in LD between breeds, so that a marker that is a good surrogate of a causal gene in one breed is of less value in another breed. Few datasets have been available to date for across breed validation. Simulated data using some of the 50k loci as if they were causal genes has allowed the prospects for across breed prediction to be quantified (Kizilkaya et al., 2009), in the best-case scenario in the absence of non-additive gene effects such as dominance or epistasis. In the simulations, two populations were available, one which represented purebreds (i.e. Angus) and one which represented multibreeds (8 different sire breeds, including Angus, mated to straightbred and crossbred commercial cows). Those analyses show that predictive ability would be very high if the causal genes were on the marker panel (results not shown), but results (Table 2) are much poorer when LD among the markers on the panel are relied on to predict performance. Further, they show that the predictive ability of the 50k panel erodes considerably when the number of simulated causal genes is increased. The

best-case predictive ability therefore varies from correlations around 0.4 for 50 genes down to 0.2-0.3 for 500 genes. These correlations correspond to marker panels that would account for up to 18% genetic variation for 50 genes down to only 4-9% variation for 500 genes.

These analyses showed that in this case, it was better to train in purebreds to predict multibreed performance than vice versa. This is the case because the LD is on average higher and extends further in purebreds than it does in multibreeds. Training in a multibreed population would benefit from access to a higher density marker panel than the currently available 50k set.

Table 2: Correlations between 50k genomic prediction in one population (purebred PB or multibred MB) and realized performance in another population (MB or PB), from 5 replicates of the training populations of some 1,000 animals for a simulated trait with heritability of 50% that results from 50, 100, 250 or 500 causal genes (Kizilkaya et al., 2009).

Causal genes	Train PB then predict MB	Train MB then predict PB
50	0.42	0.39
100	0.31	0.29
250	0.28	0.25
500	0.30	0.20

Within-breed predictions from reduced (eg 384) SNP panels. Most activities reflect the law of diminishing returns. Alternative genotyping systems allow for the simultaneous assessment of a few hundred or a few thousand SNP markers at less cost than the current $200-300 for the use of the 50k Illumina platform. Bayesian analytical techniques (Fernando and Garrick, 2008) that are useful for 50k prediction can also be used to identify subsets of informative SNPs. The creation of subsets of 600 SNP markers obtained from choosing the 20 markers on each bovine chromosome with the highest model frequency, a measure for marker support, was undertaken to repeat the analyses shown in Table 1 on 600 marker subsets. The corresponding results are in Table 3. These data demonstrate relatively little loss of predictive ability in selectively reducing the panel from 50k to 600 SNP.

Table 3: Correlations between genomic predictions from a 600 SNP panel comprising the 20 most-supported SNP on each chromosome and realized performance for validation of Angus sires in independent Angus datasets for backfat (BFat), calving ease direct (CED) and maternal (CEM), carcass marbling (Marb), carcass ribeye area (REA), scrotal circumference (SC), weaning weight direct (WWD) and yearling weight (YWT).

Trait	Train 2 & 3 Predict 1	Train 1 & 3 Predict 2	Train 2 & 3 Predict 3	Overall
BFat	0.64	0.58	0.67	0.63
CED	0.64	0.47	0.68	0.61
CEM	0.56	0.58	0.60	0.55

Marb	0.70	0.69	0.61	0.67
REA	0.54	0.58	0.55	0.56
SC	0.55	0.51	0.48	0.51
WWD	0.62	0.46	0.66	0.49
YWT	0.68	0.51	0.72	0.55

Reduced panels of 600 markers per trait are still too many to populate a single 384 marker panel, particularly if the panel is to simultaneously target several traits. Further, the results shown in Table 3 for each trait reflect three panels of 600 markers, although some SNP may be in common in two or more panels. Using secondary screening procedures to select among these SNP for a subset of informative markers for marbling and using these in a prediction equation to obtain the equivalent of a genomic EPD enabled the genomic EPD to be validated in an independent population of 698 Angus steers (Nkrumah, pers. comm.). In this case, validation involves quantifying the genetic correlation between the genomic EPD or marker score and observed phenotype, in a bivariate analysis similar to those used to estimate genetic correlations between any pair of traits. The resulting estimates of the genetic correlations for 50, 100, 150 or 200 markers were 0.28. 0.29, 0.39 and 0.43. The genetic correlation between the genomic EPD and the observed phenotype will ultimately be required in order to combine genomic EPD with conventional pedigree and performance-based EPD in the context of a national cattle evaluation (Kachman, 2008).

Panels that are constructed to combine 100-200 of the best markers for each trait provide the opportunity of reassessing the genomic EPD using all the say 384 markers on the panel, rather than just the 100-200 markers selected for a particular trait. The estimated genetic correlations between carcass phenotypic observations and the molecular scores from a 384 panel based on the subset of SNP described in the previous paragraph were 0.49 for marbling and 0.43 for ribeye area (Nkrumah, pers. comm.). However, estimating genetic correlations requires substantial amounts of data, and more reliable estimates can be obtained using progeny test records.

The markers on the single 384 SNP multitrait panel were further validated by estimating the genetic correlation between marker score and progeny test performance on a new sample of 275 Angus AI bulls that were not used in any of the training analyses. The results of those analyses were estimated genetic correlations of 0.59 for marbling, 0.32 for backfat, 0.58 for ribeye area, 0.44 for carcass weight, 0.39 for heifer pregnancy and 0.35 for yearling weight (Nkrumah, pers. comm.). Such a panel would account for 10% genetic variation in the poorest trait and 35% variation for the best traits.

Ideally, the genomic EPD or marker scores on such panels would be used in national evaluation along with available pedigree and phenotypic information to improve the accuracy of EPD on selection candidates.

Conclusions

Clearly, the current studies have a strong focus on Angus cattle, and a more comprehensive approach to phenotypes than those presently available through national cattle evaluation. Fertility traits remain poorly represented. Predictions from 50k panels might account for 50% genetic variation when used in the same breed as the training population and substantially less when used in other breeds. Reduced panels can account for 25%-35% genetic variation for targeted traits. The prospects for modifying selection programs to exploit high-density 50k and/or low-density (e.g. 384) SNP panels looks encouraging, although less so than previously published simulation results. Future panels can only improve, as further analysis is undertaken on available resource populations. The role of marker tests as a selection tool is now maturing to the extent that they are likely to complement, rather than compete with, national cattle evaluation.

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