Marker Assisted Selection in the Beef Industry: Developments and Research Needs

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Introduction

In recent years, the beef industry has benefited from elevated calf prices, unfortunately the costs of production have also increased. An annual cow cost of \$571.73 was reported by the Southwest Standardized Performance Analysis in 2006 (SPA; Bevers and Dunn, 2008; Figure 1). Input cost steadily rose through the 1990s, but since 2002 they have dramatically accelerated. This escalation has been credited to higher feed costs, fuel prices, repair, and interest rates. Bevers and Dunn (2008) predicted that the next five years in the cattle business will be marked by some of the most dramatic changes that the industry has seen in 50 years due to the occurrence of a combination of economic circumstances (i.e. production costs, emerging ethanol industry, increase in land values, etc.) and legislation (i.e. country of origin labeling, failure to repeal the death tax, etc.). In response to these events, producers need to be strategic in planning for enhanced production efficiency and selecting cattle to fit their changing management goals.

Production efficiency of agricultural animal industries has greatly progressed in the last 50 years. For example, the dairy industry has used the combination of artificial insemination and aggressive genetic selection to increase the annual milk yield per cow while reducing the size of the national dairy herd; through nutrition, management, and genetic selection, the poultry industry has developed a broiler which requires 1/3 the time and a threefold decrease in the amount of feed needed; in the pork industry, genetic selection practices have resulted in a decrease in the amount of feed needed to produce a pound of pork by approximately half (USDA, 2007). The beef industry has also seen benefits of using genetic information such as, expected progeny differences (EPD) and parentage verification as part of the selection process. In order for producers to remain financially solvent in today's and future beef industries, development of tools to assist genetic improvement programs has become more important than ever. This paper will review the concept of marker assisted selection (MAS) in the beef industry and present recent results that can potentially contribute to DNA-based genetic improvement programs.

Figure 1. Annual cost per female from 1991 to 2006 (Bevers and Dunn, 2008).



Review of Literature

Phenotypic selection for economically important traits such as post-weaning growth has been extensively used because of the ease of measurement and high levels of heritability for those particular traits (Dekkers, 2004). However, an increase in calving difficulty occurred because of the desire to select animals for these traits. In recent decades, producers have combined the use of phenotypic appraisal with EPD to make selection decisions. Genetic improvement through selection and the incorporation of technologies such as: artificial insemination, sire testing programs, and hormonal control of the female reproductive cycle have been an important contributor to the dramatic advances in productivity (Dekkers and Hospital, 2002; Van Eenennaam, 2007). As DNAbased technologies continue to evolve and further knowledge is gained about systems biology of agricultural animals, there is great potential to use these tools as an aid in selection decisions.

Agriculture animal research and its funding topics have greatly changed due to recent developments in molecular biology. One of the most noteworthy milestones includes the completion of sequencing the bos taurus genome (USDA, 2007). This contributed to the understanding of genetic variation in economically important complex traits as well as the identification of loci and chromosomal regions that contain loci that affect traits of importance in livestock production (Andersson, 2001). With this knowledge, tools such as marker assisted selection (MAS), and whole genome selection (WGSL), can be explored within the realm of genetic improvement in the beef industry. However, it is important to state, "data sets to evaluate the longterm effectiveness of MAS or WGSL are not yet available."

Types of DNA Markers

The concept of DNA markers has been discussed for several decades in the beef industry. In its infancy, markers were developed to aid animal identification and kinship analyses to maintain the accuracy of pedigree records at the request of cattle breed associations (Heaton et al., 2002; Glowatzki-Mullis et al., 1995). Previously, parentage was determined by the inheritance of blood groups and enzyme polymorphisms in the serum proteins (Williams et al., 1997). However, with the introduction and evolution of DNA technology, use of several types of genetic markers replaced blood typing.

Williams et al. (1997) stated that DNA markers need to be robust, reliable and display a large number of alleles so that individuals can readily be distinguished from each other in parentage testing. This criterion was taken into consideration with the discovery of highly polymorphic, short tandem repeats, termed microsatellites (MS), which were amenable to direct amplification by polymerase chain reaction. Microsatellites consist of short stretches of nucleotide repeats, flanked by unique sequences which provide primer binding sites for amplification (Tautz, 1989). These markers are very useful in parentage analysis due to their large number of alleles, random distribution throughout the genome, and Mendelain inheritance (de Oliveria et al., 2005). With the development of DNA technology, many microsatellite loci have been described in the cattle genome through genetic mapping efforts (Williams et al., 1997). The International Society of Animal Genetics (ISAG) has chosen nine microsatellites to be used internationally as a parentage marker set. These markers are BM1824, BM2113, INRA023, SPS115, TGLA122, TGLA126, TGLA227, ETH10 and ETH225 (Bicalho et al., 2006).

Advances in DNA sequencing, computer software, and bioinformatics have facilitated the identification of an additional marker from amplified segments of genomic DNA termed, single nucleotide polymorphism (SNP). Single nucleotide polymorphisms are a fundamental unit of genetic variation and are appealing as markers because of their abundancy in the bovine population (Heaton et al., 2002). Single nucleotide polymorphism is the most common form of sequence variation with one SNP about every 1000 base pair (bp) in animal genomes (Vignal et al., 2002). In trait association studies, SNPs are preferred over MS because they are more ubiquitous in genomes and may influence gene function (i.e., as a SNP can change triplet codon and subsequent amino acid sequence of proteins; Zhang et al., 2002).

Molecular markers have been used to identify loci or chromosomal regions that affect single-gene traits and quantitative traits. Single-gene traits include genetic defects, genetic disorders, and appearance. Quantitative traits include those that are routinely recorded, those difficult to record (feed efficiency, product quality), as well as unrecorded traits (disease resistance; Dekkers, 2004). Genetic markers can be used to identify specific regions of chromosomes where genes affecting quantitative traits are located, known as quantitative trait loci (QTL). Gene mapping and discovery programs that vielded SNPs and MS technologies have resulted in the detection of an abundance of quantitative trait loci (QTL) for various beef cattle traits (Van Eenennaam et al., 2007).

Marker Assisted Selection

Marker assisted selection uses information about chromosomal or candidate gene regions in selection practices to identify individuals with favorable combinations of alleles (Davis and DeNise, 1998). The markers used in MAS programs are generally linked to, or underlie, a QTL. Therefore, through genotyping technology, DNA deviations (i.e., alleles) can be accurately identified and this information then used in combination with traditional and/or EPD selection to increase the number of favorable alleles for a certain trait. Success in this type of selection is challenging

90

as most economically important traits that will benefit from MAS are complex and controlled by many genes, influenced by the environment, have a tendency to be lowly heritable, and/or are difficult and expensive to measure (i.e. disease resistance, feed efficiency, etc.) (Dekkers, 2004; Van Eenennaam, 2006).

Marker detection is the first phase of a MAS program where DNA polymorphisms are used as linked or direct markers to detect QTL segregating in particular populations with specific allele frequencies. If one or more markers are found to be associated with QTL then the size of the QTL allelic effect and the location of the region in the genome are estimated. Direct marker QTL have been reported in beef cattle for Pompe's Disease (Davis and DeNise, 1998), muscle hypertrophy (Charlier et al., 1995; Grobet et al., 1997), and tenderness (Barendse et al., 2004; Casas et al., 2006; Van Eenennaam et al., 2007). Linked markers have been detected for horn development (Georges et al., 1993), birth weight (Rocha et al., 1992), preweaning growth, fat and ribeye area (Beever et al., 1990).

The second phase of a MAS program is validation (Van Eenennaam et al., 2007) or evaluation segment where the markers are tested in target populations or families to determine whether the detected QTL are segregating in those populations (Davis and DeNise, 1998). The National Beef Cattle Evaluation Consortium (NBCEC, http:// www.nbcec.org), defines validation to mean the independent verification of associations between genetic tests and phenotypes, as claimed by the company. In 2007, NBCEC facilitated a validation study for three commercially available genetic tests (GeneSTAR Quality Grade, GeneSTAR Tenderness and Igenity TenderGENE) for quantitative beef quality traits. All three of the genetic tests involved a marker panel, where the test involved genotyping more than one marker locus. Results yielded that

tenderness could be improved by selecting for the favorable calpastatin and μ -calpain genotypes included in the GeneSTAR Tenderness and Igenity *TenderGENE* marker panels. It was also found that the GeneSTAR Quality Grade panel may also be associated with an increased percentage of USDA Choice or Prime grade carcasses. Validation of the effects of genetic markers in independent populations appears to be vital to implementation of genetic testing technology as some producers may be reluctant to invest in unproven markers (Van Eenennaam et al., 2007).

The third and final phase of an MAS program is the implementation of markers which have shown to be predictive in independent populations. Individual markers and marker panel data should be used in combination with phenotypic and EPD information for the prediction of genetic merit of individuals within the population (Davis and DeNise, 1998). In early generations of selection programs, the use of marker and phenotypic information appeared superior to phenotypic selection alone (Lande and Thompson, 1990), also MAS was shown to be most efficient in large populations in addition to early generations of selection and when the trait occurs before measurement (Meuwissen and Goddard, 1996). Selection also appears more efficient if markers are evaluated in every generation (Gimelfarb and Lande, 1994). Marker assisted selection may increase the annual rate of genetic gain in livestock by 15 to 30% without increasing the risk involved in breeding schemes (Ge, et al., 2001). Edwards and Page (1994) estimated the total genetic gain of using MAS to range from 44.7 to 99.5%, depending on the model. However, as strong as these publications appear, application of MAS in the beef industry has not been heavily implemented or studied thoroughly in large populations of beef cattle.

ETH10 Microsatellite Association with Growth and Carcass Traits in Brangus Cattle.

Microsatellites have been identified in both coding and non-coding sequences of the genome and have been utilized to determine the chromosomal locations of numerous genes. Therefore, it is possible that a percentage of the previously identified livestock MS flanking sequences are located within regions of conserved sequence.

Farber and Medrano (2003) reported that ETH10, a MS marker included in the ISAG parentage panel, was a GT repeat located in the promoter region of the signal transducer and activator of transcription—6 (STAT6) gene on bovine chromosome 5. Biologically, STAT6 is involved in the signaling of growth hormone (GH; Han et al., 1996). Growth hormone regulates postnatal bone and muscle growth and fat metabolism in mammals (Etherton and Bauman, 1998). ETH10 has been strongly associated with marbling in Wagyu cattle (Barendse, 2002).

The International Brangus Breeders Association (IBBA) has required parentage testing for artificial insemination (AI) sires and embryo transfer donor dams. An association analysis utilizing data mining techniques was conducted to investigate the association of ETH10 genotypes with growth and ultrasound carcass phenotypes of cattle registered with IBBA. Genotype and phenotype records registered with IBBA were queried from the association database (n = 2,222 individual's born between 1983 and 2007). A study of 13 allele and 38 genotype frequencies revealed that individual alleles could be grouped into two different-sized classes: small ≤ 215 bp in size, or large ≥ 217 bp in size. This procedure yielded genotypes in the categories of small/small, small/large, or large/ large. Results of the association between ETH10 genotypes and phenotype traits are presented in

Table 1. Frequencies of the small/large and large/ large genotypes were 44.7 and 45.3%, respectively. Associations of genotype to phenotype were evaluated and cattle with small/large genotypes had larger (P < 0.05) birth weight than cattle of the large/large genotype ($36.84 > 35.86 \pm 0.3$ kg). Concomitantly, cattle with the large/large genotype had greater percent fat within LM ($3.51 < 3.67 \pm$ 0.08%; P < 0.05) and more LM per body weight ($0.17 > 0.16 \pm 0.001$ cm²/kg; P < 0.05) than cattle of the small/large genotype. Implications of this study suggest ETH10 genotypes appear to be associated with growth and ultrasound carcass trait levels in Brangus cattle. In addition, these results provide rational for additional investigations involving STAT6 as a candidate gene in studies of the growth endocrine axis (DeAtley et al., 2008). This study is an effort to continue building tools used in selection practices for the genetic improvement of beef cattle and is part of the Masters project of Kasey DeAtley at New Mexico State University.

Trait	Genotype		
	Small/Large	Large/Large	SEM
Frequency, %	44.73	45.32	
Actual birth weight, kg	35.27 ^a	34.35 ^b	0.31
Adjusted birth weight, kg	36.84 ^a	35.86 ^b	0.32
Actual weaning weight, kg	278.08	276.29	2.85
Adjusted weaning weight, kg	287.07	288.95	2.18
Actual yearling weight, kg	456.79	454.31	3.66
Adjusted yearling weight, kg	461.31	458.08	3.67
Actual Ultrasound LM area, cm ²	72.05	71.98	0.73
Adjusted Ultrasound LM area, cm ²	71.86	71.83	0.72
Actual Ultrasound Fat Thickness, cm	0.62	0.64	0.02
Adjusted Ultrasound Fat Thickness, cm	0.61	0.63	0.02
Actual Ultrasound Intramuscular fat, %	3.56 ^a	3.71 ^b	0.08
Adjusted Ultrasound Intramuscular fat, %	3.51 ^a	3.67 ^b	0.08
Actual Ultrasound Rump Fat, cm	1.01	1.04	0.05
LM area/body weight, cm ² /kg	0.16 ^a	0.17 ^b	0.00
ADG kg/d	1 09	1.08	0.02

Table 1. LS means for growth traits and ETH10 genotypes grouped small/large and large/ large in Brangus cattle (3/8 Brahman x 5/8 Angus; n = 2222; DeAtley et al., 2008).

^{ab}Within a row, means without a common superscript differ (P < 0.05).

Marker Panels

Advancement of DNA marker discovery programs resulted in various markers linked or underlying OTL. Commercialization of this technology has vielded marker panels containing various numbers of DNA markers. For example, MetaMorphix, Inc. (MMI; http://www.metamorphixinc.com) offers a marbling panel that includes 128 markers and a tenderness panel that includes 11 markers. Marker panels appear beneficial as they test more than one marker locus and MMI uses them to assist with management decisions. This is referred to as marker assisted management (MAM) and entails using DNA-marker test results to predict the phenotype of the animal being tested. This information can then be used to sort individual cattle into management groups that are most likely to achieve specific end points (eg. Quality grade "Choice or better"). The word "assisted" implies that markers can be used in conjunction with other information on the individual animal such as breed composition, age, weight, condition score, and ultrasound measurements, to assist in sorting animals into groups that can then managed in a uniform manner to target a specific performance goal or market (Van Eenennaam, 2007).

Whole Genome Selection

Meuwissen et al. (2001) suggested a markerbased approach to selection in the absence of phenotypes known as "whole genome selection" (WGSL). Whole genome selection enables the use of single nucleotide polymorphisms (SNP) and haplotype information within beef cattle (USDA, 2007). Animals are genotyped at high-density with 30,000 or more SNPs evenly distributed throughout the genome. Statistical methodology is utilized to determine the genomic regions that contribute to phenotype or additive genetic merit. The statistical technology that underlies WGSL is an extension of association analysis conducted with microsatellite and SNP markers between genotypes and phenotypes. However, associations are achieved for all regions of the genome at once rather than one locus at a time (Sellner et al., 2007). For instance, Illumina now provides an assay that includes ~58,000 SNP throughout the bovine genome (Illumina BovineSNP50 Infinium assay; http://www.illumina.com/pages.ilmn?ID=256).

Benefits of using WGSL will include the ability to obtain precise genetic improvement as SNP markers can be used as a monitor of selection for more than one trait throughout the genome (USDA, 2007) and to increase the rate of response to selection. Potential disadvantages include dramatically increasing the rate of inbreeding and loss of diversity among livestock breeds, as well as the cost of this genotyping procedure (~\$400/animal; Dr. M.G. Thomas, personal communication). For example, individuals who have desirable alleles on one chromosome and undesirable alleles on another will produce progeny that will be different than if parents were heterozygous at both chromosomes. Progeny that inherited both of the favorable alleles would then be more desirable for selection. With these thoughts in mind, Sellner et al. (2007) suggested that the application of WGSL strategies will most benefit the livestock industries that use them within the context of selection indices rather than for the estimation of single trait breeding values.

While DNA technology continues to evolve at a rapid pace, one issue still needs to be addressed, "what is the best way to unite marker information with selection tools used today (i.e., EPD)." Two USDA funded research efforts are currently under way to explore this issue. The first is being conducted by Mark Thallman and co-workers of the USDA/ARS Meat Animal Research Center to genotype 2,000 AI sires and evaluate the ability to associate whole genome SNP data with phenotype and how to incorporate this information into breeding values. Phenotypes in this study will be derived from breed associations. The objectives of the second effort will be funded by USDA-NRI competitive grants program to develop analysis software and bioinformatics infrastructure for whole genome animal selection, validation, and application technology to a range of animal species. Specific to the beef industry, this effort will enable the application of genomic evaluation to a range of economically important traits (Thomas, 2008).

Conclusions and Implications to Genetic Improvement of Beef Cattle

A combination of economic and political circumstances will create a dramatic change in the beef industry within the next five years. Therefore, producers need to be planning for enhanced production efficiency and selecting cattle to fit their changing management. DNA marker technology has evolved from blood typing to the discovery of microsatellites and SNPs which are included in panels for specific traits of the entire bovine genome. This paper reviewed the concept of marker assisted selection (MAS) in the beef industry and presented recent results that can potentially contribute to DNA-based genetic improvement programs. Marker assisted selection and WGSL are tools that have the potential to be very beneficial in selection practices; however, the methodology of including this information as part of selection tools used frequently today (i.e. EPD) needs research and development.

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