Recent Advances That Impact Skeletal Muscle Growth and Development Research[1]

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ABSTRACT: Numerous technological advances and scientific insights have had profound effects on our understanding of skeletal muscle growth and development. The objective of this review is to highlight a new technology and recent findings on the functional responses of skeletal muscle/satellite cells to physiological stimuli. First, recent technological advances have facilitated global gene expression profiling experiments. This type of research has, for the first time, provided researchers with insights into cell/tissue-wide response to a given treatment. These experiments have dramatically increased our understanding of the extent to which cells/tissues respond. Furthermore, these experiments have implicated previously underappreciated genes as playing potentially vital roles in biological events. Secondly, recent advances have suggested that the cell culture model utilized can greatly influence the results and conclusions obtained from an experiment. Under standard culture conditions, satellite cells obtained from aged rats are capable of only a few rounds of replication before becoming senescent. Under conditions of reduced oxygen content, the number of rounds of replication is greatly increased. These results demonstrate that experiments using traditionally accepted in vitro culture conditions might be flawed. Finally, recent studies have identified a population of pluripotent stem cells in skeletal muscles termed side population cells. These cells possess the ability to efflux Hoechst dye, which distinguishes them from all other cells that cannot efflux the dye. These cells are capable of differentiating into many other tissue types in vitro and in vivo. With these new technologies and insights, our portrait of skeletal muscle growth and development continues to evolve.

Key Words: Cells, Cell Cultures, Differentiation, Gene Expression, Skeletal Muscle

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Introduction

The growth and development of skeletal muscle has long been of interest to animal scientists. Not only will a better understanding of this process lead to improved strategies to increase the efficiency of lean tissue deposition in domestic animals, but it also has human health implications. Thus, there is an ever-growing need to define the molecular mechanisms controlling embryonic and postnatal skeletal muscle growth and development.

Throughout the history of skeletal muscle growth and development research, there have been a number of landmark discoveries. The ability to grow myoblast/myotubes in cell culture (Rinaldini, 1959), the discovery of the satellite cell (Mauro, 1961), and the discovery of myoD (Lassar et al., 1986) to name a few. Our intent here is to discuss one technology and two research advances that we believe will have dramatic effects on how skeletal muscle growth and development research is conducted. First, we will discuss several microarray-based gene expression profiling experiments that have been conducted with skeletal muscle. Traditionally, researchers have taken a reductionist approach (i.e., one gene/protein at a time) to studying skeletal muscle growth in vivo and in vitro. However, with the advent of high-throughput technologies, such as complementary DNA (**cDNA**) microarrays (Schena et al., 1995), more systems-based biological studies are becoming increasingly possible (Kitano, 2002). Second, we will discuss the affects that atmosphere may have on in vitro experiments. Cell culture has long been used as a technique to study skeletal muscle growth and development in vivo. Recent research suggests that atmospheric conditions can dramatically affect cell culture results. Finally, we will discuss some recent findings with skeletal muscle-derived stem cells. Recent studies have suggested that not only satellite cells, but also stem cells,

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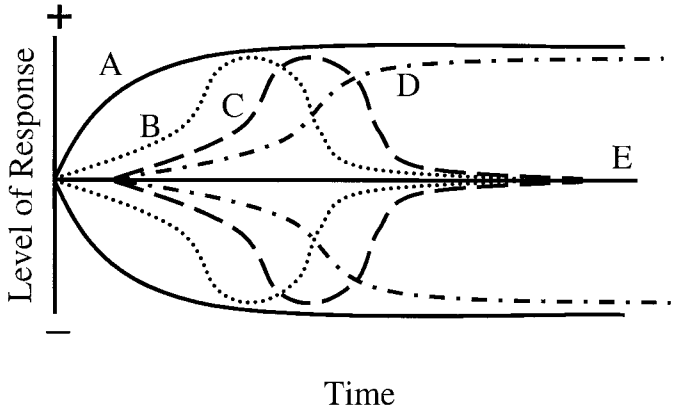

Figure 1. Potential changes in messenger RNA (mRNA) levels in response to a stimulus. A) The mRNA level may rise and remain elevated. B) The mRNA level may rise then return back to baseline levels (i.e., immediate response gene). C) The mRNA level may rise in a delayed fashion and then return to a baseline level of expression. D) The mRNA level may rise in a delayed manner and remain elevated. E) Alternatively, the mRNA level may not change. The mirror image of each of these response lines is also possible.

reside in skeletal muscle (Jackson et al., 1999; McKinney-Freeman et al., 2002).

Microarray Gene Expression Analysis

To further our understanding of skeletal muscle growth and development, we need to identify genes that play critical roles in the different stages of skeletal muscle growth and development. Pinpointing these genes has traditionally been done on a gene-by-gene basis (i.e., a single gene is identified as suggestive and studied independently). This systematic evaluation has several benefits: 1) experiments can be designed so that each gene can be thoroughly investigated, and 2) the idea that a single gene(s) controls an important trait is compelling. Furthermore, if a trait like muscle hypertrophy is regulated by a small subset of genes, it should be relatively easy to design strategies to manipulate these genes for medical and commercial use.

Until recently, scientists were constrained by a lack of technology allowing analysis of global changes in messenger RNA (**mRNA**) levels. Today, advances in gene transcript profiling techniques, such as microarray and similar technologies, allow for genome-wide or tissue-specific examination of global changes in gene transcription in response to an experimental stimulus (Figure 1). The promise of these new technologies lies in their potential to tie specific changes in gene expression to a phenotype of interest. It is beyond the scope of this review to discuss issues related to the way microarray experiments are conducted, or to discuss the different platforms utilized. For those discussions, we would direct you to a number of recent articles (Strausberg and Austin, 1999; Hedge et al., 2000; Brazma et al., 2001). For those readers interested in the fundamental differences in different gene expression profiling arrays, such as macroarray vs microarray and cDNA spotted vs oligonucleotide array, we would direct you to Freeman et al. (2000). Furthermore, it is beyond the scope of this discussion to evaluate different approaches to the statistical analysis of microarray experiments (see Wolfinger et al., 2001; Kerr and Churchill, 2001a,b). However, by no means are these lists complete, as this field is quickly evolving. It is also important to note that microarrays are not the only high-throughput gene expression profiling system. Other systems, such as serial analysis of gene expression (Velculescu et al., 1995), subtractive hybridization, CuraGen GeneCalling (New Haven, CT), or Lynx Therapeutics Megasort (Hayward, CA) are also used. However, to date, microarray technology has been utilized to the greatest extent.

In this section, we will review the results of several studies that have utilized microarrays to gain a greater understanding of the changes in gene expression that accompany 1) aging of skeletal muscle, 2) muscle fiber type differences, and 3) physical activity level. We will finish this section with a discussion of the availability of microarrays for livestock species and the need for complementary technologies, such as proteomics.

Effect of Age on Skeletal Muscle Gene Expression

Although the changes in gene expression during aging do not directly impact animal agriculture, it is an important area of research. In humans, identifying genes that are involved in the diminished muscle mass and impaired muscle function seen during aging is critical to combating these problems. To analyze important questions about the effects of aging on skeletal muscle, several microarray studies have been conducted.

Jozsi et al. (2000) used Atlas human macroarrays from Clontech (Palo Alto, CA) to examine the changes in gene expression in the vastus lateralis that accompanies aging. Their results suggest that skeletal muscle in older men had a similar baseline stress-response expression profile to exercised muscle from young men. This study indicated that genes differentially expressed in older muscle had an attenuated response to resistance exercise in senior men. Not only is aged skeletal muscle stressed at basal activity levels in comparison to young skeletal muscle, but it also cannot respond to the extent to which younger muscle responds to increased physical activity.

Previously, several studies have demonstrated that reduced caloric intake could increase life expectancy in rats and mice (Weindruch and Walford, 1988; Fishbein, 1991). Microarray analysis has been conducted with Affymetrix (Santa Clara, CA) GeneChip technology. See Lockhart et al. (1996) for a description of Affymetrix-based gene expression analysis on the impact of caloric restriction on aging in the skeletal muscle of the mouse (reviewed in Weindruch et al., 2001). A compari-

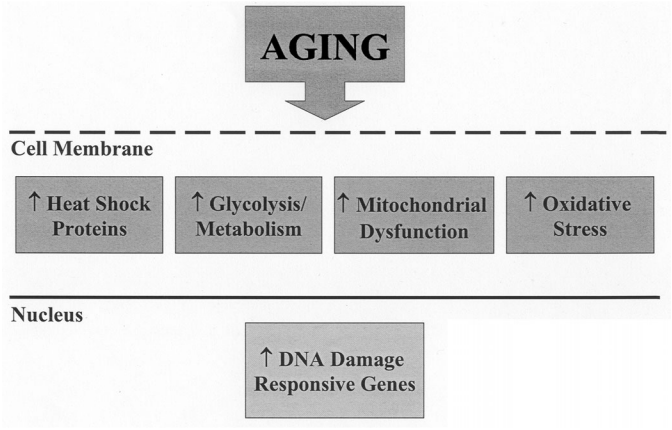

Figure 2. Changes in gene expression in skeletal muscle associated with aging. Differentially expressed genes were involved in DNA damage, metabolism, and stress response. Each system is shown relative to its location within the cell.

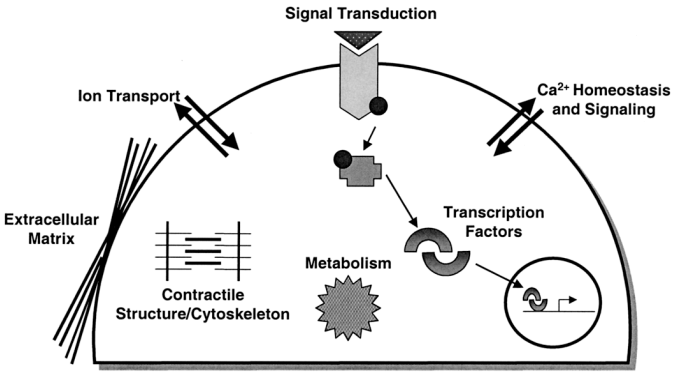

Figure 3. The changes in gene expression in the red soleus vs white quadriceps muscles. Differentially expressed genes were involved in Ca^{2+} homeostatis and signaling, contraction and cytoskeletal structure, extracellular matrix, ion transport, metabolism, signal transduction and transcriptional regulation. Each system is shown relative to its location within the cell.

son of gastrocnemius muscle from 5- (adult) and 30-mo-old (old) mice indicated an increased stress response (i.e., increased heat shock protein, DNA damage, inducible and oxidative stress, inducible gene expression, decreased energy metabolism (i.e., reduced glycolysis), increased neural damage and repair, and increased mitochondrial dysfunction in aged skeletal muscle (Figure 2). In contrast, caloric restriction increased protein metabolism (i.e., increased protein synthesis and degradation), energy metabolism (i.e., increased glycolysis, gluconeogenesis and pentose phosphate shunt), and biosynthesis of fatty acids and nucleotide precursors, and decreased macromolecular damage (i.e., decreased heat shock factors, detoxification systems, and DNA repair systems). Caloric restriction appears to completely reverse or at least alleviate many of the changes in gene expression observed in aged skeletal muscle. It is important to note that tissues capable of cellular proliferation do not respond identically to postmitotic skeletal muscle (Weindruch et al., 2001).

As it is with many diseases, the mouse is a commonly used model for aging in humans. Recent work by Welle et al. (2001) compared Affymetrix oligonuleotide microarray analysis results of aging in human skeletal muscle to that in mice. In that study, they examined the changes in gene expression between eight healthy young men (mean: 23-yr-old) and eight healthy old men (mean: 71-yr-old) to the changes in gene expression reported by Lee et al. (1999) between 5- and 30-mo-old mice. The results of this comparison demonstrated that the effects of aging were often not the same between the two species. This finding underscores the need for caution in the use of the mouse as a model for other species. However, it is difficult to document that the physiological age of the tissues examined in humans and mice were identical. Thus, the observed differences could be due to physiological age differences between species.

Effect of Red vs White Skeletal Muscle on Gene Expression

A gene expression profiling experiment that has implications on animal production is a study conducted by Campbell et al. (2001). They investigated the changes in gene expression between the white quadriceps muscle, which is comprised of 100% type-IIb muscle fibers, and the red soleus, which is comprised of 70% type-I and 30% type-IIa muscle fibers in female ICR mice. Using Affymetrix GeneChips, they identified 49 differentially expressed genes, 27 of which were expressed at a higher level in the quadriceps muscle, and 22 genes of which were higher in the soleus muscle. In general, these genes could be subclassified into the following categories: 1) Ca^{2+} homeostasis and signaling, 2) contractile structure/cytoskeletal, 3) metabolism, 4) extracellular matrix, 5) ion transport, 6) signal transduction, 7) transcription factor/coregulator, and 8) miscellaneous (Figure 3). As expected, the group with the greatest number of genes, whose expression differed, was that of energy metabolism. The next largest group was that of the transcription factors and coregulators, which suggests that regulation of fiber type at the transcriptional level may be greater than previously appreciated. Furthermore, these candidate genes offer new inroads necessary to define the transcriptional controls underlying the differences between red and white skeletal muscle.

In terms of animal agriculture, we know that muscle that is composed of predominately white/glycolytic/type IIb myofibers grows at a faster rate than muscle composed of red/oxidative/type I myofibers (Swatland, 1994). Alternatively, we know that the meat- processing characteristics of glycolytic myofibers are inferior to

that of oxidative myofibers (Xiong, 1999). Any strategy devised to either increase skeletal muscle growth or improve meat-processing characteristics by changing skeletal muscle fiber-type composition would need to bring about reciprocal changes in gene expression. It is distinctly possible that information provided by this experiment has supplied us with a starting point to begin to break the antagonism between increased skeletal muscle growth rate and decreased meat quality. If we could identify strategies to increase oxidative myofiber growth rate without converting it to a glycolytic myofiber, we could truly benefit the meat industry by dramatically improving meat quality.

Effect of Increased Physical Activity on Gene Expression

The structural adaptation of skeletal muscle to work overload is well characterized (Goldberg, 1967). However, a comprehensive understanding of the molecular events underlying skeletal muscle hypertrophy remains elusive. To investigate the global changes in gene expression induced by work overload, microarray analysis of gene expression was performed on overloaded rat skeletal muscle. Rats were randomly assigned to work overload, which was induced in the soleus muscle by gastrocnemius ablation, or to a control group, which received a sham operation. The soleus was collected after 3 d of work overload from each rat and total RNA was isolated and analyzed (Carson et al., 2002).

In the past, many microarray experiments have not been statistically analyzed. This needs to change and progress is being made. We statistically analyzed our microarray data in two different ways. First, we performed an ANOVA test coupled with the bootstrapping of residuals to determine a *P*-value for each gene. This analysis provided us with a list of 19 genes with a type I error rate of 5%. Due to the cost of conducting the experiment and the small number of animals utilized in this study, we wanted to be as comprehensive as possible in identifying differentially expressed genes, so we also performed a false discovery rate analysis. This returned 125 genes, of which 5% were false positives (Carson et al., 2002).

We hoped to identify potential pathways and specific genes that may play important roles in skeletal muscle hypertrophy. As with any broad-based analysis, microarray data is most useful as a tool to locate candidates for detailed investigation. Work overload altered the mRNA levels of metabolism and intracellular genes and increased the expression of transcription factors, extracellular matrix, and immune response genes (Carson et al., 2002). In addition, the expression level of genes involved in cell-cycle regulation and protein metabolism increased (Figure 4).

One of the advantages of global gene expression analysis is the identification of potential pathways that were not previously implicated. The practical value of global analysis lies in its ability to gather individual, differential expression changes into an overall portrait of a biological event. This overview can identify interactions that previously may have been overlooked. However, such an overview is not possible with traditional molecular techniques. The number of transmembrane and intracellular signaling genes that were differentially expressed as a result of work overload intrigued us—particularly the number of genes whose expression level increased, which can increase Janus kinase/signal transducers and activator of transcription pathway signaling activity (Figure 5) (Carson et al., 2002). Alternatively, other labs may be more interested in the number of immune related genes whose expression levels change in response to work overload.

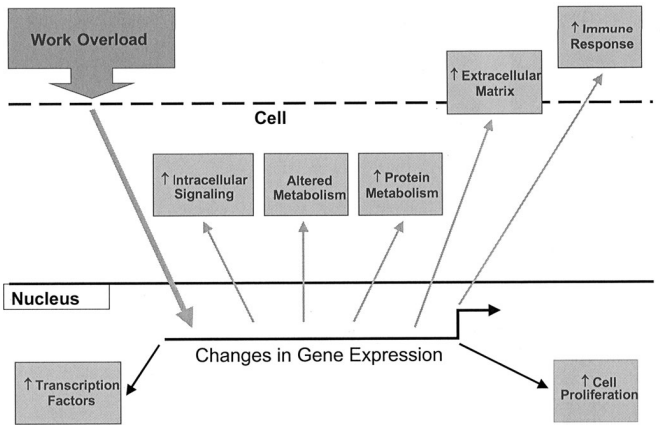

Figure 4. The changes in gene expression in the rat soleus in response to 3 d of work overload can be parsed into different cellular responses. Physical activity is converted into a chemical signal, which results in changes in gene expression. These genes, whose expression level changed, play important roles in the physiological response of skeletal muscle, such as altered metabolism and increased cellular proliferation.

An important point to consider is that although the microarray analysis was conducted with skeletal muscle, this tissue contains a variety of cell types. Muscle cells, such as myofibers and satellite cells, are highly

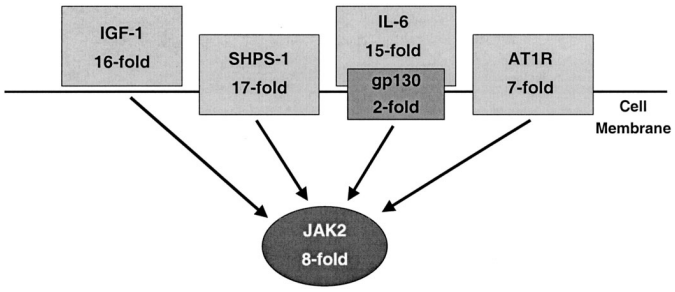

Figure 5. Some identified changes in gene expression in the rat soleus in response to 3 d of work overload. The arrows represent pathways that have been reported to occur within at least one cell type.

abundant, but other cell types, such as fibroblasts, nervous tissue, smooth muscle, and endothelial cells, are also present. Work overload is an insult to the muscle tissue and results in immune cell infiltration. Since all of these cell types contribute to muscle hypertrophy, it is impossible to determine precisely which cells account for specific mRNA changes without performing in situ gene expression analysis of each gene. This raises an interesting problem of systems-based research. Once an experiment is completed, future individual gene-based experiments are often required to better understand the molecular mechanisms involved.

In animal agriculture, we know that maximal skeletal muscle growth is repressed in growing animals. Several lines of evidence support this contention. First, the double-muscle phenotype is the result of the inactivation of myostatin (Grobet et al., 1997; Kambadur et al., 1997; McPherron and Lee, 1997). Thus, skeletal muscle growth is inhibited by functional myostatin. Second, work overload can stimulate an increased rate of skeletal muscle growth in a rapidly growing rat (Goldberg, 1967). These two phenotypes suggest there is a large untapped potential for increased skeletal muscle growth. However, reproduction problems will limit the introgression of the myostatin null allele into commercial cattle herds. In addition, myostatin-null alleles do not exist in other livestock species. Furthermore, producers are not going to exercise livestock to increase skeletal muscle growth. However, if we can determine the molecular mechanisms whereby physical activity and/or double muscling alleviate the repression of muscle growth, we should be able to develop strategies to increase postnatal skeletal muscle growth. Obtaining a global picture of gene expression in these phenotypes is an initial step in that direction.

Microarrays for Livestock Species

Information obtained from microarray data offers a unique opportunity to gain a broad sense of an organism's genetic response to stimulus. Microarray analysis could benefit behavioral, genetic, nutritional, physiological, and reproductive evaluation of livestock. Furthermore, microarrays can be used to evaluate the beneficial or detrimental effect of a treatment (i.e., toxicogenomics; Waring and Ulrich, 2000). In livestock species however, the only microarray that is commercially available is a small one for cattle (Band et al., 2002; http://www.anigenicsinc.com). The only microarrays for pigs and chickens are those used within individual labs. Today, we are primarily limited to using model organisms in an attempt to answer questions of economic importance to the livestock industry. However, this will rapidly change in the near future.

Although changes in gene expression can be indicative of changes in protein production, it is important not to assume that differential mRNA production will always result in corresponding protein levels and activity. In addition to microarray data, it would be very informative to have proteomic information. Proteomics is simply defined as the global analysis of changes in protein expression (for reviews, see Honore, 2001; Lawrie et al., 2001; Martin and Nelson, 2001). Proteomics takes advantage of the ability to couple two-dimensional electrophoresis with high throughput technology to separate and identify proteins of interest. Factors such as mRNA stability and transcription, protein translation efficiency, and protein modifications all play a role in the ultimate impact a gene will have. Microarray and proteomic analyses should be viewed as tools to identify interesting areas that warrant further investigation. Although these are exciting molecular advancements, both must be used with caution and with the knowledge that these changes are only suggestive of the ultimate molecular events.

Low Oxygen

Traditional muscle-cell culturing methods have focused on understanding the mechanisms controlling myoblast proliferation and differentiation. However, the atmospheric conditions used during this in vitro period have been largely ignored. Recent experiments have suggested that maintaining cells under more physiological atmospheric conditions may have many benefits. Since the 1930s, cell culture experiments have used a combination of 5% CO_2 and 95% air (Parker, 1938) to help maintain media pH. Cells are exposed to atmospheric conditions that contain approximately 20% oxygen. In contrast, the level of oxygen found in vivo is a magnitude or more less than this. The partial saturation of oxygen found in mature skeletal muscle is reported to be between 1 to 10% (Greenbaum et al., 1997; Richardson et al., 1998). Recently, studies have been performed that have sought to address the effects of culturing cells in a more physiologic environment.

Morrison et al. (2000) and Studer et al. (2000) first reported that central nervous system and neural crest stem cells had increased rates of proliferation, reduced apoptosis, and increased dopaminic neuron generation when cultured in lowered vs traditional oxygen conditions. Based on these results, Chakravarthy et al. (2001) examined the effect of decreased oxygen on the activation and proliferation of satellite cells from aged rats. Under standard cell culture conditions, satellite cells isolated from aged rats undergo only a couple of cycles of replication. Cells that were cultured under atmospheric conditions containing approximately 3% oxygen had a significant increase in proliferation rate and formed larger myotubes than control cells cultured in 20% oxygen. Proliferating myoblasts cultured in lowered oxygen had increased protein levels of G1/S cyclins and cyclin-dependent kinases, as well as decreased levels of the cell cycle inhibitor $p27^{Kip1}$ (Chakravarthy et al., 2001). These results indicate that even mature satellite cells that are mitotically inactive under traditional culturing conditions can be stimulated to proliferate in the right environment.

Csete et al. (2001) found similar results using whole muscle fiber cultures. There was an increase in the chemotaxis and proliferation of satellite cells cultured in lowered oxygen, as well as increased survival of the fiber itself. It is also interesting that some of the satellite cells that were adherent to the fiber could take on an adipocyte phenotype. Furthermore, the percentage of adipose cells on fibers maintained at 20% oxygen was greater than that on fibers maintained at 6% oxygen. These results imply that there are pathways in the cell-regulating, cell-proliferation, and cell-fate determination that are responsive to the level of oxygen exposure.

The implications of this line of research are quite staggering. Generally, we would like to assume that the results from cell culture experiments could be extrapolated to an in vivo situation. In situations where cell culture results could not be recapitulated in vivo, it is distinctly possible that traditional atmospheric conditions may have caused these confounding results. It is not easy to culture cells in a lower oxygen environment because special equipment is needed to regulate and monitor oxygen levels. However, we need to seriously consider accepting these challenges as the new standard for cell culture if we are to obtain meaningful data. Acceptance of this new standard should improve the transfer of cell culture-obtained knowledge to an in vivo setting. It will still be an absolute requirement to perform in vivo experiments to validate cell culture findings as being biologically meaningful. This line of research is new enough that we do not yet know what truly constitutes physiological oxygen concentration vs hypoxia and hyperoxia. Furthermore, there is a question of whether optimal oxygen concentrations are organism specific (e.g., mammalian vs amphibian).

The results of Csete et al. (2001) question whether we can manipulate the differentiation of satellite/stem cells located within skeletal muscle to differentiate into either skeletal muscle or adipose. If we wanted to maximize the production of lean meat (i.e., low marbling score), it would be advantageous to maximize the percentage of cells differentiating into skeletal muscle. Conversely, if we wanted to produce a meat product with high levels of intramuscular fat, it would be beneficial to ensure that adequate numbers of cells were directed to differentiate into adipose cells. Would it be possible to do so in a programmable fashion? Could we maximize skeletal muscle production throughout most of the growing period and then only toward the end of the feeding period switch to adipose production or vice versa?

Skeletal Muscle-Derived Stem Cells

There have been several recent reviews that addressed the physiology (Hawke and Gary, 2001) and stem cell potential (Seale and Rudnicki, 2000; Seale et al., 2001) of muscle satellite cells. Considerable effort has been focused on the role of these cells in modulating skeletal muscle growth and repair. Satellite cells were the first stem cell-like cells isolated from skeletal muscle, although further potential stem cell populations have since been described. The use of fluorescence-activated cell sorting (**FACS**) has revealed several of these putative stem cell populations, the most interesting of which is a recently discovered subpopulation of muscle cells termed side population (**SP**) cells.

Goodell et al. (1996) first characterized SP cells when they were trying to stain murine bone marrow cells with Hoechst 33324 dye. They used FACS and found that a small portion of the cells could exclude the Hoechst dye. Upon further analysis, these cells had many of the phenotypic markers for hematopoietic stem cells (**HSC**). Hematopoietic stem cells are multipotential and can take on either a myeloid or lymphoid phenotype. The cells contain multidrug resistance proteins that enable them to efflux the dye. The stem cell potential of this population was confirmed in vivo in mice that received a lethal dose of radiation. The bone marrow of these mice was destroyed by the radiation treatment, but the intravenous injection of a small portion of the SP cells was able to reconstitute the bone marrow, blood, and lymph systems. SP cells have since been isolated from human, porcine, and rhesus marrow (Goodell et al., 1996).

Skeletal muscle also has a small portion of these HSC-enriched SP cells (Gussoni et al., 1999; Jackson et al., 1999). Muscle-derived SP cells from male mice were able to reconstitute the marrow compartment of lethally irradiated female *mdx* mice (Gussoni et al., 1999), a Duchenne's muscular dystrophy model. They also found that 90% of the spleen cells were positive for Y chromosomes and were donor derived. The muscle of *mdx* mice is dystrophin negative, but after the addition of the wild-type male SP cells, there was a small proportion of donor-derived dystrophin-positive myofiber nuclei. The muscle-derived SP cells were not as effective as marrow SP cells at replacing the bone marrow of irradiated mice, however, since it took 10 times more muscle SP cells to achieve effective reconstitution. Donor-derived SP cells from muscle were found in the blood of irradiated mice up to 3 mo after transplantation (Jackson et al., 1999). These results indicate that satellite cells are not the only potential stem cells in mature skeletal muscle and, in fact, are more differentiated than SP cells. In support of this contention, McKinney-Freeman et al. (2002) reported that muscle-derived SP cells could be fractionated into hematopoietic (Sca-1 positive and CD45 positive) and myogenic cell populations (CD45 negative). A note of caution, however: these results question the notion of adult-derived stem cells. These two cells populations had differing abilities to differentiate into different cell types. The CD45 negative cells were myogenic in vitro and in vivo. In contrast, the CD45-positive hematopoietic cells were only weakly myogenic in vivo and not in vitro.

Blanton et al. (1998) described two distinct populations of primary pig myoblasts using FACS and culturing. Two days after isolation, there was a homogeneous

population of smaller myoblasts, as well as a population of larger diameter cells that consisted of myoblasts and fibroblasts. They found that at d 2, the predominant population was that of the smaller myoblasts, although since these cells were activated to proliferate, their size increased. None of the smaller myoblasts was visible after two passages; Barrafio et al. (1995) showed that this population of cells could be recovered from myoblast populations that were induced to differentiate. Following differentiation, there is a small portion of cells that fail to fuse with the myotubes, and these cells represent a potential long-term stem cell population.

Skeletal muscle contains not only satellite cells that can differentiate into skeletal muscle, but also a subset of cells that are capable of differentiating into other cell types. This leaves a number of open questions. Are stem cells and satellite cells the same, or are they two separate populations? If they are two separate populations, are satellite cells simply partially differentiated stem cells? How can we identify stem cells and satellite cells in skeletal muscle? How can we independently study stem cells and satellite cells in vivo? Regardless of these cell population questions, it appears that we need to change how we study satellite cells in cell culture. Traditional satellite cell studies are conducted by isolation of single nucleated cells from skeletal muscle and subsequent evaluation in cell culture. Thus, these cultures contain stem cells and satellite cells, as well as other cell types (i.e., fibroblasts). Traditionally, we have investigated the activation, proliferation, and differentiation of satellite cells in cell culture. If satellite cells are capable of only so many rounds of replication before reaching senescence, whereas stem cells are capable of multiple rounds of replication, would it not be beneficial to specifically identify strategies to enhance stem cell activation, proliferation, and subsequent differentiation into skeletal muscle? Similarly, we would also want these strategies to maximize satellite cell activation, proliferation, and differentiation. We should then be able to maximize the efficiency of livestock growth.

The use or activation of satellite cells and other potential stem cell populations will continue to be important in the future. The use of pharmacological or other methods to stimulate the activation of muscle stem cells is one potential mechanism to increase muscle mass. Ex vivo expansion of myoblast populations and subsequent transplantation is another possibility. These experiments would certainly be aided by the use of a more physiological environment, as described earlier during expansion.

Implications

Great strides have been made in our understanding of skeletal muscle growth and development. These advancements have come about because of technological innovations and scientific discovery. It is our belief that microarray analysis of gene expression, atmospheric culture conditions, and skeletal muscle-derived stem cells are advances that will have profound influences on our understanding of skeletal muscle growth and development. However, future advances will be necessary if we are to successfully develop new strategies to enhance lean tissue deposition in livestock and/or prevent muscle loss in at risk individuals.

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Reducing the cost of beef production through genetic improvement in residual feed intake: Opportunity and challenges to application[1]

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ABSTRACT: There is considerable individual animal variation in feed intake above and below that expected or predicted on the basis of size and growth rate. This difference in intake is calculated as residual (or net) feed intake (RFI). Genetic variation in RFI of beef cattle exists both during growth (slaughter generation and replacement females; heritability estimates since 1996 range from 0.16 to 0.43) and in adult cattle (the breeding herd; the one published heritability estimate is 0.23). Evidence shows that selection for lower RFI measured postweaning will lead to a decrease in feed intake by young cattle and by cows, with no compromise in growth performance or increase in cow size. Results from a single generation of divergent selection on postweaning RFI between 8 to 12 mo of age demonstrated favorable correlated changes in average daily feed intake (9.2 ± 0.2 vs. 9.8 ± 0.2 kg/d), RFI (–0.20 ± 0.11 vs. 0.17 ± 0.10 kg/d), and feed:gain ratio (F:G; 7.0 ± 0.2 vs. 7.6 ± 0.2 kg/kg) in Angus feedlot steers. In Angus cattle, the genetic correlation between postweaning RFI with average daily feed intake by the cow is high (0.64), and the correlation between postweaning RFI and cow RFI is very high (0.98); however, the correlation between postweaning RFI and cow F:G is low (–0.06). These genetic correlations indicate that selection against postweaning RFI has the potential to lead to a decrease in feed intake and improvement in feed efficiency of growing animals and mature animals. Measurement of feed intake might occur in central test stations, or on-farm, and uniform guidelines are required to ensure that standardized and accurate data are generated. Ways of utilizing information generated in genetic evaluations are discussed. An EBV for feed intake after a phenotypic adjustment for growth performance (growth rate and BW) seems most practical. Such EBV would best be used in an economic selection index to account for genetic correlations with other traits in the breeding objective, including feed intake of the breeding herd, and the economic value of feed in relation to other traits. Further research is needed to examine these genetic relationships and to find ways for cost-effective identification of superior cattle.

Key Words: Beef Cattle, Feed Intake, Genetic Correlation, Heritability, Selection

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Introduction

Providing feed to animals is a major cost input in almost any animal production system. This has long been recognized by the pig and poultry industries, in which cost of feed is easily quantified. These industries have made significant improvements in feed efficiency through both genetic and nongenetic means (Luiting, 1991). Although the cost of providing feed to grazing animals is more difficult to quantify in extensive grazing industries, the provision of feed is a major cost in beef production, and improvement of the output of beef per unit of feed used over the whole production system would be of significant economic benefit.

The majority of national genetic improvement programs for beef cattle have emphasized selection to improve outputs, such as BW, and more recently, fertility and carcass traits. There is a need to also consider avenues for reducing inputs in order to improve efficiency of production and to increase profit. Avenues for genetic improvement of production system feed efficiency include choice of breed, crossbreeding and selection within breeds. Research has shown that there is considerable individual animal variation in feed intake

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above and below that expected or predicted on the basis of size and growth rate (e.g., mice: Archer et al., 1998; poultry: Luiting and Urff, 1991; pigs: Foster et al., 1983; cattle: reviewed by Archer et al., 1999b). This difference in intake is generally calculated as residual feed intake **(RFI).** In some reports RFI is also called net feed intake, referring to its derivation as actual feed intake net (or less) of expected feed intake for BW maintained and ADG by an animal over a test period. The term "net feed efficiency" is also used and refers to feed efficiency net of size and level of production. This paper reviews new evidence for the potential of within-breed selection on RFI to improve production system feed efficiency and the application challenges to industry adoption.

Genetic Variation in Feed Efficiency of Beef Cattle

Feed intake is generally correlated with output traits, and therefore examination of feed intake or production outputs in isolation from each other usually provides little or no indication of the efficiency of production. To make comparisons between animals, many researchers have considered feed intake and production outputs over a limited part of the production cycle and expressed "feed efficiency" using an index, which combines feed intake (the input) with production (the output). Evidence for genetic variation in indices of feed efficiency, including RFI, published for beef cattle up to 1996 was reviewed by Archer et al. (1999b). Since 1996, genetic variation in RFI has been reported in a range of beef cattle breeds in studies from Australia (Arthur et al., 2001b), Britain (Herd and Bishop, 2000), Canada (Liu et al., 2000), and France (Renand et al., 1998).

The efficiency of a beef production system depends on the summation of many traits that include feed intake of both the breeding herd and slaughter generation, growth traits, and other cow traits, such as mature size and reproductive rate (Archer et al., 1999b). Selection for lower RFI (a measure of net feed efficiency, which accounts for feed required to maintain BW and for growth) measured postweaning has the potential to lead to a reduction in the intake of young cattle and of cows, with no compromise in growth performance or increase in cow size. This is not the case for selection to reduce feed:gain ratio (F:G) in which the genetic correlation with growth rate can lead to an increase in cow size and feed intake, which is not always desirable (Archer et al., 1999b).

Residual Feed Intake: Opportunity

That individuals of the same BW require rather widely different amounts of feed for the same level of production was acknowledged by Byerly (1941) in his preparation for experiments to determine whether or not individual differences in net efficiency of laying hens are inherited. In growing beef cattle, Koch et al. (1963) recognised that differences in both weight maintained and weight gain affect feed requirements. They suggested that feed intake could be adjusted for BW and weight gain, effectively partitioning feed intake into two components: 1) the feed intake expected for the given level of production and 2) a residual portion. The residual portion of feed intake could be used to identify animals, which deviate from their expected level of feed intake, and was heritable (0.28 ± 0.11), with efficient animals having lower (negative) RFI. While the utility of RFI for within-breed genetic improvement in feed efficiency is the subject of this review, it is worth noting that the concept of RFI can also be used in nutrition studies to detect differences in the efficiency of feed utilization not revealed by measurement of ADFI, ADG or F:G, presumably because of the correlation between these traits. The report by Okine et al. (2001) provides an illustration of the use of RFI to detect differences in efficiency of utilization of energy in feeds.

Literature estimates of genetic variation in RFI of growing cattle published to 1996 were summarized by Archer et al. (1999b). Some more recent estimates are presented in Table 1. Low values for the heritability of RFI reported in some studies appear to reflect higher measurement error (e.g., Herd and Bishop, 2000; CRC, 2001). Nevertheless, these new reports continue to show that there are both phenotypic and genetic variation in feed efficiency of growing cattle beyond that explained by differences in BW and level of production.

The opportunity to improve whole-herd production efficiency through exploitation of genetic variation in RFI is dependent not only on the existence of genetic variation in young cattle but also on the magnitude of the genetic correlations with other key production traits. These traits include growth and feed intake during finishing, carcass and meat quality traits at slaughter, and cow traits, such as mature size, feed intake, milk production, and lifetime reproductive performance. In young beef cattle, results from postweaning tests show that RFI has strong, favorable genetic correlations with F:G of the growing animal (Table 1). Estimates for the genetic correlation for postweaning RFI with measures of fatness at the end of the RFI test are positive but variable (Table 1). They are evidence for a genetic association of low RFI (high efficiency) with lower fatness (increased lean). The variation in estimates for this correlation presumably reflects differences between the actual measurements recorded and the age of the cattle being tested. For example, the genetic correlations reported for RFI of weanling bulls and heifers tested from 8 to 12 mo of age with subcutaneous rib fat and rump fat depths were 0.17 ± 0.05 and 0.06 ± 0.06 (Arthur et al., 2001b) and weaker than reported for steers and heifers tested in a feedlot (RFI with subcutaneous rump fat depth 0.42; CRC, 2001), possibly the result of greater genetic expression of fatness in the feedlot cattle due to older age and a higher-energy diet (CRC, 2001). If this genetic correlation with fatness is expressed in progeny destined for slaughter or in daughters entering the cow herd, then selection

Table 1. Literature estimates published since 1996 for the heritability of residual feed intake in growing beef cattle and genetic correlations with selected postweaning test and mature cow traits

				Postweaning test		Genetic correlation Mature cow		
Breed	Sex[a]	Number	Heritability	F:G[b]	Fatness	RFI[c]	BW	Source
Hereford	M	540	0.16 ± 0.08	0.70 ± 0.22	–0.43 ± 0.23[d]	—	–0.09 ± 0.26	Herd and Bishop (2000)
Limousine and Charolais	M	1,629	0.21 to 0.39[e]	—	0.70[f]	—	—	Renand et al. (1998)
Beef and dairy	M	282	0.29	—	—	—	—	Liu et al. (2000)
British	M & F	1,180	0.39± 0.03	0.66 ± 0.05	0.17 ± 0.05 to 0.06 ± 0.06[g]	—	—	Arthur et al. (2001b)
British	F	751	0.23[h]	—	—	0.98	–0.22	Archer et al. (2002)
Charolais	M	792	0.39 ± 0.04 to 0.43 ± 0.06[e]	0.85 ± 0.05	—	—	—	Arthur et al. (2001c)
British and tropically adapted	S & F	2,155	0.18	—	0.42[i]	—	—	CRC (2001)

[a]M = males; S = steers; F = females.
[b]Feed:gain ratio.
[c]Residual feed intake.
[d]Estimated lean content.
[e]Two ages/feeding regimen and two methods for estimating residual feed intake were used.
[f]Whole body fat.
[g]Scanned subcutaneous fat depth at rib and rump.
[h]Mature cow RFI.
[i]Scanned subcutaneous rump fat thickness.

for low RFI might affect market suitability and reproductive performance of the progeny. Results from divergent selection on postweaning RFI found no change in subcutaneous fat depths in progeny in weanling tests (Herd et al., 1997), no compromise in meeting market specifications by feedlot steers (Richardson et al., 1998), and no change in subcutaneous fat depths in cows (Arthur et al., 1999).

It would be desirable that the genetic correlations for RFI measured on seedstock animals in a postweaning test, with RFI and F:G of their progeny in the feedlot were high, but these correlations are not reported yet. However, there is evidence that this genetic correlation is likely to be high. Arthur et al. (2001d) reported results for Charolais bulls tested as weanlings from 9 to 14 mo of age and then again as yearlings from 14 to 19 mo of age. The genetic correlations were high: 0.75 ± 0.12 between RFI in weanling tests and RFI in yearling tests and 0.54 ± 0.17 for RFI in the weanling tests with F:G in the yearling tests. Furthermore, results from a single generation of divergent selection on postweaning RFI demonstrate favorable correlated changes in RFI and F:G in feedlot steers (Richardson et al., 1998).

Knowledge of the genetic relationships between feed efficiency traits measured in weanling tests with mature cow performance traits is required for breeding programs that are designed to improve whole herd production efficiency. Genetic correlations between postweaning RFI and mature cow size are low or zero (Table 1), indicating that breeding to improve feed efficiency in growing animals though selection against postweaning RFI need not be accompanied by an increase in cow size. This is not the case if selection to reduce postweaning F:G is employed because of the stronger genetic correlation of postweaning F:G with cow size (–0.29 ± 0.24, Herd and Bishop, 2000; and –0.54, Archer et al., 2002). The genetic correlation between postweaning RFI with feed intake by the cow is high and with RFI of the cow very high (0.64 and 0.98, respectively; Archer et al., 2002). There are few reports of the genetic correlations of feed intake and RFI from young growing animals to mature adults for comparison. Niewhof et al. (1992) found a genetic correlation between RFI of dairy heifers measured postweaning with ME-intake during first lactation of 0.52 and with RFI of 0.58. Archer et al. (1998) found a genetic correlation between RFI of mice measured postweaning with ADFI at maturity of 0.50 and with RFI of 0.60. The genetic correlations for postweaning F:G with cow feed intake and cow F:G appear to be low (0.15 and 0.20; Archer et al., 2002) suggesting that selection to reduce postweaning F:G to likely to be accompanied by only small reduction in cow feed intake and F:G. These genetic correlations indicate that selection against postweaning RFI has the potential to lead to a reduction in feed intake by cows with little change in cow size, thus improving the efficiency of the cow herd. This is an important advantage over selection for increased postweaning growth or decreased F:G that can be accompanied by an increase in cow size, which is not always desirable. It is not known whether genetic reduction in cow feed intake would be accompanied by a reduction in foraging activity of cows at pasture, which might not be desirable. Reduction in physical activity, at least within the confines of the test

environment, has been shown for low-RFI animals (e.g., laying hens: Luiting et al., 1991; pigs: De Haer et al., 1993; young beef bulls: Richardson et al., 1999).

Because RFI is by definition phenotypically independent of the production traits used to calculate expected feed intake, it allows comparison between individuals differing in level of production during the measurement period. This independence of RFI from production has led some authors to suggest that RFI may represent inherent variation in basic metabolic processes. For example, genetic variation in maintenance energy requirement per kilogram of metabolic BW is closely associated with genetic variation in RFI in young Hereford bulls (genetic correlation 0.93 ± 0.06; Herd and Bishop, 2000). In laying hens, variation in RFI is mainly caused by variation in maintenance energy expenditure between hens with similar egg mass production and BW (Luiting et al., 1991). In a typical beef cattle herd, the feed energy for maintenance represents 60 to 75% of the total energy requirements of individual breeding cows, and the cost of maintaining cows is clearly an important factor in determining the efficiency and profitability of beef production systems (Archer et al., 1999b). It seems likely that there will be a genetic association between RFI and maintenance efficiency of the cow, but this remains to be demonstrated.

Predictive Value of RFI

There is evidence for genetic variation in RFI measured in young cattle, and the estimates for heritability and genetic correlations with other traits raise expectations for favorable direct and correlated responses in the next generation that include a reduction in RFI and feed intake with little change in size or growth rate for both young cattle and for cows and thus an improvement in feed efficiency in both groups. The validation of the predictive value of RFI in bringing about these favorable changes comes from demonstration of the direct and correlated responses to selection.

The most comprehensive study of the responses to selection on postweaning RFI in beef cattle is that conducted by NSW Agriculture at the Agricultural Research Centre, Trangie, NSW Australia, between 1993 and 2001. The design of the breeding program and postweaning test procedures are described by Arthur et al. (2001b) and the establishment of divergent selection lines for postweaning RFI by Arthur et al. (2001a; 2001b). The following sections present results for the direct and correlated responses to this divergent selection.

Response to Selection— Postweaning Traits

Parents were divergently selected on the basis of their own RFI measured over a postweaning test from 8 to 12 mo of age and their bull and heifer progeny were subsequently evaluated for postweaning RFI under the same test regimen used to test their parents. After 5 yr of divergent selection (1999-born animals; approximately two generations) the direct response was –0.54 ± 0.18 kg/d in the low RFI-line and 0.70 ± 0.17 kg/d in the high RFI-line (Arthur et al., 2001a). Selection for low RFI (more efficient cattle) was accompanied by corresponding reduction in daily feed intake (9.4 ± 0.3 vs. 10.6 ± 0.3 kg/d) and reduced (improved) F:G (6.6 ± 0.2 vs. 7.8 ± 0.2 kg/kg). Yearling weight (384 ± 7 vs. 381 ± 7 kg) and postweaning ADG (1.44 ± 0.03 vs. 1.40 ± 0.03 kg/d) were not affected by divergent selection on postweaning RFI.

Response to Selection—Cow Traits

Preliminary results for the correlated response in cow traits following divergent selection for postweaning RFI were reported by Herd et al. (1998) and Arthur et al. (1999). The cows had been separated into high- and low-efficiency herds based on their own postweaning RFI to form the parent generation for divergent selection. Herd et al. (1998) measured pasture intake by 41 lactating cows that had previously been ranked as either low postweaning RFI (high efficiency) or high RFI (low efficiency), when tested as young heifers on a pelleted ration. The low-RFI cows were 7% heavier (618 ± 16 vs. 577 ± 11 kg), had similar rib fat depths (12.0 ± 0.7 vs. 11.7 ± 0.8 mm) and rump fat depths (15.8 ± 0.8 vs. 15.6 ± 0.8 mm), and reared calves of similar BW to the high-RFI cows (111 ± 4 vs. 104 ± 4 kg) but consumed no more feed than the high RFI cows. The advantage in efficiency of the low RFI cows, when expressed as a ratio of calf BW to cow feed intake, was 15% (9.3 ± 0.5 vs. 8.1 ± 0.4 kg/kg.d, $P = 0.07$). The study suggests a phenotypic association between postweaning RFI of the young female and her later efficiency as a cow/calf unit at pasture.

Arthur et al. (1999) reported results for 284 4-yr-old cows retested for RFI on a pelleted ration after weaning their second calf. Only cow RFI and feed intake over the 70-d test differed between the RFI selection lines, with high efficiency cows having a lower RFI (–29 ± 11 vs. 18 ± 11 kg) and consuming less feed (1093 ± vs. 1144 ± 16 kg) than low-efficiency cows. There were no significant differences in BW (551 ± 7 vs. 550 ± 7 kg) and rib fat depth (4.9 ± 0.3 vs. 5.2 ± 0.3 mm) at the start of the test, nor in ADG over the test (1.20 ± 0.04 vs. 1.21 ± 0.04 kg/d),) between the high-efficiency and low-efficiency lines. Milk yield, measured once during lactation by the calf weigh-suckle-weigh method on 104 cows, did not differ between high- and low-efficiency lines (4.4 ± 0.2 vs. 4.1 ± 0.2 kg/d). The results indicate that females, which were more efficient as weanlings, required less feed as mature cows, with no compromise in performance.

Response to Selection—Steers on Pasture

One cohort of steers born following a single generation of divergent selection for postweaning RFI, as de-

scribed by Arthur et al. (2001a), were evaluated for their growth and feed efficiency on improved pastures (Herd et al., 2002c). The cohort of 53 steers (22 from the low-RFI line, progeny of six sires; 31 from the high-RFI line, progeny of five sires) had pasture intake measured using alkanes as markers. This experiment demonstrated a favorable response in growth and feed efficiency on pasture by steers whose parents had been selected for low postweaning RFI. Significant regression coefficients for traits measured on the steers with their mid-parent EBV for postweaning RFI were used as evidence for genetic association. Steers from the low-RFI selection line tended to grow faster than steers from the high-RFI selection line (0.50 ± 0.02 vs. 0.42 ± 0.02 kg/d; $P < 0.1$), consistent with the negative regression coefficient for ADG with mid-parent EBV for RFI (–0.11 ± 0.05; $P < 0.05$). The difference in daily pasture intake between the selection lines was not significant (3.04 ± 0.11 vs. 3.23 ± 0.14 kg DM/d; $P > 0.1$), nor was the regression coefficient with mid-parent EBV for RFI (0.28 ± 0.29; $P > 0.1$). Feed conversion ratio was 6.4 ± 0.4 kg/kg for low-RFI selection line steers and 8.5 ± 0.8 kg/kg ($P = 0.1$). The positive regression coefficient for F:G with mid-parent EBV for RFI (2.9 ± 1.5; $P < 0.1$) provided evidence for low RFI in the parents being genetically associated with superior efficiency of feed conversion on pasture by their steer progeny, with an approximate three-unit improvement in F:G accompanying a 1-kg reduction in mid-parent EBV for postweaning RFI.

Response to Selection—Steers in the Feedlot

A cohort of Angus and of Angus-crossbred steers born following a single generation of divergent selection for postweaning RFI, as described by Arthur et al. (2001a), were evaluated for their growth, feed intake, feed efficiency, and some carcass attributes in the feedlot. Results were reported by Richardson et al. (1998). For the Angus steers, there was no difference between the progeny of parents selected for low RFI or for high RFI in BW at the start of the RFI tests (283 ± 6 vs. 293 ± 6 kg, respectively), ADG over the test (1.35 ± 0.05 vs. 1.30 ± 0.04 kg/d), and BW at the end of the test (369 ± 7 vs. 375 ± 6 kg). Steers in the low-RFI selection line had lower DMI over the tests (9.2 ± 0.2 vs. 9.8 ± 0.2 kg/d), lower F:G (7.0 ± 0.2 vs. 7.6 ± 0.2 kg/kg) and lower RFI (–0.20 ± 0.11 vs. 0.17 ± 0.10 kg DM/d) than did steers in the high-RFI line. Individual feed intake was not recorded for the crossbred steers. There were significant differences between the selection lines in carcass traits measured ultrasonically before slaughter. The low-RFI line steers had less subcutaneous fat depth at the 12/13th rib and rump (Angus: rib 7.1 ± 0.5 vs. 8.3 ± 0.4 mm; rump 8.3 ± 0.6 vs. 10.2 ± 0.6 mm; crossbred: rib 10.1 ± 0.2 vs. 12.2 ± 0.2 mm; rump 13.3 ± 0.2 vs. 14.3 ± 0.2 mm), and a smaller cross-sectional area of the longissimus dorsii muscle (Angus: 48.5 ± 1.1 vs. 51.4 ± 0.9 cm^2; crossbred: 48.2 ± 1.1 vs. 50.4 ± 1.1 cm^2). Richardson et al. (1998) concluded that the steer progeny of low-RFI (high efficiency) parents grew as fast, or faster, than steers of high RFI (low efficiency) parents but ate less feed per unit gain and produced carcasses of acceptable fat finish with no compromise in retail meat yield, and as a consequence, should be more profitable to feed in a feedlot.

Postweaning RFI and Nutrition Interactions (Genotype × Environment)

Genes conferring advantage in net feed efficiency in a particular test environment may not necessarily confer advantage in other environments. Tests for postweaning RFI usually employ medium-to-high energy density rations both for practical reasons, such as ease of feed handling and measurement of feed intake, and to contain sufficient energy so as not to inhibit potential animal performance. For example, test rations with metabolizable energy contents of 10 and 12 MJ/kg DM for weanling seedstock and feedlot RFI tests are recommended in the Australian Net Feed Efficiency Standards Manual (Exton, 2001). Such metabolizable energy contents are well above those of pastures typically grazed by cows or by steers before feedlot entry. It is then legitimate to ask if the progeny of bulls and cows found to be genetically superior for net feed efficiency, as identified by low RFI of a medium-to-high energy test ration, will grow as well and be more efficient on pasture compared to progeny whose parents displayed a greater appetite and higher RFI when similarly tested. From the studies reported above on the Trangie RFI divergent selection lines, there is no evidence that selection for low RFI (high efficiency) measured postweaning on a high-quality, pelleted ration available ad-libitum was accompanied by inferior growth performance by cows and their calves on pasture (Herd et al., 1998; Arthur et al., 1999), or by steers on pasture (Herd et al., 2002c). Moreover, evidence was presented indicating improvement in feed efficiency on pasture accompanied selection for low RFI (Herd et al., 1998; Herd et al., 2002c).

Measurement of RFI

Measurement of feed intake with current technology is expensive, and so the cost of measurement compared to the benefits obtained is an important issue if performance testing of animals for feed efficiency is to be used to select animals. In Australia, a standards manual—*Testing Beef Cattle for Net Feed Efficiency* (Exton, 2001)—has been produced by the Australian Performance Beef Breeders Association, representing breed societies, and forms the basis of a national accreditation scheme to ensure that standardized and accurate data are generated for genetic analyses. This provides uniform guidelines that enable a cattle breeder to measure feed intake of animals, either in centralized testing facilities or on-farm, and to use this information in a genetic evaluation.

Given that measuring feed intake is expensive, the length of a RFI test and the amount of data collected needs to be optimized to reduce the cost of testing animals. The current recommendation to the Australian industry for a 70-d RFI test is based on the results reported by Archer et al. (1997). They showed that for British breed cattle tested for RFI, with feed intake recorded daily and animal BW measured weekly, that while 35 d was adequate to measure feed intake, 70 d was required to accurately measure growth and RFI. Archer and Bergh (2000) analyzed data from centralized tests in South Africa for young bulls from five breeds and four biological types to conclude that while a test of between 42 and 56 d was sufficient for measurement of growth rate, feed intake required 56 to 70 d to measure accurately, and RFI required around 70 to 84 d. Differences between the two studies for minimum periods for measurement of growth rate and feed intake were attributed to differences in the procedures used to measure BW and feed intake.

For RFI tests conducted following Australian standards, if the accuracy in measuring growth could be improved, then it might be possible to reduce the length of the RFI test, with a consequent reduction in the cost of testing and an increase in the number of animals that can be tested per year at the same testing facility (Archer et al., 1999a). Advances in livestock weighing technology that incorporate animal electronic identification allow automatic frequent capture of animal BW. Preliminary evaluations have shown that more frequent weighing of cattle can improve the accuracy of measurement of growth (Archer et al., 1999a; Graham et al., 1999; Tatham et al., 2000) and thereby offer the potential to reduce the length of the standard 70-d RFI test. However, to confirm these results and to determine the optimal length of test with frequent weighing, more animals with good genetic links need to be tested, and a comprehensive genetic analysis conducted, as done by Archer et al. (1997).

Cattle may be tested for RFI either at centralized test facilities or on-farm. Archer et al. (1999b) reviewed the merits of both test regimens, and Australian experience is that both will be used by cattle breeders. An issue common to both approaches is the influence of pretest environmental affects on subsequent test performance. Archer et al. (1999b) recognized two approaches might be used to remove differences due to the previous history, one biological and the other statistical. A common pretest adjustment phase might be used to biologically remove differences between animals measured in a test group. An alternative approach is to restrict comparisons between animals to those raised in the same environment from conception to measurement (i.e., in the same contemporary group), as currently occurs with other traits recorded in BREEDPLAN, the national program for genetic evaluation of beef cattle in Australia (Skinner and Sundstrom, 1997). The Australian standards manual requires a minimum pretest adaptation period of 21 d and testing of animals in contemporary groups. Comparisons of RFI may be less influenced by pretest environmental affects than are growth-related traits. For example, Herd and Bishop (2000) showed that RFI over a performance test was not affected by differences in pretest rearing treatments, in contrast to growth related traits, such as start-of-test BW and end-of-test BW, and, in some years, ADG and F:G. Age of dam is another nongenetic factor known to influence liveweight and growth of young cattle. Arthur et al. (2001d) showed that where age of dam affected ADG, feed intake, F:G, and final BW, it did not affect RFI in weanling tests on Charolais bulls.

Using Feed Efficiency in Selection Decisions

The method used to incorporate feed intake and growth information in selection decisions is an important issue for consideration and is discussed in detail by Archer et al. (1999b). Combining feed intake and growth information into an index for feed efficiency does not add any new information to that which is obtained directly from the component traits (Kennedy et al., 1993). Where use of postweaning feed intake and growth as separate criteria traits in an economic selection index is theoretically optimal, currently the level of usage of economic selection indices in the beef industry is low. For the medium term, it is likely that a large proportion of bull breeders and bull purchasers will continue to base decisions on EBV for individual traits. Presentation of separate EBV for feed intake and growth, which are antagonistic and highly correlated, is likely to cause difficulty in interpretation as it is difficult to compare an animal with high intake and high growth rate with another with lower intake but lower growth also. Conceptually, an EBV for feed intake after adjustment for differences in growth performance (i.e., RFI) would be easier to interpret than an EBV for feed intake unadjusted for growth, as the correlation between growth EBV and the adjusted feed intake EBV would be lower and comparisons between feed intake of animals with different growth performance would be simplified. Therefore an EBV for RFI, calculated using a phenotypic or genetic adjustment for growth performance, may be the best way to present the information. However, EBV for RFI should be presented as feed intake EBV with an adjustment for growth, rather than as EBV for "efficiency" per se. Moreover, the EBV, or its component traits, should be used in an economic selection index to optimize selection decisions based on all available information not just feed efficiency.

Industry Adoption

In Australia, BREEDPLAN EBV are accepted as the most appropriate method of estimating genetic merit of an animal for a given trait (Sundstrom, 1997). Recent research and extension has focused on developing EBV for RFI for those cattle breeds already enrolled in

GROUP BREEDPLAN and that have begun testing cattle for RFI (Exton et al., 1999). The breed societies control the databases and determine which traits will be included in the BREEDPLAN analysis, accuracy levels for publication, and cost structures for their members. The Australian Performance Beef Breeders Association referred to above is responsible for implementing policy regarding testing for RFI and subsequent submission of data for development of EBV. This association has developed a standards manual (Exton, 2001) for the measure of net feed efficiency and forms the basis of a national accreditation scheme to ensure that standardized and accurate data are generated for to use in a genetic evaluation.

Trial EBV for net feed intake (i.e., RFI) were published in the 1999 Autumn Australian Angus GROUP BREEDPLAN genetic evaluation report (sire summary). Trial BREEDPLAN single-trait EBV for net feed intake were published for Australian Angus, Hereford, and Poll Hereford bulls in 2002. The Angus RFI EBV were computed using 2,128 animals with individual feed intake records. The EBV generated ranged from –1.41 to +1.14 kg/d, compared to an average feed intake by the cattle of about 12 to 13 kg/d (Angus Society of Australia, 2002; D. J. Johnston, personal communication). This implies that there exists genetic variation in feed intakes ranging from at least 10% below to 10% above that expected on the basis of an animals size and growth rate. This provides an opportunity to select low-RFI bulls for use in breeding programs to reduce the feed cost of beef production. Fewer records existed for the Hereford and Poll Hereford breeds, EBV being computed using 579 animals with individual feed intake records. The EBV generated ranged from –0.63 to +0.90 kg/d (Australian Hereford Society, 2002).

Challenges to Application

Measurement of feed intake with current technology is expensive, and this is the major barrier to industry adoption. Lack of comprehensive demonstration of the whole farm economic benefit for the beef cattle breeder and his clients under the specific conditions of their farm enterprise is also a barrier to adoption to cost-sensitive farmers. Modeling studies can be illustrative (e.g., Arthur et al., 1996; Exton et al., 2000; Tatham et al., 2000; Archer and Barwick, 2001), but more research is required to demonstrate improvement in individual animal utilization of pasture and supplements, benefits to pasture sustainability, and improvement in whole-farm enterprise efficiency in good seasons and drought seasons. Reduction in manure and methane emissions are other tangible benefits that can be expected from genetic improvement in RFI (Basarab et al., 2001; Herd et al., 2002b) but remain to be demonstrated.

In the past, most beef cattle breeding programs involved comparatively low levels of investment in recording traits on which to base selection decisions. The cost of measuring RFI requires an increased level of investment. Breeding program design incorporating two-stage selection can reduce the number of potential sires that need to be evaluated for RFI and thereby reduce the cost of investment in performance test information number and optimize the return (Archer and Barwick, 2001). Designs using performance test information on bulls only, or including information from progeny tests, were profitable relative to designs without RFI measurement. Including information from progeny testing can improve the accuracy of selection and genetic gain, but accounting for risk and market share is required to justify progeny testing for this expensive-to-measure trait at the level of an individual business (Archer and Barwick, 2001).

An alternative to costly direct RFI testing would be to identify one or more traits that are genetically correlated with RFI and could be used to indirectly select for efficiency. These traits could include phenotypic markers measured from a blood sample or genetic markers. Measurements of marker traits made on an individual or on related animals can then be used to make inferences about the genetic merit of the selection candidate. The direct and indirect approaches are not mutually exclusive, and using both methods in tandem may provide the most cost-effective strategy to identify animals of superior genetic merit for RFI. For example, a phenotypic marker might be used as a pretest screen to identify animals on which further measurement is warranted. The use of selection against the concentration of the hormone IGF-1 in blood to improve growth, feed efficiency, and carcass lean content has been patented for livestock species by an international patent variously registered as WO9635127, AU694025, NZ306348, and EP0830607 by Owens and others in 1996: "Selection of Livestock Using IGF levels." This invention has been shown to be reliable for identification of genetically superior pigs and is the basis of commercial mass screening of pigs and selection to improve growth and feed efficiency and to reduce carcass fatness of pigs (Luxford et al., 1998ab; Hermesch et al., 2001). Recent results in beef cattle show circulating levels of IGF-1 are genetically associated with growout and finishing performance of beef cattle and may prove useful as a genetic predictor of carcass and feed efficiency traits (Johnston et al., 2001; 2002; Herd et al., 2002a). A genetic and economic evaluation of the use of IGF-1 as an indirect selection criterion in beef cattle showed it can increase the profitability of selection decisions and would best used as a screening test to identify animals to be placed into RFI tests in a two-stage selection program (Wood et al., 2002).

Recent interest in gene mapping of cattle to identify genetic markers associated with production traits suggests the possibility of using genetic markers in a breeding program to aid selection for feed efficiency. However, it is unlikely that use of phenotypic or genetic markers will obviate the necessity for direct measurement of feed intake and efficiency of some individuals in the medium term, although markers may still play

a role in improving the cost effectiveness of measuring feed intake and efficiency.

Other barriers to industry adoption exist, for example, capacity of RFI test stations and availability of measurement equipment, disease quarantine barriers to cattle movement to and from test facilities, the scheduling of testing between weaning, and sale of bulls. Our knowledge of the genetic relations for RFI with other traits is incomplete, especially for the relationships of postweaning RFI with cow efficiency at pasture, reproduction, and maternal traits. Indications from dairy cattle show a favorable genetic correlation between RFI of growing heifers and lactating heifers (Nieuwhof et al., 1992). In beef cattle, a very high genetic correlation between postweaning RFI and mature cow RFI was reported by Archer et al. (2002), and there is a favorable phenotypic association with efficiency on pasture (Herd et al., 1998). The genetic correlations for RFI measured on seedstock animals in a postweaning test, with RFI and F:G of their progeny in the feedlot are not yet known, but evidence presented above indicates that they are likely to be high. Lack of an inexpensive, accurate method to measure pasture intake by individual animals (Archer et al., 1999b) prevents testing for RFI on pasture and restricts the opportunity to demonstrate correlated responses in feed efficiency at pasture. Finally, only a handful of cattle breeds has been investigated thus far.

Implications

Genetic variation in feed efficiency of cattle exists both during growth (slaughter generation and replacement females) and in adult cattle (the breeding herd). Strong genetic relationships exist between feed intake and efficiency measured postweaning and these traits in the breeding herd. Selection for lower residual feed intake (a measure of net feed efficiency that accounts for feed required to maintain body weight and for growth) measured postweaning will lead to a decrease in feed intake by cows, with no increase in cow size. Significant barriers to industry application remain. Measurement of residual feed intake is very expensive compared with other traits currently measured and used in genetic improvement programs. Further research is needed to examine the genetic relationships between residual feed intake and other traits in the breeding objective and to find ways for cost-effective identification of superior cattle.

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The history of energetic efficiency research: Where have we been and where are we going?

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ABSTRACT: The development of energetic efficiency concepts followed a recognized pattern of knowledge evolution that began with novel insights leading to creative new concepts. The second phase integrated concepts from other fields to create new applicable principles. The third phase was the adoptive or dissemination phase, yielding solutions to industry or societal problems. It is our contention that animal energetics has been in the adoptive phase for approximately 100 yr. Concepts developed during the early phase of nutritional energetics included the concept that life is a combustion process, the laws of thermodynamics, and the Law of Hess. Subsequent efforts established relationships between gas exchange and heat production and established the concept that food not only functions as fuel, but also as a body-building material. Much of the research effort for the last 100 yr has been to 1) devise bases for evaluation of foods that could be related to energy requirements and energy expenditures and 2) establish causes of energy expenditures. Much of the effort has focused on general and broadly applicable processes (e.g., mice to elephants) of biology or broad-based populations within species. Little effort has been focused on the amount or causes of individual variation in efficiency of energy utilization by cattle, even though differences among individuals have long been recognized. Observed maintenance requirements and energetic efficiencies, for example, have not been substantially altered during the last 100 yr of intensive beef production. Reasons for the lack of change in energetic efficiencies include a lack of a consistent selection goal, loose and inconsistent definitions of efficiency, concentration on output characteristics, and emphasis on population similarities rather than individual variation. It is time to assess new or different tools and concepts to enhance efficiency of dietary energy use by beef cattle. Application of older (e.g., residual feed intake) and newer (e.g., QTL, gene expression microarray) technologies offers the potential to realize improved maintenance and system energetic efficiency through identification of individual animal phenotypic and genomic uniqueness.

Key Words: Beef Cattle, Energy Metabolism, Genome Analysis, Maintenance, Ruminants

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Introduction

The knowledge of efficiency of energy utilization by ruminants developed via a recognized pattern of evolution (Malone, 1994). In this evolutionary pattern, the process is initiated through novel, fundamental insights leading to creative concepts, e.g., the Laws of Thermodynamics, "life as a combustion process." The second step is the integration of complementary concepts from other fields of inquiry to create principles applicable to the field of inquiry; e.g., the chemical reaction of formation of high-energy phosphate bonds is applied to explain biological processes, or physiological principles are applied to life processes. The last phase of this maturing evolutionary process is the adoptive or dissemination phase, yielding solutions to industry or societal problems, e.g., the chemical analysis of feedstuffs, and the development of net energy feeding systems. It is our contention that animal science energetics has been largely in the adoptive/dissemination phase for the past approximately 100 yr. It is time to look for new integrative tools with which to enhance beef cattle dietary energy use efficiency.

Historical Energetics

The historical development of nutritional energetics was reviewed by Brody (1945), Kleiber (1961), and Blaxter (1962). We have relied on these treatises for much of this synopsis. Utilization of dietary energy has been

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a subject of research since the eras of Leonardo da Vinci (1452–1519), Joseph Priestly (1733–1804), and Antoine-Laurent Lavoisier (1743–1794). From these and other philosophers and researchers, the generalization that life is primarily a combustion process developed. This concept relating metabolism to combustion permitted the formulation of the following equation.

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{heat}$$

After those pioneering works, new objectives of research in nutritional energetics became 1) to establish relationships between gas exchange and heat production, 2) to devise bases for evaluation of foods that could be related to energy requirements and energy expenditures, and 3) to establish causes of energy expenditures. The Laws of Thermodynamics and the Law of Hess were developed. The adiabatic bomb calorimeter was developed by Berthelot (1827–1907), which enabled reproducible and accurate determination of the gross energy contents of organic compounds, feed, feces, and urine. Another essential advance was the development of the concept that foods should be partitioned into carbohydrates, fats, and proteins because their metabolism differed. Primary contributors to this concept were Baron Justus Von Liebig (1803–1873) and his students. Liebig maintained that a considerable part of animal food, especially minerals and proteins, do not function as fuel, but as material for bodybuilding. In 1881, Lunin concluded that animals need some unknown substances, other than protein, fat, carbohydrates, and minerals. Those substances were later termed *vitamins* by Casimir Funk (1912).

Considerable effort, over a period of 100 yr or so, was devoted to establishing relationships between gas exchange and heat production. One of Liebig's students, Carl Von Voit, utilized the open-circuit respiration apparatus of Max Von Pettenkofer (1818–1901), the prototype of modern instruments, to do extensive energy balance experiments. Instrumentation of this type was utilized extensively by the groups of Henry Armsby, Wilbur Atwater, Oskar Kellner, and Max Rubner (all students of Von Voit), among others. Recently, although more mechanically and/or electronically sophisticated, instruments based on similar principles have been in use at Beltsville (Flatt et al., 1965), Colorado State University (Johnson, 1986), and Clay Center (Nienaber and Maddy, 1985), among others. Some of the early instrumentation, such as that of Regnault (1810–1878), were of the closed-circuit type. Closed-circuit systems were used extensively for man and smaller animals and some for larger animals (e.g., Hannah Institute, Wainman and Blaxter, 1958) but were never as widely used as the open-circuit type. Work in this area—to a large degree—culminated in 1965 with the publication of the Brouwer equation (Brouwer, 1965). The equation developed to calculate heat production (H, kcal) from oxygen consumption (O_2, L), carbon dioxide production (CO_2, L), methane production (CH_4, L), and urinary nitrogen (N, g),

$$H = 3.866 \times O_2 + 1.200 \times CO_2 - 0.518 \times CH_4 - 1.431 \times N$$

has been used almost exclusively for the calculation of heat production from indirect calorimetry measurements since its publication.

Direct calorimetry, the direct measurement of heat produced by the animal, is also founded in the work of Lavoisier, Atwater, Armsby, and Blaxter, and others, used instruments based on the principles developed by Lavoisier. Although instrumentation has changed immensely, calorimeters in use at the University of Nebraska (Nielsen et al., 1997a) are founded in those concepts.

In conjunction with establishing relationships between gas exchange and heat production and establishing causes of animal energy expenditures, several groups devoted tremendous effort toward devising bases for evaluation of foods that could be related to energy requirements and energy expenditures. The Starch Equivalent System, developed by Oskar Kellner and his group (Kellner and Köhler, 1900) was a net energy-based system in which the energy values of feedstuffs were expressed relative to that of starch to meet the energy needs of the animal for fattening. The Kellner system has likely had the greatest influence in the practical feeding of livestock. It was used as the primary system throughout Europe and Russia for many years and serves as the basis on which many others have been built. Atwater and associates (Atwater and Bryant, 1900) developed the Physiological Fuel Values system. Atwater's system was based on metabolizable energy values of carbohydrates, fat, and protein, with the energy values of protein adjusted for the energy value of excreted urea. The Physiological Fuel Values system remains the basis for expressing the energy (caloric) content of foods for humans and laboratory animals. Armsby (1903; 1917), also using respiration calorimetry of the Atwater-Rosa type, defined metabolizable energy (physiological fuel value) as the net energy plus heat increment of feeding. He and associates developed many of the principles on which current net energy systems are based. Current energy systems used in the United Kingdom (ARC, 1965; 1980; AFRC, 1990), France (INRA, 1978; 1989), and Australia (ACC, 1990) are grounded in principles derived from those earlier efforts.

The general equation ME = RE + HE has been recognized since the days of Von Liebig, but, for many years, the primary effort of energetics researchers was to describe and quantify the ME of food and heat produced (HE), with retained energy (RE) seemingly a secondary consideration. Lawes and Gilbert (1861) first employed the comparative slaughter method in experiments. Those experiments were of considerable interest because they demonstrated for the first time that carbohy-

Table 1. Disposition of dietary energy by Kellner's fat steer and contemporary U.S. steer or overall beef production system (U.S. data extrapolated from NRC, 1996)

Item	Kellner "well fed ox," Mcal/d	% of GE intake	Today 600 kg feedlot steer, Mcal/d	% of GE intake	Beef system, cow through feedlot, %
Gross energy input	52.9	100	43.0	100	100
Fecal energy	15.9	30	6.5	15	39.6
Urine energy	1.7	3	1.7	4	4.9
"Marsh gas"	3.4	6	1.1	3	5.4
Heat of tissue syn.	6.3	12	8.9	21	8.0
Idling heat	17.3	33	17.2	40	36.3
Retained in empty body	8.3	16	7.6	18	5.8

drates were the major source of energy leading to the synthesis of fat. Blaxter (1962) stated that "during the last 100 yr, the complete bodies of about 250 cattle and 60 sheep have been analyzed" by the scheme that partitioned the animal into weight of gut contents, body water, body fat, body protein, and body minerals. Garrett et al. (1959) popularized the comparative slaughter technique in their classical manuscript, the Comparative Energy Requirement of Cattle for Maintenance and Gain. This concept was further developed and published in an article titled a System for Expressing Net Energy Requirements and Feed Values for Growing and Finishing Beef Cattle (Lofgreen and Garrett, 1968), which stands as the basis of the system incorporated into current NRC (1984; 1996) recommendations. It should be noted that this system, like other systems currently in use, is rooted in the concepts developed by Armsby, Atwater, Kellner, Brody, Kleiber, Blaxter, and others, but, unlike many of the systems, requirements and value of feedstuffs to meet those requirements were based on the measurement or estimation of energy retained, rather than energy losses.

Much of the essence of the last 50 yr of animal energetics research can be found in 15 publications from the prior symposia on energy metabolism of farm animals held every 3 yr beginning in 1958. Researchers A. J. H. Van Es (1994) and W. P. Flatt (2000) have recently summarized interesting portions of the history of the people and their work. Also of note is a report (NRC, 1935) of a conference sponsored by the Committee on Animal Nutrition of the National Academy of Science held at Pennsylvania State College in 1935 that features papers by Forbes, Mitchell, Brody, Klieber, and Ritzman.

Energy Use Efficiency

An overview of energy efficiency can be gained by an example of typical diet energy disposition (Table 1). A comparison of Kellner's (1909) respiration calorimetry-monitored "well-fed ox" with a contemporary feedlot steer (extrapolated from NRC, 1996 slaughter balance derivation) portrays moderate differences, except for the markedly lower fecal loss associated with currently used high-grain diets. The fattening steers retain from 16 to 18% of consumed energy. The largest loss is to the maintenance function, "heat of idling," followed by fecal losses and heat of tissue synthesis. On a whole-herd basis, the fecal and maintenance components become predominant, providing, perhaps, a view of the largest efficiency improvement targets. Beyond digestive losses, e.g., as a fraction of the herd's needs for metabolizable energy, the maintenance component predominates, comprising approximately 73% of ME requirements.

The term *efficiency* demands a numerator and a denominator along with terms and units of each. All have taken many forms when used to define "beef cattle energetic efficiencies" particularly when gross, partial, or net efficiencies are defined. The numerator is the caloric content of the product (megacalories of product) or its proxy, whereas the denominator is defined in units of diet (diet input). The units of diet can be weight, or megacalories or joules of GE, DE, TDN, ME, or NE. Additionally, the diet input can be divided into that provided for animal maintenance and that provided for product above maintenance; e.g., product/(total ME minus ME required for maintenance). Thus, enumerable ratios have, and are, being used to describe "energy efficiency of beef production." These efficiency ratios always embody three components:

1. Diet energy cost of maintaining the animal per unit of time.
2. Diet energy cost per unit of product.
3. Rate of product per unit of time (product/fixed maintenance cost).

However defined, the determination of partial efficiencies, e.g., body tissue energy gain/ME above maintenance, would appear to be a straightforward, simple process. But in practice, it becomes a complex problem with multiple levels of confounding, making it difficult, if not impossible, to precisely define *the* partial efficiency or maintenance energy requirement of the producing animal. A prime example of this complication is the frequently observed shifting maintenance requirements as animals adapt to changing levels of alimentation. For example, Marston (1948) reported a shifting of fasting heat production **(FHP)** of sheep in

direct proportion to their prior plane of nutrition. Additional frequent confounders include changing diet digestibility, pattern of fermentation, microbial growth, and protein supply concomitant with changing levels of production or alimentation. Add to these the changing nutrient flux, metabolism, hormonal control, and product composition likely with changing level of alimentation and the simplicity of measuring or calculating "partial efficiency" becomes even murkier. Perhaps this is where a modeling approach, e.g., Oltjen and Sainz (2000), may prove most helpful.

Variations in Maintenance Requirement. Kellner (1909) found that small dogs produced 2.8× more heat/BW at fasting than large dogs, but approximately equal FHP per unit of surface area. Classical mouse to elephant research with mature animals found FHP to be proportional to $BW^{0.734}$ (Brody, 1945) or to $BW^{0.756}$ (Kleiber, 1947), leading to the widely accepted concept of metabolic body size = $BW^{0.75}$. The accuracy of the 0.75 exponent, and the veracity and applicability to define maintenance requirements, has been widely challenged. Some early examples include the following: level of alimentation prior to fasting (Marston, 1948), age (Graham et al., 1974), breed (Frisch and Vercoe, 1977), race (Geissler, 1985), sex (Webster et al., 1982), leanness (Graham et al., 1967; Webster, 1982), unique species (i.e., ovine; Blaxter, 1989), cold adaptation (Young, 1975), and choice of regression model (Calder, 1987). All are examples of factors that have been shown to challenge the universality of FHP = 77 $BW^{0.75}$. The ARC (1980) energy requirement system adopted the exponent of 0.67 for cattle to better fit the young vs. the older, heavier animal's needs. Webster et al. (1974) in a paper entitled the Irrelevance of Fasting Metabolism suggested that the requirement of varying ages or weights of cattle are better predicted from regression rather than measurement of heat from a fasted animal. From a review of literature from several species, Blaxter (1972) indicated that if fasting is measured on mature animals of varying BW within a species, the appropriate exponent ranges from 0.83 to 0.93. Other reviews have, however, concluded that no significant advantage is gained by using exponents other than 0.75 (Garrett and Johnson, 1983; AAC, 1990).

An additional factor contributing to variation in maintenance is that some breeds/animals likely have differing abilities to adapt to changing environments or levels of alimentation. Examples include Africander vs. *Bos indicus* or *Bos taurus,* in which the decline in FHP as pasture quality declined was greater for Africander cattle (Frisch and Vercoe, 1977). A report by Reynolds and Tyrrell (2000) found maintenance energy of lactating Angus cows to be equal to expected Holstein requirements in contrast to the widely observed lower requirements of Angus or Hereford cattle when not lactating. The implication is that Angus or beef cattle in general may adapt to lower maintenance when fed at lower levels of alimentation.

Physical Activity. Except for recommendations of increasing maintenance requirements of grazing animals (NRC, 2001), the use and variation of energy in physical activity by cattle has been largely ignored. Thermogenesis of individual human subjects associated with activities that are not purposeful exercise has been shown to be highly variable, heritable, and predictive of weight gain (Snitker et al., 2001) and low in obese individuals (Schoeller, 2001). Snitker also found that the measurement in respiration chambers of these "activities of daily living" correlates (r = 0.53) to individuals' free-living activity. These types of movements, sometimes called *fidgeting,* can elevate sitting or standing thermogenesis by 50 to 80% (Levine et al., 2000) and can be monitored in free-living individuals with inclinometers and accelerometers (Levine et al., 2001a). General usefulness of these monitors is apparently limited by the need to calibrate them to individual subjects (Levine et al., 2001b).

Anatomical Variations. Many attempts have been made to explain the anatomical, physiological, and biochemical causes of varying FHP/BW. Variations in fat-to-lean tissue mass have been widely ascribed to explain group or individual heat production differences, however, not always as demonstrated by McNiven (1984). She imposed nutritional regimens on ewes to change body fat percentage dramatically and showed little difference in FHP or maintenance heat production per unit of BW in these groups. Visceral organ tissue, particularly hepatic, consumes O_2 at a much higher rate/mass than the whole animal and is positively correlated with animals or circumstances varying from mean basal metabolic rates. The basal metabolic rates of divergent human subjects have been successfully regenerated from the mass of individual organs and tissues, separately determined, multiplying by the O_2 consumptions/kg of each tissue and summing these to equal that of the whole subject. Changes in the ratios of visceral organ to whole-body mass also parallel changes in fasting or maintenance heat production in response to changes in level of alimentation, stage of fetal growth, young to old, small to large BW species, or *Bos indicus* vs. *Bos taurus* cattle (Ferrell et al., 1986; Huntington et al., 1988; Johnson et al., 1990).

Physiological Factors. Many "maintenance control factors" have been proposed. In addition to the above, these include T3, Na^+/K^+ATPase, proton leak, uncoupling proteins, leptin, acetyl-CoA carboxylase 2, malonyl CoA, sympathetic tone, α_2-agonists, and calcium/calmodulin-dependent muscle protein kinase. Knowledge of these factors has not resulted in the ability to select animals to change their maintenance cost of production. However, this research has helped to define the general requirements of groups of animals, and many very interesting concepts have evolved. Uncoupling proteins (UCP) are widely distributed in tissues beyond the UCP1 found in brown adipose of most newborn animals. These proteins facilitate a proton leak across the inner mitochondrial membrane, estimated to be responsible

for 20 to 30% of basal metabolism oxygen consumption (Brand 2000). Those observations led to the hope that the major controller of animal metabolic rate had been found. The excitement was quenched by the report (Enerback et al., 1997) that UCP2 knockout mice produced no effect on lipid stores or energy balance and that UCP may function as regulators of reactive oxygen species (Echtay et al., 2002) rather than as uncouplers of oxidative phosphorylation. Some enthusiasm was revived with the reports that mice with overexpressed UCP3 were hyperphagic, lost adipose mass, and had higher metabolic rates (Clapham et al., 2000) and that UCP3 is a molecular determinant of T3 effects on resting metabolic rate (deLange et al., 2001). When hypothyroid rats were given T3, UCP3 mRNA and protein were upregulated, resting metabolic rate was increased 45%, and muscle mitochondrial nonphosphorylating respiration increased 40%. Additionally, work of Lebon et al. (2001) found that T3 increased muscle tricarboxylic acid cycle flux by 70% with no increase in ATP synthesis, indicating accelerated proton leak.

The role of UCP in the control of proton leak or conductance has again been challenged. The mitochondria of UCP3 knockout mice showed unchanged respiration or proton leak rates (Cadenas et al., 2002). The mice overexpressing UCP3 did show greater proton conductance, but they did not respond to known enhancers, or inhibitors. Analogous responses were found by introducing human UCP3 into yeast mitochondria (Harper et al., 2002). Uncoupling was increased, but not in proportion to increased protein; it was responsive to neither activators nor inhibitors.

Proton leak variation between cold-blooded and homeothermic animals, as well as large and small species, has also been linked to membrane lipid unsaturation, particularly to the relative content of docosahexanoic acid (Hulbert and Else, 2000). For example, rat liver mitochondria have a greater 22:6 fatty acid content than a similarly sized lizard along with approximately five times greater proton leak rates. They cite previous research showing that the heart rate of mammals ranging from mice to whales was correlated to the 22:6 content of cardiac lipids (Gudbjarnason et al., 1978). Attention is also given to a general relationship in other membranes of lipid composition to Na^+K^+ATPase activity.

The injection of leptin into rabbits resulted in marked increases in stored body lipid cycling (Reidy and Weber, 2002). Lipolysis and triacylglycerol/fatty acid cycling was increased 50%, primary cycling 85%, metabolic rate 14%, and fuel use was shifted away from carbohydrate toward lipid. The authors postulate that the general role of leptin secretion by adipocytes is to maintain normal body mass, adjust lipid stores via changes in metabolic rate, fuel selection, T3 secretion, UCP levels, and diet intake. They conclude that leptin levels function to adjust the "idling rate" of animals via substrate cycling and UCP-induced proton leak.

Potential Genotype Interactions. Beginning in the 1960s and continuing through the present, the genetic growth rate potential of the beef cattle population in the United States was increased through the introduction of breeds of cattle from the continent of Europe. Attributes of these imported breeds evolved within unique production environments with differing emphasis regarding desired productivity, creating a diversity of genetic potential for production. The assimilation of these breeds into the U.S. beef industry since their introduction was stimulated by cow/calf producers' desire for heavier weights at weaning and a postweaning industry desire for more efficient gain during the finishing period coupled with consumer demand for leaner products during the 1970s and 1980s. These goals could be met by systematically using breeds (Gregory and Cundiff, 1980) differing in mature size and growth relative to the British breeds. Feeding and slaughtering cattle at physiologically younger ages contributed to the latter goals but created problems with meeting industry standards for quality of meat produced (National Beef Quality Audit, 1995), creating the need to again alter production practices. The changes resulted in a need to address the energy requirements for production of beef cattle.

The industry assumed constant energy requirements for maintenance per unit of metabolic body size and efficiency of production among these diverse producing animals (Garrett et al., 1959). This assumption ignored earlier research, demonstrating that animals differing in production "potential" varied in gross (Armsby and Fries, 1911) or maintenance efficiency. Taylor et al. (1962) utilized twins, both monozygotic and dizygotic, to investigate the effect of genetic factors on feed efficiency. These researchers concluded that a proportion of the variation in feed efficiency was under genetic control, but efficiency during any given period can also be affected by previous nutrition. Ferrell et al. (1986) and Koong et al. (1982) conducted studies with lambs and rats to test the effect of previous nutrition on an index of maintenance, fasting heat production. Level of nutrition preceding the measurement of fasting heat production significantly affected the DM requirement for maintenance per unit of metabolic weight in both species. Additionally, the requirements were not static but reflected the most recent feeding level, which is analogous to the shifting FHP noted previously.

Sutherland et al. (1974) suggested that growth rate and efficiency of feed use were variables critical to evaluation of the economical production of meat animals. In the review, the authors considered the physiological parameters possibly affecting gross feed efficiency drawing from research involving many species. Evidence was provided in several species; enhancing growth rate during the postweaning interval was an effective means to improve efficiency and this could be accomplished by increasing body size (Sutherland et al., 1970). Timon and Eisen (1970) pointed out that genetic studies investigating feed efficiency failed to

adequately address the issues of correlated responses in appetite, body composition, or the effect of test protocol, that is, fixed time interval, weight interval, and so on. Evidence from these studies suggested that observed differences in gross efficiencies realized through selection for growth could not be attributed to genetic changes in partial efficiencies for fat and protein deposition. A correlated increase in ad libitum intake (appetite) was observed in the selected mouse lines (Sutherland et al., 1970). Work by Leymaster and Jenkins (1985) reported a positive relationship for ADG between 32 and 73 kg in sheep and the rates of accretion for carcass and offal lipid, protein, and ash. The accretion rates of offal protein had the greatest direct and indirect effects on ADG. Results are critical because work reported by Koong et al. (1985) documented the effect of nutritional environment on metabolically active body tissue and the positive relationship to fasting heat production. Increased emphasis on output performance could create a correlated response in mass of metabolically active organs increasing energy requirement for maintenance. Jenkins et al. (1986) determined significant additive breed effects among Brown Swiss, Hereford, and Angus. Scaled for weight at slaughter, Brown Swiss tended to have the greatest amount of internal tissues, with Hereford the least and Angus intermediate. A similar ranking was observed for yield of milk at time of peak lactation. Taylor et al. (1986) reported that as genetic potential for milk production increased, maintenance efficiency decreased.

With additional breeds available to the industry, cattle began to be classified by output production characteristics, such as growth, carcass attributes, mature size, and milk production potential based on research evaluating performance from birth through slaughter (Mason, 1971; Cundiff et al., 1986). Responding to inquiries by the cow/calf segment of the beef industry, Ferrell and Jenkins (1982) found approximately 73% of the feed ME consumed by a mature cow is expended to maintain body mass. However, the ability to adjust energy expenditure for maintenance is influenced by genetic potential for performance, with animals of greater genetic potential for productivity exhibiting reduced ability to lower maintenance requirements (Frisch and Vercoe, 1977; Taylor et al., 1986). Ferrell and Jenkins (1985) reported that during the postweaning phase, Simmental were less efficient than Hereford at restricted levels, but at ad libitum intakes, more efficient. Jenkins et al. (1991) provided evidence that a breed with greater potential for mature size and lactation yield had greater daily heat production at restricted feeding rates than a breed with lower production potential; however, as rate of DM intake per unit weight increased, the ranking reversed between the two breeds. Solis et al. (1988) reported breed differences in energy requirements for maintenance among Jersey, Holstein, Brahman, Hereford, and Angus. Mating systems designed to utilize between- and within-breed differences in energy expenditure for maintenance offer an opportunity for improving energy efficiency.

Introduction of these breeds to the U.S. beef cattle inventory provided an opportunity to assess potential variation among the breeds for efficiency of energy use to improve efficiency. Thiessen and Taylor (1986) evaluated the variation in weight change relative to feed intake among 25 breeds of cattle fed ad libitum from 12 wk of age. Results documented: 1) efficiency (gram weight gain per unit of feed intake) decreases as the animals aged, 2) additive genetic variation among the 25 breeds evaluated increased as the animals grew older, and 3) relative to additive genetic variation, a greater proportion of the variation existed within breeds. This work was a continuation of investigations initiated to study weight changes and efficiency (Taylor et al., 1962; Taylor and Young, 1966). Using monozygotic and dizygotic twins, these researchers suggest that variation existed in the efficiency with which an animal used feed to maintain BW and variation existed among the rates of decline in efficiency among twin pairs. Using monozygotic twins, Hotovy et al. (1991) observed significant genetic variation for FHP and ME required for maintenance, suggesting selection to reduce energy expenditure for maintenance would be successful.

Based on an evaluation involving 25 breeds, Thiessen et al. (1985) reported a genetic coefficient of variation for ad libitum feed intake of approximately 12 to 15% for cattle ranging from 12 to 72 wk. Assuming that feed intake is proportional to mature weight to 0.73 power, then variation among breeds can be evaluated for animals fed ad libitum that are in weight equilibrium (Taylor et al., 1981). The constant is an index of the relative food capacity of mature animals (Kleiber, 1961) and should characterize the genetic potential for appetite. Using feed intake and weight data from the ad libitum animals at weight stasis, this proportionality held among mature cows of the nine breeds; daily DM intake $= 0.195BW^{0.73}$. Jenkins and Ferrell (unpublished data) observed variation among breeds in maintenance efficiency at weight stasis for these nine breeds of cattle varying in genetic potential for mature size, milk production, postweaning growth rate, and ad libitum feed intake. Breed estimates of the regression constant ranged from a high of 0.224 for Angus to a low of 0.167 for Limousin, suggesting substantial genetic variation in appetite (Jenkins and Ferrell, unpublished data). Relative to BW at weight stasis, genetic potentials for DM intake/BW of Angus, Hereford, Red Poll, and Charolais were greater than the pooled mean appetite and Limousin, Pinzgauer, and Simmental exhibited lower genetic potential for appetite. Braunvieh and Gelbvieh approximated the sample mean.

In spite of the above-noted selection pressures, the maintenance requirements of cattle appear to have been largely unchanged for the last 100 yr (Table 2). Kellner's (1909) estimates, translated from starch equivalents, surface area base, suggested an ME re-

Table 2. History of maintenance requirement estimates, kcal of ME per $BW^{0.75}$, of cattle fed corn, hay, or straw

System	Base requirement	Corn[a]	Hay[a]	Straw[a]
Kellner, 1909	5.2 kg of SE/454 kg of BW[b]	116	158	313
NRC, 1963	135 kcal of DE/$BW^{0.75}$	111	111	111
NRC, 1976	77 kcal of NEm/$BW^{0.75}$	110	125	129
NRC, 1984	77 kcal of NEm/$BW^{0.75}$	112	131	178
NRC, 1996	77 kcal of NEm/$BW^{0.75}$	112	131	178

[a]Requirements for cattle fed corn, hay or straw diets expressed as ME/ $BW^{0.75}$.
[b]Starch equivalent.

quirement of cattle fed grains and oil meals of 116 kcal/$BW^{0.75}$, not unlike NRC (1963; 1976; 1996), which range from 110 to 112 kcal/$BW^{0.75}$. The very high estimates of the maintenance requirement for ME from forages determined by the "fat-forming ability" Kellner system were shown to be inaccurate. Such very low efficiencies are only applicable when describing the partial efficiency of ME use for growth. The early NRC systems ignored these low efficiencies but then developed a more modest "forage inefficiency" adjustment.

Evans et al. (2002), as shown in Figure 1, has provided some indirect evidence of slight increases in cattle maintenance energy requirements. The average EPD for maintenance requirements were predicted from mature BW and milk production records. Requirements for cows increased 100 Mcal/yr over a 20-yr period prior to 1990, after which they leveled out. The 100-Mcal rise, however, represents only a 2.5% increase in yearly needs.

Individual Animal Variation. Animal-to-animal variation within class, breed, sex, etc., in maintenance requirement has been noted in several experiments (Table 3). The reported CV for maintenance energy requirements in beef cattle range from 10 to 12%, suggesting that substantial animal-to-animal variation exists for this trait. These variations, coupled with the heritability estimates of Hotovy et al. (1991), as well as indications of the heritability of residual feed intake measures (Herd and Bishop 2000; Herd et al., 2003), suggest ample room for improvements through selection.

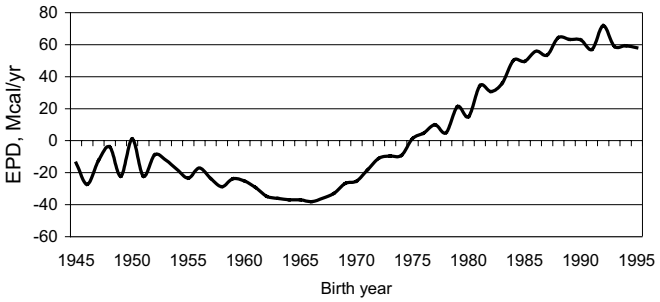

Figure 1. Average EPD (Mcal/yr) for mature cow maintenance energy requirements by birth year in Red Angus cattle (Evans et al., 2002).

Ferrell (1986) reported weight changes for mature cows representing breeds differing in mature size and milk production potential and fed at 120 kcal per unit metabolic body size or ad libitum. Relative to metabolic body size within assigned feeding level, the ADG of individual cows varied, indicating variation among animals in efficiency of metabolizable energy use at approximately weight stasis and positive weight change (production). Nielsen et al. (1997a,b) successfully practiced divergent selection for high and low heat production (**HP**) in mice for 15 generations. Correlated responses were observed for feed intake (increased intakes in the high FHP line and decreased intakes in the low FHP line; respectively), composition (reduced fat in the high line relative to low FHP line), litter size (larger litter size in the high line vs low line) and activity. These results suggest that even though additive genetic variation exists in measures of energy use, implementing selection criteria to change the basal metabolism to improve energetic efficiency will affect other traits in the producing animal.

*Residual Feed Intake **(RFI)** as an Efficiency Measure.* In an attempt to develop a selection method without the negative consequences of selection for growth rate, several researchers have investigated individual animal deviation from regression of feed intake as predicted from mean BW and gain during growth trials of 70 d or more. The heritability of RFI ranged from 0.16 (Herd and Bishop, 2000) to 0.39 (Arthur et al., 2001). Steer progeny from parents selected for low RFI also had lower RFI (–0.15 vs. +0.16), consumed less feed (8.03 vs. 8.45 kg of DM/d) as yearlings, but weighed the same (423 and 428 kg BW) at the end of the trial as steer progeny from parents selected for high RFI (Richardson et al., 2001). Body fat of the low RFI steers was not significantly lower, averaging 21.9 vs. 23.1%, although carcass fat/final weight was lower and protein gain during the 70 d test was higher. The authors conclude that selection for RFI is unlikely to have negative consequences regarding mature weight and potentially positive effects on cow maintenance requirements. Changes in meat quality noted by McDonagh et al. (2001) have some negative potential but are expected to have minor practical importance.

Efficiency of Product Formation. The partial efficiency of energy use for product synthesis has been actively

Table 3. Estimates of the variation in maintenance energy requirement between individual animals within group or species

Reference	Species	Measure	% ME_m variation
Van Es (1972)	Cattle	CV	5 to 10
Webster, et al. (1982)	Cattle	CV	14 to 35
Kirchgessner and Muller (1991)	Sows	CV	11.8
	Humans	CV	12.4
Hotovy et al. (1991)	Cows	Range	15

investigated for many years. Kellner (1909) found a 57% partial efficiency of body energy storage from the ME of grains added to a maintenance diet of steers. Brody (1935) reported a partial efficiency of ME use for milk production of 0.61, not unlike recent NRC values. It does appear likely that these partial efficiencies have been little altered.

Partial efficiency variations by product or by feedstuff source, however, are considerable. Although not totally conclusive, most investigations indicate the ranking (most to least) for partial energetic efficiency of product is as follows: lipid > milk > protein > fetal tissue. The apparently low efficiencies of protein (30 to 50%) and fetal tissue synthesis (~10%) may be a matter of bookkeeping. Are higher costs of concomitant protein turnover or increased maintenance best included in the cost of the product? Biochemical estimates of ATP/mole of amino acid incorporated into a protein chain, even at 5 mol/mol, show relatively high efficiencies of ~75%.

The major discrepancy between theoretical as compared to observed product formation efficiencies occurs when low quality, fibrous feed ME is utilized for growth. The very low partial efficiencies of 30% or lower have been "explained" as resulting from a high heat increment of acetic acid use (Blaxter, 1989). However, there is substantial experimental evidence that acetic acid can be used efficiently for growth (Johnson, 1972; Orskov et al., 1979). The mechanism responsible for the high heat increment of fibrous diet use for growth, thus, remains a mystery, to intrigue contemporary energeticists.

Baldwin (1995) has summarized the energy flux through the multitude of physiological/biochemical tissue and organ tasks of growing, lactating, or idling animals, e.g., Na/K pumping, futile cycles, protein, urea, lipid, and lactose synthesis. These elegant models have illustrated the dynamic and interactive nature of supplying these energy needs from varying substrate mixtures to meet varying physiological tasks, for example, varying lipid/VFA/protein mixture ratios can result in very different efficiency responses when these nutrients are used for maintenance as compared to their use for growth. These relationships are not easily applied to diet nutrient use, however, due to difficulty of quantifying substrate uptakes from the gastrointestinal tract. Substrate inputs from nutrients default to static estimates of moles per unit of chemical component digested in the gut (Bannink et al., 2000; Mills et al., 2001).

Law of Diminishing Returns. Many energetics scientists noted the applicability of this law to animal efficiency. Brody (1945) cites the philosophy that "the man blessed with plenty of this world's goods requires a correspondingly larger increase in his good fortune than does the poor man in order to derive the same amount of pleasure." Brody's chapter 5, "Principle of Diminishing Increments," provides extensive evidence of its fit to data for growing steers, rabbits, hens, and lactating cows. J. T. Reid of Cornell expounded frequently on the "A-TDN" concept of lower digestibility and efficiency at increased intakes (e.g., Reid, 1962; Moe et al., 1965). Sir Kenneth Blaxter in Scotland used the Mitscherlich equations to describe diet GE use by ruminants (Blaxter and Boyne, 1978). The research by Ferrell and Jenkins (1998) provides additional impetus to the need to consider this phenomenon in beef cattle energy requirement and efficiency evaluations. Use of NRC (1996), Level 2, allows prediction of level of intake depression; however, it may need refinement because the partial efficiencies of feedstuff energy use were established from estimates of absorbed energy using "maintenance level" digestibility. Actual DE or ME intakes of the animals used to determine NE_g were likely to have been lower than assumed. NRC dairy (2001) has also incorporated procedures to estimating digestibility depression at increasing levels of diet intake.

Future Directions

The history of describing the energetic efficiency of beef cattle has been focused on groups or genotypes and the factors that determine their diet energy requirements. The publication from the Committee on Animal Nutrition of the National Academy of Sciences, Nutrient Requirement of Beef Cattle, has expanded exponentially with each succeeding issue over the last 40 yr. More and more factors have been defined, such as breed/genotype, environment, and BW at maturity, that impact energy, and other nutrient requirements. Part of the expansion results from the deliberate attempt to document the scientific basis for these concepts.

Although these definitions represent important improvements in projecting needs or responses of cattle, we are recommending a change of research emphasis for the future. The focus should be on methods to assess individual animal differences in energetic efficiency, particularly on variations in energy requirements for

maintenance of mature beef cows. This, of course, is not a new dream of energeticists, but one that may be currently reachable. To accomplish the goal, a practical means of identifying individuals of merit must be developed to replace the too costly and cumbersome respiration or slaughter balance methods.

Greater activity within the integrative component of knowledge generation is needed to create new tools required for conducting the studies at the appropriate scale. Research protocols applied today are predicated on integrative research from the late nineteenth century. During the adoptive phase of the last 50 yr, the precision of many measurements may have been increased as have the ability to store and analyze the data, but it is for traits that were identified in the nineteenth and early twentieth centuries.

Recently, Oddy and Herd (2001) suggested that there are five mechanisms contributing to variation in efficiency under genetic control that could be studied, which are as follows: 1) feed intake, 2) digestion of feed, 3) metabolism, 4) activity, and 5) thermoregulation. To this list we would add those that have received most of the attention: 6) rate or gain, 7) BW, and 8) prolificacy. Also, metabolism must be separated into at least two components: 3a) maintenance and 3b) growth metabolism. None of these traits can be ignored, if only to ensure minimum or no negative consequences.

If we assume the processes identified above are correct, what phenotypes can be identified within each of these processes? What measurements need to be recorded? When should it be recorded? For example, informative data to improve energetic efficiency on a mature, grazing ruminant may not be the same as that needed for postweaning animals with access to high-quality diets. Is it possible to accurately determine the energy efficiency of the beef cattle system by making measurements only on young growing animals consuming high concentrate diets? As Webster questioned (see above), is fasting heat production a robust indicator of maintenance efficiency?

Possible Techniques, RFI. The several reports of relative feed intake measurements on individual animals, discussed briefly above, are encouraging. Genetic antagonisms appear inconsequential in most traits examined and the tool may indeed prove useful to define system energetic efficiency. Use of RFI for individual evaluation of large numbers of animals is, however, still cumbersome and several confounding factors are undoubtedly part of this compound trait. Other possibilities may also arise. Variations on this theme may be observed/expected ratios expressed either as observed to expected gain ratio or apparent maintenance requirement. In any case, component process energy loss measurements will need to be made on the growing animals and, particularly, mature cows to calibrate the method at least during development phases.

*Heart Rate **(HR)** Option.* This technique extrapolates to daily HP from short-term measurements of O_2/HR and long-term recordings of HR. The technique probably can be useful, but only under special circumstances and limited conditions. The need to "calibrate" each animal and then to show they are not "stressed" by the measurement process present serious limitations. Dr. A. Brosh (Agric. Res., Israel) estimated that in mature, untrained cows, some 50 or more percentage would not "calibrate." That is, they would have heart rates during O_2/HR calibration, as normally conducted in a handling chute, that are 10 or 20% or more above their HR average for the balance of the day. Perhaps for development of indexes, one could train young animals and thus calibrate O_2/HR for the majority of a group, as we can generally train them to be apparently calm in chambers. Calibrated O_2/HR monitoring combined with the inclinometer/accelerometers technique may provide a way to investigate activity energy loss variations in production circumstances.

Chips, ChIPs, SniPs, QTLs and Regulons. The most likely infusion of new tools with the most potential to realize improved maintenance and system energetic efficiency will come through identification of individual animal genomic message uniqueness. As stated by a recent technology perspective (Shannon and Arao, 2002), "developments in microarray technology will soon allow the entire human genome to be displayed on one or a small number of chips, providing a powerful tool for discovering and mapping of global regulation networks." Their transcription perspective described the use of microarray expression profiling using a combination of cDNA chips and chromatin immunoprecipitation to investigate expression groupings termed *regulons.* Although bovine genome mapping, sequencing, and regulon functions lag behind prokaryote and human descriptions, there are multiple candidates such as the maintenance and/or energy loss control factors discussed above to allow the development of targeted energetics microarrays. Such energy flux message profiling and/or QTL will likely need to be calibrated with simultaneous individual animal evaluations using classical methods, e.g., nutrient flux, O_2 consumption, etc. Once developed, these assays can be used to screen thousands of individuals identifying energetic uniqueness of value to the beef cattle industry.

Implications

The discovery that feedstuff nutrient use for the maintenance of animal life and support of animal product formation is a combustion process provided the basis for understanding dietary energy use by animals. Thousands of experiments exploring feedstuff and diet digestion, coupled with measures of either heat loss or product energy retention, have been used to create elaborate, useful net energy schemes to predict animal performance and/or requirements. Despite these advances, neither the requirement of energy for maintenance nor the partial efficiencies above maintenance have changed materially in the last 100 yr, and major mysteries remain unsolved (e.g., the cause of the high

heat increment of forages). New insights into factors controlling the need for and use of energy will likely be required to move forward. It is expected that techniques now becoming available will provide such insight, which in turn, will allow progress toward increased energetic efficiencies in the future.

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Technology to complement forage-based beef production systems in the West

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ABSTRACT: Forage-based beef producers in the Western United States are faced with numerous challenges to remain sustainable and profitable. Several technologies are available to assist ranchers, but the American public must be convinced that ranchers are sound stewards of public and private lands. New coalitions to resolve environmental conflicts have been formed over the last 10 yr that seem to have helped educate the public that proper grazing management is a sustainable practice. Methods are available to help ranchers economically evaluate enterprises and aid producers in deciding which technologies to adopt. New developments in fencing, water development and placement, and supplement placement should improve cattle distribution in large pastures. The use of complementary forages remains one of the most profitable technologies available. Swath grazing technologies are being tested to decrease feeding costs. Developments in plant genetics offer a variety of applications to beef producers that could improve animal performance. In the future, molecular technologies involving transgenic organisms may offer the opportunity to produce "designer" forages, ruminal microbes, and animals, but such applications have yet to be tested. Adoption of technologies that improve environmental quality and enhance profits for forage-based beef cattle producers will influence their sustainability.

Key Words: Beef Production, Forages, Genetic Selection, Rumen Microorganisms, Transgenic Plants

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Introduction

Forage-based beef production in the West faces an increasing number of challenges that may impact its sustainability. Many ranchers in the western US may be required to remove their livestock from public lands unless they can demonstrate that these animals do not pose an ecological threat to the landscape. Federal legislation such as the Multiple-Use Act, the Threatened and Endangered Species Act (ESA), and the Federal Clean Water Act could place additional economic pressure on already stressed beef cattle operations. Our objective is to review available or new technologies that offer solutions to some of the challenges faced by western livestock producers. We have chosen to start with examples of large-scale, whole-ranch technologies related to rangeland resources that have been successfully implemented and have had a high economic rate of return. Some of these technologies, such as fencing, water and supplement placement, have been around for a long time and have recently received renewed interest by resource managers to improve livestock grazing distribution. Then we reduced the application scale and chose examples of genetic modification of plants and animals at the gene level. These technologies have not yet been implemented on a practical basis; however, they demonstrate the wide range of possible applications of new scientific knowledge.

Conflict Resolution

The National Wildlife Federation and the Natural Resources Defense Council (2001) recently presented a white paper that charged the Bureau of Land Management (BLM) with failing to protect ecological integrity, water quality, biological diversity, and threatened and endangered species habitat. This report suggested that if the BLM failed to adopt a conservation agenda for lands under its jurisdiction, management responsibilities for those lands should be transferred to other federal agencies. The report promoted the establishment of conservation areas, Wilderness units and National Monuments, and suggested that livestock producers who use public lands in the western U.S. should be required to demonstrate that their management is ecologically sustainable. If the public fails to see that grazing is compatible with multiple values of rangelands, application of technology alone will not save the range livestock industry. Therefore, an important technology for range

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livestock operations might be categorized as conflict resolution. Changing legislation and demographics have caused ranchers and environmentalists to reexamine the current methods through which conflict is managed. For years, some environmental groups have sought to eliminate cattle grazing on public and private lands. Ranchers have viewed the ESA as an immediate threat to their livelihood. These conflicts have been reenacted in every western state, with very few constructive outcomes. Throughout the western United States, a number of organizations have been formed in response to conflicts that appeared to be unsolvable under the current social structure.

In Montana, elk numbers had been escalating steadily since the mid 1980s. Ranchers near the Beartooth Wildlife Management Area decided to seek solutions for the growing elk herds found on private lands. Chase Hibbard, Bill Milton and other ranchers formed a group that included members from the US Forest Service, Montana Department of Fish, Wildlife & Parks, BLM, Montana State Lands, and sportsman's groups. The team decided that everyone involved had to concur they were benefiting from the proposed solution, or there would be no agreement (Dagget, 1998). The group was called the Devil's Kitchen Management Team, and they agreed on a management proposal that was submitted to the Montana Fish and Wildlife Commission in 1993. The formation of this group and their management solution changed the way wildlife and public grazing resources are managed in the state of Montana. Local landowners were allowed to participate in setting wildlife harvest targets for private lands near the Beartooth Wildlife Management Area, which increased forage available for use in beef production systems.

The formation of the Malpai Borderlands Group in southwestern New Mexico in 1994 is another example of the reorganization of ranchers and conservationists to solve a resource management conflict. In a recent address, Under Secretary of Agriculture Mark Rey (2002) recognized this group for their forward thinking. Ranchers bring their cattle to the 130,000 ha Gray Ranch for a grassbank of stockpiled forage and in return, they place conservation easements on their own ranches. Ranchers use an equal amount of forage as set aside in their easement. To date, the Malpai grassbank has rested 10,000 ha on five ranches (Rey, 2002).

A number of environmental laws have made it difficult for production agriculturists to remain in business in the western US. It has become apparent that ranchers must become active participants in land policy decisions. This process will help educate environmental and ranching communities. There are numerous groups all over the western U.S. that have become active environmental educators in an effort to resolve resource management conflicts.

Whole Ranch Evaluation

Many technologies available to ranchers can increase livestock production; however, whole ranch evaluation approaches that include partial budgeting can help ranchers economically evaluate enterprises. A number of private and state entities have implemented programs to assist ranchers with economic evaluation of their business, and may also conduct workshops and sell software. Most of these programs are designed to help establish ranch goals, inventory resources, explore possible enterprises, plan changes and monitor and adjust those plans (Richards and George, 1996). Total Ranch Management, developed by a Texas Extension group, has served as the basis for the Western Integrated Resource Education (WIRE) program that involves four land-grant universities and their extension programs. This type of structured evaluation, and the use of personal computers, has helped producers examine their entire operation and has lead to the adoption of technologies that are nontraditional yet highly profitable.

A number of individuals and private companies have advocated whole ranch evaluation. One of the most notable of these is Gregg Simonds. Simonds was asked by the Deseret Ranch Management Team to evaluate the economics of implementing irrigation technology, and through the use of whole ranch evaluation methods, Simonds showed the ranch management team that they would be financially better off if they did not adopt this technology (Dagget, 1998). Based on enterprise evaluation, Simonds suggested changes in production practices over a 12-y period on the Deseret Ranch that resulted in decreased total cost per pound of calf produced from over $0.90 to $0.62. Production changes implemented included moving from an early-spring calving season to a late-spring calving season, and the addition of a yearling operation to take advantage of year-round marketing opportunities (Simonds, 1991). Simonds (1991) suggested that the tremendous variability present in biological and financial environments does not make it possible for a single fixed strategy to maximize long-term profitability.

An assessment of these types of whole ranch evaluations concluded that due to the programs, ranchers had improved or protected 14% of the rangeland used in their operations, over half had increased their ranch profit and a majority had implemented at least one new technology (Richards and George, 1996).

Fencing

One of the major problems associated with grazing cattle on large pastures in the western United States is poor distribution of grazing. Grazing systems have been used to improve distribution, however, since this topic has been reviewed extensively (Launchbaugh et al., 1978), we will examine the use of fencing to manage distribution. Cattle tend to congregate near water sources and on level terrain where forage is abundant (Ares, 1953). This results in portions of the pasture that are grazed too heavily and other areas where little grazing takes place. It also contributes to erosion and

poor water quality in many watersheds (Kauffman and Kruger, 1984). The use of fencing to control livestock distribution and increase forage use is usually one of the most cost effective methods used to improve cattle production on large ranches (Ohlenbusch et al., 1995). Recent developments in electric fence technology have allowed producers to employ fencing in areas where it was previously cost prohibitive. Electric fences often cost 25% to 50% of conventional fencing. Less labor is required to install electric fencing, and it can be installed at rates three to five times faster than five-strand barbed wire fencing (Lacey, 1985). The availability of low cost solar panels, energizers, and batteries has provided power to many remote areas of large ranches. This technology has also allowed producers to develop intensive grazing systems on highly productive pastures.

Water Development and Placement

Water development and placement can also be used to manipulate livestock distribution on rangelands. Very few ranch investments return higher annual rates than stockwater developments (Roberts and Wennergren, 1965).

Ganskopp (2001) evaluated the effects of moving water and salt locations to improve beef cattle distribution in large (825 ha) pastures in Oregon. Cattle were fitted with global positioning system collars to assess their location in the pasture. Mean distance to water was unaffected by location which demonstrated cattle followed the movements of the water tanks. Ganskopp (2001) concluded that cattle made less effort to remain near salt than near water and moving drinking water was the most effective tool for altering cattle distribution. Porath et al. (2002) investigated cattle distribution on pastures with off-stream water and trace mineral salt. They reported that early in the grazing season (July) cattle with access to off-stream water were located farther from the stream in the latter part of the day. There were no differences during the late season (August) in distances from the stream between cattle with off-stream water and trace mineral salt and those without.

Changing water location and providing off stream water in pastures with riparian areas is also a method to improve steambanks. McInnis and McIver (2001) conducted a study on the same pastures as Porath et al. (2002). They reported that off-stream water and salt attracted cattle into the uplands enough to reduce the proportion of uncovered and unstable streambanks from 9% to 3%. Providing off-site water can also improve animal performance. Porath et al. (2002) demonstrated that cows and calves with off-stream water and trace-mineral salt gained more than cows and calves that did not have access to off-stream water. Willms et al. (1995) found that grazing steer performance increased 23% when an alternate water source was supplied compared with steers that had access only to a dugout.

Despite recognition that water development has been one of the most effective methods to improve livestock distribution in large pastures, cost effective technologies have limited its use. Recent improvements in solar-powered pumps have led to increased use of watering sites and wells that would not have been possible due to the lack of electrical power. Nose pumps are another cost-effective recent technology that have been employed to keep cattle out of riparian areas and lure them to other adjacent locations. The U.S. Fish and Wildlife Service has encouraged the use of nose pumps as a method to keep cattle from entering riparian areas.

Supplement Placement

Another technology used to improve distribution on rangelands has been the placement of supplements. Ares (1953) demonstrated that a cottonseed meal-salt mix placed away from water could be used to reduce over-grazed areas by 50% and increase properly grazed areas by 84%. Recently, Bailey and Welling (1999) examined the use of dehydrated molasses supplements to improve grazing distribution in foothills rangelands. Three pastures that averaged 642 ha in size were divided into difficult and moderate terrain. Each terrain subunit was randomly assigned to control or supplement treatments. Dehydrated molasses supplement barrels and salt were moved every 7 to 10 d during the fall and winter. A greater proportion of cattle were observed in areas with supplement (32%) than areas without supplement (3%). Supplement placement increased forage utilization in areas with moderate terrain by 24% and by 11% in areas with difficult terrain. Bailey and Welling (1999) concluded that placement of dehydrated molasses supplements could be used to improve uniformity of grazing by beef cattle in foothill ranges although it was more effective in moderate terrain. Bailey et al. (2001) conducted a study to examine the distance cattle grazed from dehydrated molasses supplements. Three pastures were used to determine if supplement placement could increase forage utilization in underutilized areas. Forage utilization was increased 14% at distances up to 600 m from the supplement. Fifty-three percent of the cows were observed within 600 m of the supplement, and overall cows spent 37% of their time within 600 m of supplement. Supplement placement was an effective tool to modify cattle grazing distribution; however, other research has indicated that forage characteristics, such as forage quality and quantity, are the most important factors affecting cattle distribution (Harris et al., 2002).

Complementary Forages

Use of complementary forages involves combining different forage species with dissimilar growth patterns to help maintain consistency in forage production and nutrient intake by cattle. In the West, rangeland forages are usually the base to which introduced forages

are added. The objective often is to increase livestock production per land area in a cost efficient manner. Gray (1973) reported that complementary grazing was the single item most highly correlated with increased net profit for cow-calf producers in the Great Plains. Launchbaugh et al. (1978) described the use of improved pastures and farmed forages to reduce per animal costs and increase net returns to cattle producers. Smoliak and Slen (1974) found that complementary grazing in Canada reduced land requirements per animal unit by 77% and increased beef production by 60%. By using complementary forages, individual animal performance is usually increased due to improved forage quality, and stocking rate can be increased due to increased forage production. Other advantages of using complementary forages can include more efficient use of individual forages, improvements in range condition (Gillen and Berg, 2001), and increased resource management flexibility. Over seven calf crops, Sims (1993) compared cow-calf pairs grazing sagebrush-mixed prairie native rangeland with pairs grazing the same rangeland plus winter wheat and summer annual forage to replace 30% of the rangeland for each cow unit. Using the complementary forages increased stocking rate by 32%. Cow body weight at weaning was heavier, and Angus × Hereford cows had improved reproductive rates on the complementary forage system compared with native rangeland alone. In addition, weaning weights were 90 kg heavier for calves on the complementary forage system (Sims and Bailey, 1995). Stocking rates and total season livestock production per ha were higher when steers grazed Old World bluestem (*Bothriochloa ischaemum* L.) combined with native pasture compared with grazing native pasture alone (Gillen and Berg, 2001). Coleman et al. (2001) compared native tallgrass prairie (primarily *Andropogon gerardii* Vitman., *Schizachyrium scoparius* [Michaus] Nash, and *Sorgastrum nutans* [L.] Nash) under continuous grazing management with the addition of wheat pasture grazing or substitution of plains bluestem (*Bothriochloa ischaemum*, var. ischaemum) pasture grazing combined with wheat pasture grazing for cow-calf production. Cows grazing plains bluestem and wheat pasture lost less weight and body condition compared with cows grazing native tallgrass prairie or native prairie and wheat pasture, however, no differences were seen in calf weaning weights or in reproductive efficiency. The plains bluestem-wheat pasture system produced greater net income per hectare than either of the native tallgrass prairie systems. Gillen et al. (1999) compared two sequence grazing systems; one of native mixed grass prairie (primarily *Schizachyrium scoparium* [Michx.] Nash, *Bouteloua curtipendula* [Michx.] Torr., and *Androgpogon hallii* Hack.) and Old World bluestem, and the second of Eastern gamagrass (*Tripsacum dactyloides* [L.] L.) and Old World bluestem, for crossbred beef steers. Sequence grazing is defined as using two or more units of land containing different forage species and grazing them in succession. Steer gains during a 103-day grazing period did not differ between the two systems, however, due to a substantially greater stocking rate, the Eastern gamagrass-Old World bluestem system resulted in 150% greater beef production per hectare. Alfalfa (*Medicago sativa* L.) is commonly used as a complementary forage. Including alfalfa at as little as 35% in pasture mixtures results in improvements in animal gains (Popp et al., 2000). Yearling steers gained as much as 1.5 kg/d and total liveweight production ranged from 107 kg/ha under dryland conditions to 1946 kg/ha under irrigation when alfalfa was grazed. Grazing alfalfa can pose management difficulties due to its bloat potential. However, traditional plant breeding was used to develop AC Grazeland, a cultivar of alfalfa with reduced bloat potential when grazed (Popp et al., 2000). Many complementary forage species have been extensively evaluated including alfalfa, bermudagrass (*Cynodon dactylon* L.), Eastern gamagrass, foxtail millet (*Setaria italica* (L.) Beauv.), kochia (*Kochia scorparia*), oats (*Avena sativa* Linn.), orchardgrass (*Dactylis glomerata* L.), pearl millet (*Pennisetum glaucum* L.), perennial ryegrass (*Lolium perenne* L.), reed canarygrass (*Phalaris arundinacea* L.), rye (*Secale cereale* L.), smooth bromegrass (*Bromus inermis* Leyss.), sudangrass (*Sorghum bicolor* (L.) Moench), triticale (*Triticosecale* spp.), wheat (*Triticum aestivum* L. subsp. *aestivum*), and the wheatgrasses (*Agropyron, Elymus, Pseudoroegneria, Pascopyrum*, and *Thinopyrum* spp.). Recently, Vogel and Jensen (2001) reported survival and forage production under rangeland conditions of 105 accessions of the perennial *Triticeae* that were chosen to represent a wide range of germplasm. Species evaluated came from 8 genera and included commonly grown species as well as a large number of species not previously evaluated in the Central Great Plains. These authors identified several new species that may have potential for inclusion in rangeland forage systems, including mammoth wild rye (*Leymus racemosus*), *Leymus sabulosus*, and *Leymus chinensis.*

Swath Grazing

Swath or windrow grazing is an alternate feeding technique designed to lower production costs by allowing the cow to harvest cut forages directly. Cut hay is left in windrows through the winter, and cows graze the windrows under controlled conditions, usually with electric fencing. Ranchers from Nebraska to Canada are using this method to reduce their winter feeding costs (Surber et al., 2001). Thomson (1999) estimated that swath grazing saved an average of $36.00 per ton compared to baling, storage and feeding costs, and resulted in a savings of $0.55 per cow per day and $0.21 per calf per day. Surber et al. (2001) estimated a minimum savings of $16 per acre, assuming a harvest of 1.5 tons per acre of meadow hay. Volesky et al. (2002) baled alternating windrows of cool-season perennial species with the remaining windrows left in place for

swath grazing. Forage production costs for the swath-grazing system were about $63/ha less than baling due to baling and bale moving costs. Weaned steer calves were fed baled hay or grazed windrows during each of two winters. During the 1st year, swath-grazing calves gained more than bale-fed calves, but gains were similar during the second year. Feed costs averaged $0.16·animal^{-1}·d^{-1} for swath grazing and $0.30 animal^{-1}·day^{-1} for feeding bales.

Plant Genetic Selection

Genetic improvements in forage quality can result in reductions in supplementation, reductions in acreages of complementary forages or enhanced flexibility in livestock and enterprise management (Casler and Vogel, 1999), and the development of improved cultivars can improve livestock productivity (Moore and Jung, 2001). Although improvement of forage quality through traditional plant breeding and genetic selection can be successful, very few new cultivars with improved forage quality have been developed and released (Vogel and Sleper, 1994). Improving forage quality characteristics such as digestibility may not be beneficial to a species, while anti-quality factors in plants that reduce animal performance appear to improve the survivability and vigor of a species. However, substantial genetic variation in digestibility has been reported for a wide variety of forages including alfalfa, bermudagrass, crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), indiangrass (*Sorghastrum nutans* (L.) Nash), intermediate wheatgrass (*Elytrigia intermedia* (Host) Nevski subsp. *intermedia*), orchardgrass, perennial ryegrass, smooth bromegrass, and switchgrass (*Panicum virgatum* L.; Vogel and Sleper, 1994). Ranges in IVDMD as large as 10% within a forage species have been reported, and heritabilities have been estimated to be 0.3 or higher. Documented progress has been made in improving digestibility via genetic selection in at least 7 forage species, and the reported rates of change of 0.7 to 2.5% per year are similar to long term gains for grain yield in many cereal crops (Casler and Vogel, 1999). Genetic progress in selection for reduced NDF content has been reported in smooth bromegrass (Casler, 1999) and reed canarygrass (Surprenant et al., 1988). However, these reductions in NDF content were associated with reduced forage yield.

It is possible to dissociate yield and nutritive value. Belanger et al. (2001) reported success in improving the nutritional value of timothy without reductions in forage yield. Forage yield and digestibility have both been improved in a number of species. Vogel and Sleper (1994) reported a 34% increase in yield, 12% increase in IVDMD, 42% increase in ADG, and a 132% increase in gain/ha for bermudagrass. In addition, the improvements made in IVDMD have been repeatable across a wide range of environments and management systems, including on-farm tests (Vogel and Sleper, 1994). Selection for increased Mg content has been successful in Italian ryegrass (*Lolium multiflorum* Lam.) with a 56% increase in forage Mg, a 10% increase in gains by grazing ewes and lambs, and a reduction in incidence of hypomagnesaemia in ewes (Mosely and Baker, 1991). Similar results have been obtained in tall fescue (*Festuca arundinacea* Schreb.; Sleper et al., 1989; Crawford et al., 1998). Variation in UIP content and minor success in increasing UIP has been demonstrated in alfalfa (Broderick and Buxton, 1991).

Plant toxins often give a competitive advantage to plants, and the resulting toxicity to cattle is merely a secondary effect. Reed canarygrass cultivars have been developed with reduced levels of alkaloids (Kalton et al., 1989), sudangrass with decreased potential to cause prussic acid poisoning (Haskins et al., 1990), and sweetclover cultivars with lower levels of coumarin (Gorz et al., 1992). Most anti-quality compounds are the result of specific pathways found in plants, and many are not necessary for growth or development. With increased understanding and characterization of these pathways, "blocking" genes or down-regulation of these pathways might prove a useful way of reducing the levels of toxin compounds.

Genetic Modification of Plants

New technologies, which complement improvements made in pasture science, include advances in DNA and molecular genetics (Vercoe, 1996). Molecular approaches offer the opportunity to produce "designer forages." Opportunities to design forages with beneficial characteristics include forages containing specific antibodies or vaccines (Ma et al., 1995; Mason et al., 1996), expression of UIP (McSweeney et al., 1999), or enhanced fiber digestion (Carpita et al., 2001). McSweeney et al. (1999) stated that there are two strategies to improve forage quality prior to ingestion. One is maximizing the content of desirable compounds such as amino acids presented to the small intestine, and the second is reducing the content of undesirable compounds such as lignin and secondary products that are toxic.

Tabe et al. (1995) suggested that there are two major biotechnological approaches to improving forage protein quality for ruminants; introducing condensed tannins into forages such as alfalfa to increase the UIP fraction, and enriching forages with specific proteins that have a reduced ruminal degradability. When condensed tannins and polyphenolic secondary plant products are found at high levels (40 to 50 g/kg DM) in forages, CP and DM digestibility are reduced (McMahon et al., 2000). However, tannins at moderate levels (5 g/kg DM) have been shown to reduce the degradation of leaf protein in the rumen, increase duodenal nonammonia N flow, increase absorption of essential amino acids from the small intestine (Baba et al., 2002), increase milk production, prevent bloat in cattle and sheep (Barry and McNabb, 1999; McMahon et al., 2000), and reduce parasite infections in grazing sheep (Butter

et al., 2001). Research efforts are currently underway to genetically modify alfalfa to reexpress its tannin biosynthetic pathway or to move genes encoding steps of this pathway into alfalfa (McMahon et al., 2000).

Transgenic subterranean clover (*Trifolium subterraneum* L.), white clover (*Trifolium repens*) and alfalfa have been produced which contain genes which encode delta-zein, ovalbumin and albumin; proteins that are resistant to ruminal degradation but are readily degraded by intestinal proteases (Tabe et al., 1995; Khan et al., 1996; Christiansen et al., 2000). Christiansen et al. (2000) introduced genes encoding sunflower seed albumin into white clover to increase the content of cysteine and methionine. They were able to increase the level of albumin to 0.1% of total protein in the leaves, and demonstrated that the ability to synthesize albumin was inherited in successive generations. Khan et al. (1996) introduced a gene encoding sunflower seed albumin into subterranean clover, and the expression of the gene was stable in the first and second generation progeny. Tabe et al. (1995) introduced sunflower seed albumin into Australian commercial cultivars of alfalfa, and were able to obtain expression of the foreign protein, however, the levels of albumin achieved were presumably not high enough to affect animal production.

Ferulic acid crosslinks xylans and links them to lignin in grasses, and this reduces digestibility of the plant cell wall. Hatfield et al. (1999) speculate that targeting the enzymes that attach ferulic acid to polysaccharides could be the key step in reducing cross-linkages and improving forage grass digestibility. Other options to manipulate cell wall digestibility include altering lignin concentration and lignin composition using both genetic selection and molecular approaches. In forage legumes, selection for increased pectin content could lead to increased digestibility (Hatfield et al., 1999).

Current transformation efforts involve down-regulating enzymes in the lignin biosynthetic pathway in alfalfa and stylo (*Stylosanthes* spp.) that have resulted in reduced lignin content and increased digestibility compared with control plants (Casler and Vogel, 1999). Guo et al. (2001) produced transgenic alfalfa lines that had decreased lignin content and changed lignin composition by down-regulating two O-methyltransferase enzymes in the lignin biosynthesis pathway. Compared with control alfalfa plants, these transgenic alfalfa plants exhibited no gross changes in stem morphology as assessed by examination of stained cross sections, and no changes in pectin, cellulose and hemicellulose content. Alfalfa in vitro NDF digestibility was increased by 1 to 5.5% in the transgenic alfalfa lines compared with control alfalfa, and NDF digestibility of the stems was improved by 8% in one transgenic line. In *Arabidopsis thaliana*, a plant species that has been used extensively as a model for genetic studies, it is estimated that approximately 15% of the more than 25,000 genes identified are involved in cell wall synthesis, reorganization and turnover (Carpita et al., 2001). Tremendous progress has already been made, but for molecular breeding and transformation technology to be successful, detailed knowledge of the exact genes to manipulate, and of any possible negative consequences of genetic manipulation are necessary (Vogel and Jung, 2001).

Genetic Modification of Ruminal Microbes

Using genetically engineered ruminal microbes and microbial enzymes offers the possibility of eliminating anti-nutritional factors and toxins in plants, enhancing fiber digestion, and improving amino acid composition of ruminal bacteria (Wallace, 1994; Bonneau and Laarveld, 1999). Over 100 different genes encoding enzymes for fiber digestion have been identified and cloned from ruminal bacteria such as *Butyrivibrio fibrisolvens, Fibrobacter succinogenes, Prevotella ruminicola, Ruminococcus albus* and *Ruminococcus flavefaciens*. At least 30 genes from ruminal fungi have been isolated that encode cellulase, xylanases, mannanases, and endoglucanases. These are of particular interest due to their powerful fibrolytic activity and ability to break down very resistant cell wall polymers. In addition, cellulase and xylanase genes from ruminal protozoa have been cloned. Almost 50% of the fibrolytic genes cloned have been sequenced (Selinger et al., 1996). Protein engineering has been used to increase the catalytic activity and substrate diversity of fibrolytic enzymes from ruminal microbes. This has resulted in enzymes with up to 10 times higher specific activity, changed pH and temperature optima and increased substrate binding activity than the enzymes from which they originated (Selinger et al., 1996). Some ruminal bacterial species such as *Butyrivibrio fibrisolvens* and *Prevotella ruminicola* are found widely in ruminant animals on varied diets and are found in significant numbers regardless of the ruminal environment. These species therefore are logical choices to introduce new or enhanced genetic material into the rumen (Selinger et al., 1996).

Streptococcus bovis is tolerant to O_2 and depressed rumen pH unlike most cellulolytic bacterial species in the rumen. In addition, there are convenient gene transfer methods available for this species that make it a candidate as a host for the expression of genes from other organisms. Ekinci et al. (2002) were able to use a beta-glucase promoter found in *S. bovis* to express a cellulase gene from the anaerobic rumen fungus *Neocallimastix patriciarum* that is found in very low levels in the rumen, and is important for the degradation of crystalline cellulose. The resulting enzyme product was active against a wide variety of cellulosic substrates. The advantages of using fungal enzymes are their stability to low pH and their extremely high activity level (Ekinci et al., 2002).

Xue et al. (1997) were successful in introducing a xylanase gene from the anaerobic ruminal fungus *Neocallimastix patriciarum* into *Butyrivibrio fibrisolvens*, and achieving secretion of the enzyme. Krause et al. (2001) constructed a recombinant *Butyrivibrio fibrisol-*

vens that expressed a xylanase enzyme from the ruminal fungus *Neocallimastix patriciarum*. The recombinant *Butyrivibrio fibrisolvens* did have an increased ability to digest fiber, but it did not persist in the rumen past 22 d.

Monofluoroacetate is a toxin found in many Australian shrubs and trees that results in substantial animal deaths. Gregg et al. (1996) reported the successful introduction and in vitro expression of a gene encoding a toxin-degrading enzyme (fluoroacetate dehalogenase) into *Butyrivibrio fibrisolvens*. The recombinant *Butyrivibrio fibrisolvens* established and persisted in the rumen of sheep for over 5 mo; however, the successful colonization of a genetically modified species in the rumen is still the most difficult barrier to cross. Currently, the biggest problem is the ability to introduce and maintain the new strain in the mixed rumen population, and survival of new strains is not well understood. Other options include using nonruminal organisms such as *Saccharomyes cerevisiae* because yeast is already used as a feed additive and its genetics are well understood (Wallace, 1994).

Genetic Modification of Animals

The technology of developing transgenic animals with modified characteristics offers the opportunity to increase production efficiency, modify digestion and end products, improve metabolic efficiency, and partition nutrients (Vercoe, 1996). Bacteria appear to be a convenient reservoir of useful functional genes to introduce into animals. Several efforts in this area are currently ongoing. The one that has made the most progress involves inserting a biosynthetic pathway for cysteine, a rate-limiting amino acid for wool production, into sheep. Genes from *Escherichia coli* encoding the two enzymes necessary to convert the amino acid serine into cysteine were introduced into mice. These transgenic mice expressed the enzymes for the synthesis of cysteine, and when placed on a low sulfur amino acid diet continued to grow normally. Control mice without the enzymes for cysteine synthesis suffered considerable weight loss on the same diet. These same genes have been placed into transgenic sheep, but although low-level expression of the enzymes has occurred, not enough cysteine has been synthesized to be useful (Ward, 2000).

Another attempt at manipulating animal metabolism is the introduction into ruminants of a glyoxylate pathway that synthesizes glucose from acetate. Ruminant metabolism is unique in that there is very limited glucose absorption and only one gluconeogenic VFA, propionate. Saini et al. (1996) introduced genes encoding bacterial glyoxylate cycle enzymes into mammalian cells in vitro, and into transgenic mice. In both cases, the appropriate enzymes have been expressed. Introducing this pathway into ruminants presumably would improve metabolic efficiency. However, all efforts so far to insert these genes and achieve expression of the glyoxylate pathway enzymes in sheep have failed (Ward, 2000).

Implications

Forage-based beef cattle producers in the Western United States face two large challenges in the future. First, they must demonstrate that their production methods are compatible with the desires of the American public, especially when public land grazing is involved, and second, they must remain economically viable in times of increased competition. A number of technologies that are simple and relatively inexpensive are currently available to help meet these challenges. Advances in electric fencing, water development and supplement placement offer practical solutions to improve distribution problems. The use of complementary forages has proven to be one of the most profitable improvement practices for livestock producers in the Western US. Other technologies such as genetic modification of plant and ruminal microbial species are not currently available, but they may substantially change the way livestock producers operate in the future.

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