Breeding for Feed Efficiency: Yes We Can!

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Take-home point

Efficiency of cows can be improved further by continuing to select for more milk per cow along with modest decreases in cow size and by using genomic technologies to select for animals that eat less than expected to achieve their production.

Introduction

Feed efficiency in North America has more than doubled in the past 70 years, largely as a byproduct of selecting and managing cows for increased milk production (VandeHaar et al., 2016; Capper et al., 2009). Continued gains in feed efficiency are likely and possible as we adopt new technologies and make better use of existing ones Many factors influence feed efficiency on farms. For example, feed efficiency is decreased directly by losses of feed or products on the farm. Feed efficiency is altered indirectly by diet composition, management of cows, and genetics through effects on feed intake, milk production, maintenance requirements, digestion, nutrient partitioning, and metabolic efficiency. These topics have been reviewed recently by the authors and colleagues in an open source publication of the Journal of Dairy Science (VandeHaar et al., 2016), and we direct readers to that publication <journalofdairyscience.org/article/S0022-0302(16)30165-5/abstract> as well as to papers in the Large Dairy Herd Management Handbook soon to be published in 2017 (VandeHaar and Tempelman, 2017; Cole and Spurlock, 2017; and other chapters in the section on breeding strategies, edited by Weigel). We also recommend other recent reviews of dairy feed efficiency (Berry and Crowley, 2013; Connor, 2015; Pryce et al., 2014). In this paper, we briefly discuss the role of genomics and traditional genetics in selecting animals that are more efficient. We will focus on two areas for future improvements in feed efficiency: 1) continued increases in milk production per cow on a per unit of metabolic body weight basis, and 2) adoption of new genomic methods to select for cows that eat less than expected based on production.

Defining feed efficiency

Feed efficiency is a complex trait for which no single definition is adequate. Feed efficiency should be considered over the lifetime of a cow and include all feed used as a calf, growing heifer, dry cow, and lactating cow and all products including milk, meat, and calves. Feed efficiency could also account for whether the feeds eaten by cattle could be consumed directly by humans, how much land is required to grow feed, whether wastes are captured, and how much the cows contribute to climate change and pollution. Developing a metric that includes all relevant factors for feed efficiency would be difficult. Whereas protein could be considered the most important component of milk, energy intake generally limits milk production, and feed energy includes the energy of protein. Thus, this paper focuses on energetic efficiency.

Gross energy (**GE)** is the total chemical energy of a feed but some of it is lost as the chemical energy in feces, gasses, and urine, and some is lost as the heat associated with the metabolic work of fermenting, digesting, and processing nutrients. The remaining chemical energy is known as net energy (**NE**). Some NE is used to support maintenance functions and is subsequently lost as heat. Some NE is the chemical energy of secreted milk or accreted body tissue and conceptus. For this paper, feed efficiency is defined as the energy captured in milk and body tissue divided by the GE consumed by a cow in her lifetime, and it is highly correlated to milk energy output per unit body weight (**BW**). The major components affecting feed efficiency can be divided into 1) those that alter maintenance and the dilution of maintenance, or the portion of NE that is captured in milk or body tissues instead of used for maintenance, and 2) those that alter the conversion of GE to NE, which include diet and cow effects. To breed for improved feed efficiency, we can focus on these independently. To enhance the portion of NE that is captured in products, we can breed for continued increases in milk production per cow on a per unit of metabolic body weight basis. In the past, we have not been able to select for improved conversion of GE to NE; however, new genomic methods are becoming available.

Selecting for cows that capture NE more efficiently.

The typical Holstein cow has a maintenance requirement of ~10 Mcal of NE/day (equivalent to ~25 Mcal of GE and ~6 kg of feed; the requirement is ~8 Mcal for Jerseys). This feed is used for basal life-sustaining functions even if animal is not producing milk, growing, working, or pregnant. Any extra feed consumed above that needed for maintenance can be converted to milk or body tissues. As a cow eats and produces more, the portion used for maintenance becomes a smaller fraction of total feed intake. This "dilution of maintenance" increases feed efficiency and has been known for a long time (Freeman, 1975; VandeHaar et al., 2016).

Production relative to maintenance can be increased by increasing production or by decreasing maintenance. Maintenance is correlated to a cow's body weight, and, over the past 50 years, the body size of dairy cattle has increased. Because of this, the US genetic base for body size traits in all dairy breeds is continually being adjusted up. However, our latest analysis on 5000 Holsteins in mid-lactation (using the dataset of Tempelman et al., 2015) demonstrated no genetic correlation between BW and milk energy output (VandeHaar et al., 2014); moreover, BW was genetically correlated negatively with overall feed efficiency. In a smaller subset of that data, Manzanilla-Pech et al. (2016) showed that milk energy output had zero or negative genetic correlations with BW and that stature was genetically correlated negatively with feed efficency. Lifetime feed efficiency of dairy cows had more doubled in the past 70 years because of increased milk production per cow; however, the fact that cows have gotten larger at the same time is counter to the goal of increasing efficiency. If cows had simply gotten larger as we bred for greater milk production, this might be acceptable; however, it seems we have bred for larger cows simply because we like larger cows and think they should produce more milk. If we want more milk, we should breed for more milk. If we want more efficient cows, we use a linear index that favors more milk protein and fat and smaller, or at least not larger, body size.

At present, we don't know exactly the optimal level of milk production and body weight to maximize feed efficiency of dairy cows. We do know the following.

1. As cows eat more and produce more milk, the improvement in overall feed efficiency per lb of extra milk produced or feed consumed diminishes. This is due to simple math. If a 1400-lb cow

requires 10 Mcal of NEL per day for maintenance and eats 10 Mcal, then 100% goes toward maintenance. If she eats 20 Mcal per day and puts the extra 10 Mcal into milk (about 30 lb of milk/day), 50% goes toward maintenance. At 30 Mcal per day (almost 70 lb of milk), 33% is for maintenance; at 40 Mcal (100 lb of milk), 25% is for maintenance; and so on. With each extra 10 Mcal of feed and milk, the advantage in milk/feed from diluting maintenance decreases.

2. Breeding for smaller cows provides the same result for feed efficiency as does breeding for more milk. What matters is how much milk energy a cow produces relative to her BW. More specifically, what really matters is her BW to the 0.75 power, or metabolic BW (MBW) because maintenance requirements are directly related to $BW^{0.75}$. As a percentage, the difference in MBW is less than the difference in BW, so while a 1500-lb cow weighs 50% more than a 1000-lb cow, on a MBW basis, she is only 36% heavier.
3. Previous estimates of the maintenance requirement of cows is likely too small for today's cows. Based on a recent publication (Moraes et al., 2015), cows probably require 25% more energy for maintenance than predicted by the last NRC (2001). In addition, maintenance per unit MBW is higher for thin cows than fat cows (Birnie et al., 2000), indicating that maintenance is more related to the frame size of a cow than her actual BW.
4. We don't have measures of BW for cows that can be used to predict feed costs for maintenance in a breeding index. Instead we have estimates of BW based on classification scores. These are imperfect but are improving as new data becomes available. In the past year, the TPI was updated with new estimates for BW, and the Net Merit Index will likely be changed in August 2017.
5. To complicate this further, as cows eat more per day relative to their size, they digest feed less efficiently because it passes through the tract faster (NRC, 2001). The magnitude of this digestibility depression is not clear.
6. Efficiency on a lifetime basis is what matters. To that end, we must consider the amount of milk produced per unit of feed over the cow's lifetime, not just during lactation. Larger animals eat more feed while heifers and dry cows, but they also give more salvage value.
7. Lifetime feed efficiency likely is close to its maximum at 40,000 lb of milk/year for a cow with 1700 lb mature BW (VandeHaar, 1998).
8. We do not know with certainty whether feed efficiency for Holsteins and Jerseys is different. Jerseys might be more efficient for producing cheese, due to the higher protein and fat content of their milk (Capper and Cady, 2012). However, studies with actual measures of feed intake and production on lots of animals are needed to many any conclusions regarding breed differences.
9. If the milk and body tissues are not harvested, they are of no value. Cow deaths and unsaleable milk are major losses for feed efficiency. Both are both influenced by heritable traits (such as productive life and somatic cell score) and are not considered in the traits we use to breed for milk production and body weight.

Thus, based on all available data, we suggest that substantial gains can still be made in lifetime feed efficiency from increasing production relative to body size and that a linear index should be used to select cows for greater milk production and smaller BW together. However, top North American herds are at a point where the return in efficiency from further gains in productivity or from smaller cows certainly will be smaller than they have been in the past. Thus, along with continuing to breed for more milk per unit BW, we should also develop new methods to select for cows that convert GE to NE more efficiently.

Selecting for cows that convert GE to NE more efficiently

During the 20th century, we selected for superior genetics based on measuring phenotypes (traits like milk production) in daughters of young sires; sires with outstanding daughters were deemed genetically superior. Because DMI cannot be measured easily and routinely on individual cows in commercial farms, direct selection for feed efficiency was impossible. However, the advent of genomic selection is revolutionizing the dairy industry. Genomics enables selection for traits like feed efficiency for which daughter phenotypes are unknown.

Excellent reviews on the general methodology of genomic selection are Eggen (2012) and Hayes et al. (2010). In short, the genome (all of the DNA) of a cow consists of 30 pairs of chromosomes and 3 billion base pairs. There are 4 options for each base pair in the genome, and for most of these 3 billion base pairs, the base of the coding strand is the same for all cows. A single nucleotide polymorphism (SNP) is any place in the DNA where more than one base is found. When we genotype cows, we typically examine from 6,000 to 90,000 of these SNP across the genome, but even 800,000 SNP can be examined. An individual SNP may have no biological function, but it is linked to the DNA around it, so the SNP serves as a marker for the variation in the DNA at surrounding genes. When the small effects of 50,000 or more SNP are added together, they can help identify animals that are expected to be superior for heritable traits like milk production.

One trait of particular interest in selecting animals for feed efficiency, independently of production level, is **Residual Feed Intake** (**RFI).** RFI is a measure of actual versus predicted intake for an individual and is essentially "unjustified feed intake" (VandeHaar et al., 2016, which provides references for other great reviews on the subject). Cows that eat less than expected have negative RFI, and thus are desirable when comparing animals for selection purposes as long as RFI is only seen as one factor to use in selecting for efficiency. Selecting for high milk production relative to BW also remains an important selection objective.

Based on our data examining the feed efficiency of cows compared to their level of production (see figures in VandeHaar et al., 2016), efficiency varies considerably among cows within a production level. This variation can also be examined in intake units, or RFI. Whereas part of the variation in RFI is error in measurements, some RFI is biological. We found the pedigree-based heritability of RFI to be 0.17 based on measures in 4900 cows from across the US, Canada, Scotland, and the Netherlands (Tempelman et al., 2015). We also found that RFI was heritable at the genomc level. Based on the first 2900 cows of our study, the proportion of RFI variance accounted for by about 50,000 SNP markers was 14% (Spurlock et al., 2014), and this has been confirmed when examing 5000 cows by separate analyses at Iowa State, Michigan State, and the University of Wisconsin. However, in all of our analyses, very few SNP had major effects; instead, the additive effects of many SNP were important in identifying the efficient vs inefficient cows. Publications from those papers are forthcoming.

New breeding value equations based on the cows in our current database (7,600 cows with feed efficiency phenotypes, of which about 5,300 have genotypes) can be applied to bulls currently available in the US and used to predict which bulls will sire the most efficient daughters. We have already computed preliminary breeding values for "Feed Saved", similar to Pryce et al. (2015). The Feed Saved trait is based on the sum of RFI and the extra feed consumed for maintenance due to larger-than-average body size with Feed Saved equal to -1 x (RFI + extra feed for maintenance).

Based on our preliminary analyses, sires with superior genetics for Feed Saved would have a predicted transmitting ability of about 1000 lb of feed saved per lactation compared to the breed average. About half of the total feed saved is from RFI and half from maintenance savings. Furthermore, based on current data, we expect that the Feed Saved trait is not correlated (positively or negatively) with health or fertility traits.

Evidence that genomic selection for RFI can work in the dairy industry has been nicely demonstrated by Davis et al. (2014). In their study, genomic predictions for RFI were developed for growing heifers, and then 3,400 mature cows were genotyped and ranked based on the RFI genotypes for growth. Actual feed intake and production were then measured in the top 100 and bottom 100 at a common location during lactation. Cows from the top 10%, compared to the bottom 10%, for RFI genotype during growth needed 1.4 lb less feed per day to produce the same amount of milk. This is similar to the expected savings in feed for maintenance in a cow weighing 180 lb less. The use of genomics in selection against RFI or DMI is already beginning in Australia (Pryce et al., 2015) and the Netherlands (Veerkamp et al., 2014) and will likely occur in North America in the near future.

If selection for RFI is to be effective, it should be repeatable across diets, climate conditions, lactations, stages within a lactation, and even stages of life. Data to date suggest that it is (Tempelman et al., 2015; Potts et al., 2015; Connor et al., 2013; MacDonald et al., 2014). In addition, if genomic selection for RFI is to be used in making breeding decisions in the future, we must continue to update our database of feed efficiency. We believe this will happen and encourage producers to consider using the new genomic tools as they become available.

It is important to note that RFI is only part of feed efficiency. Selection for efficiency must also consider the optimal levels of milk production relative to body weight. The "feed saved" approach used by Pryce et al. (2015) seems reasonable, with an index to select for smaller body size and lower RFI, while continuing to select for high milk yield and desirable milk composition. Improvements in feed efficiency must not occur at the expense of health and fertility of dairy cows. Many traits must be optimized as we consider the ideal cow of the future to promote efficiency and profitability of farms and sustainability of the dairy industry (Table 1). Genomics will help us achieve these goals.

Conclusion

We have made major gains in feed efficiency in the past as a byproduct of selecting, feeding, and managing cows for increased productivity, which dilutes maintenance. To enhance efficiency further, we should take advantage of new genomic tools that will enable us to select for cows that require less feed per unit of milk by using a selection index that favors greater milk production and components, smaller cow size, and negative RFI.

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Table 1. Breeding goals for the cow of the future to enhance efficiency and sustainability. (from VandeHaar et al., 2016).

Efficiency goals	Efficiently captures (partitions) lifetime NE to product because maintenance represents a small portion of required feed NE
	Has a negative RFI, indicating greater efficiency at converting GE to NE or lower maintenance than expected based on BW
	Is profitable (high production dilutes out farm fixed costs)
	Has minimal negative environmental impacts
	Can efficiently use human-inedible foods, pasture, and high fiber feeds
	Requires less protein and phosphorus per unit of milk
	Produces milk and meat of high quality and salability
Other goals	Is healthy, long-lived, and thrives through the transition period
	Is fertile and produces high-value offspring
	Is adaptable to different climates and diets
	Has a good disposition

Notes: