Residual Feed Intake and Feed Efficiency: Differences and Implications

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Introduction

In the beef production system, 70-75% of the total dietary energy is used for maintenance (Ferrell and Jenkins 1984; NRC 1996; Montaldo-Bermudez et al. 1990). Thus, while only 5% of the total life cycle dietary energy consumption is used for protein deposition in beef cattle, swine and poultry are more efficient at 14 and 22%, respectively. The relatively large size, slow maturity and slow reproductive rates of cattle (Pitchford et al. 2002), are some of the major reasons for the inefficiency of beef production. However, maintenance energy requirements of cattle are moderately to highly heritable (h^2 = 0.22-0.71), suggesting an opportunity to select for more efficient cattle (Carstens et al. 1989; Bishop 1992). Thus, improvements in the efficiency of use of maintenance energy either through selection, nutritional considerations and/or through management strategies should result in an increase in total beef production for a given amount of feed.

Feed efficiency has been targeted as a means of reducing the cost of production in the beef industry. However, two major concepts are now competing as the selection criteria for efficient cattle. They are the traditional feed efficiency (FE) and a newer concept called residual feed intake (RFI). This review explains the concepts of the relatively newer approach of RFI, used to study the nutritional influences on feed efficiency and compares it to the traditional concepts of feed efficiency.

Feed Efficiency

Feed efficiency or efficiency of gain is usually measured as the ratio of feed consumed to gain in weight. It is the efficiency of use of the energy consumed for maintenance and growth and relates the relationship between input of feed and output of product.

Average daily gain determines the length of time the animal requires to be fed to gain a given amount of weight whereas the ratio of intake to gain determines the variable cost of putting on that gain. Various other definitions of FE and refinements are available including partial efficiency of growth, relative growth rate and the Kleiber ratio.

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Feed efficiency is of great economic importance in beef cattle production since it contributes about 70% of the total cost of gain. Thus, a 5% increase in feed to gain ratio has been reported to have an economic impact four times as great as a 5% increase in daily gain (Gibb and McAllister 1999). Results of a simulation (Table 1) suggest that feed efficiency has about up to 7 to 8 times the economic impact as a similar increase in weight gain of cattle.

Components of Feed Efficiency: Implications for Measuring Performance

Growth Rates versus Feed Efficiency

Over the years, there has been a fixation of increased rate of growth in cattle as the basis for profitability based on the assumption that there is a dilution effect of maintenance costs over a faster rate of growth due to a physiologically lower age at a fixed slaughter weight (Luiting et al. 1994). However, the selection for a faster rate of growth at a fixed end point of slaughter or mature weight favors cattle with genetically larger size (Luiting et al. 1994). The larger size animals are physiologically less mature at equal slaughter weight and are thus at a lower proportion of their mature weight. A simulation was conducted using data from actual performance of steers started on feed at 250 kg with end weights of 560 kg. Steers with a 5% increase in daily weight gain had savings of $2 per head versus $18 per head for steers with a calculated increase of 5% in FE.

Table 1. Simulated cost and saving of steers with calculated 5% increase in feed efficiency or average daily gain compared to actual performance.

	Actual Data (200 days)	Calculated 5% Increase in Feed Efficiency (200 days)	Calculated 5% Increase in Weight Gain (191 days)
Feed Intake (kg)	9.45	8.98	9.91
Feed efficiency (kg/kg gain)	6.08	5.78	6.08
Gain (kg/day)	1.55	1.55	1.63
Feed ($/ kg gain)	1.13	1.07	1.13
Feed cost ($ for total gain/day	1.75	1.66	1.84
Total feed costs	$350	$332	$352
Total costs including yardage ($0.37/day)	$424	$406	$422
Savings for 200 days @$0.186/kg feed	-	$18 per head	$2 per head

The data in Table 1 indicate that this kind of strategy leads to a higher efficiency only because of a lower degree of maturity at slaughter without the necessary increase in cost savings. Indeed, for the steers with a 5% increase in daily weight gain to be profitable, they need to be fed for an extra 9 days and gain a total of 326 kg giving extra gross revenue of $29.60 (15.5 kg of beef @ $1.91/kg). The net savings is $12 since it costs an extra $17 to feed the steers for the extra 9 days.

To be economically viable, slaughter weights have therefore, tended to be increased by producers. For example, 20 years ago large frame size cattle were not expected to produce 13 mm of subcutaneous fat at the 12th rib until their weights exceeded 544 kg and 454 kg for steers and heifers, respectively. However, for the modern large frame cattle, the weights at which they are expected to produce 13 mm of fat at the 12th rib has increased to 612 and 544 kg for steers and heifers, respectively (Basarab 1996).

Genetic scaling theory suggests that increases in growth rate leads to increased mature weight, and a consequent increase in maintenance requirements (Taylor et al. 1986). The increased mature size is thus expressed in the parental animals which then become expensive to feed leading to an antagonistic relationship between the faster growth rate of growing cattle versus the maintenance requirements and cost of maintaining the cattle population (Taylor et al. 1986). Selection for high growth rates inevitably leads to a population of cattle with increased maintenance requirements, higher feed requirements and intake, with subsequent higher feed and environmental costs.

Feed Utilization

Until recent times the efficiency of feed utilization has been quite difficult and expensive to measure and quantify compared to the rather simple measurements of growth rate. It was thus practical and the norm to measure gross feed intake and gain as measures of feed efficiency. However, Ferrell and Jenkins (1998) (Figure 1) showed that the relationship between feed (energy) intake and gain is not linear. They indicated that the maximum efficiency in daily gain may occur at less than maximum energy or feed intake. Decreases in efficiency at higher Metabolizable energy (ME) intake have been attributed to depression of ME of diet at higher levels of intake, higher heat increment of feeding at higher intakes and heavier visceral organ weights (Ferrell and Jenkins 1998). These concepts hold true assuming that all the traditional factors that influence average daily gain and impact negatively on feed intake, have been controlled. These factors include the following: 1) feed is not stale or moldy, as cattle tend to eat less when feed is not fresh, 2) amount of concentrate is enough to meet a targeted average daily gain, 3) protein content of the diet is adequate to meet requirements for maintenance and for the targeted rate of growth, and 4) there are no limiting factors to negate the targeted growth rate. Some researchers have attempted to use the concepts of Ferrell and Jenkins (1998) to increase efficiency of cattle production through the practice of limit feeding.

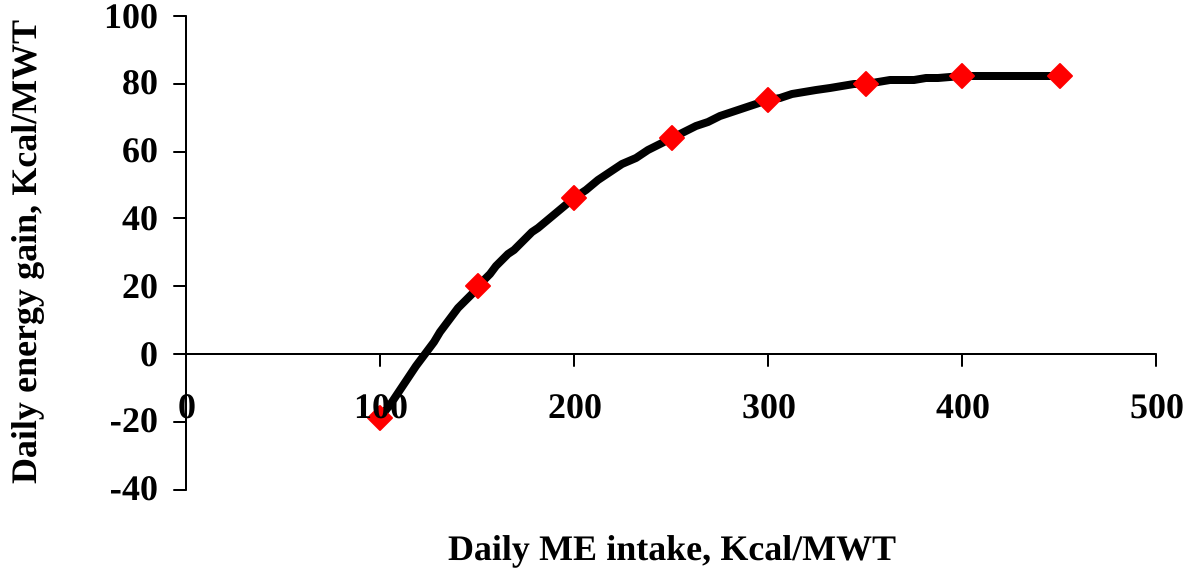

Figure 1. Relationship Between Energy Gain and Metaboli zable Energy Intake (adapted from Ferrell and Jenkins 1998).

Limit Feeding

Restricting dry matter intake without compromising average daily gain thereby improving feed to gain ratio of cattle has been defined as limit-feed also known as programmed or prescriptive feeding. Results (summarized in Figure 2) from various researchers including Galyean (1996), Plegge (1987), Zinn (1986) and Hicks et al. (1990) in the United States indicate the beneficial effects of moderate feed restriction on feed efficiency and average daily gain in the feedlot. These results indicate that with a maximum of 15% feed restriction, there is an increase of about 9% in feed efficiency. However, these data of the advantages of limit-feeding are contrary to the accepted relationships between dry matter intake, average daily gain, and feed conversion efficiency. Indeed, the economic impact of limit-feeding is debatable. Mathison and Engstrom (1995) tested ad-libitum versus limit-feeding in feedlot steers fed barley or corn based diets. They restricted feed intake by only 4% and found that there was a 22% reduction in fat cover, but the 3% improvement in feed efficiency was not significant. Their feed restriction of 4% fell below the point where there could have been an economic impact (Figure 2).

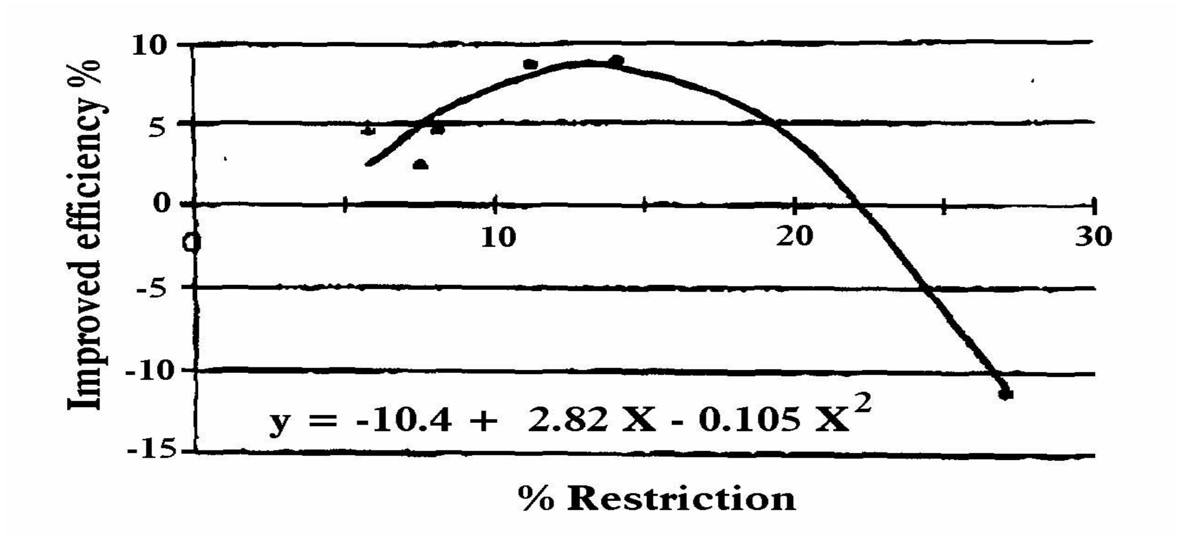

Figure 2. Improvements in Feed Efficiency With Limit Feeding (Adapted from Sainz 1995).

Mechanisms of Limit Feeding on Feed Efficiency

Increased FE by limit feeding has been postulated to be effected through more efficient utilization of nutrients and/or increased supply/digestibility of nutrients from the diet. These two mechanisms cumulatively increase efficiency through various means: 1) the rationale of improved digestibility is the reverse logic of the concept that there is a 4% decrease in organic matter digestibility for each unit increase in intake above maintenance, 2) increase in ME content of diet (discussed in section on residual feed consumption), 3) reduction in maintenance requirement possibly due to decreases in the weight and activity of the gastrointestinal organs and the liver associated with reduced feed intake, and 4) reductions in the heat increment of feeding associated with digestion, passage, protein, and fat accretion in the body tissues especially a perceived increase in lean tissue accretion relative to fat gain.

Evidence to support these assertions has been limited. Relative to the role of different diets and the advantages of limit feeding, Mathison and Engstrom (1995) stated that the digestibility of corn-based diets decreases in feedlot cattle as intake increases, while there may be little or no decrease in digestibility of barley-based diets (Delphino, Mathison and Smith 1988). These results indicate that limit-feeding and the nutritional influence on feed efficiency may not be effective with barley-based diets. In addition, the limited works on the effectiveness of limit feeding in cold environments indicate that limit feeding may not be effective in cold environments such as Western Canada (McKinnon et al. 2001).

Residual Feed Intake (Net feed Efficiency)

The Theory

The limitation of using FE to measure performance and the lack of economic improvements in the breeding herd has led to a shift in focus in recent times in using a concept known as residual feed intake (RFI) or net feed efficiency (NFE) in identifying efficient animals. As indicated previously, FE is highly correlated with growth rate and may be confounded with maturity patterns, body size, composition of gain and appetite of cattle (genetic correlations of –61 to –95%) (Mrode et al. 1990; Fan et al. 1995; Liu et al. 1998, Arthur et al. 2001). On the other hand, residual feed intake is the difference between the metabolizable energy intake (MEI) and metabolizable energy required for maintenance and gain (MER) (Fan et al. 1995; Liu et al. 1998). Mathematically, RFI or residual metabolizable feed consumption (RMFC) in kg d^{-1} is calculated as RFI = MEI - MER. Residual feed intake is independent of growth and maturity patterns, and is a more sensitive and precise measure of feed quality based on energy intake and energy requirements (Fan et al. 1995; Liu et al. 1998). Practically, RFI estimates efficiency of use of feed consumed by subtracting observed dry matter intake (DMI) of an individual from DMI predicted by an equation developed from the relationship between DMI, daily gain and metabolic mean weight across fed contemporaries (Basarab et al. 2003). When MEI = MER the RFI = 0 and means the energy requirements of the animal are completely met. A positive RFI means that MEI > than MER and means the animal's energy intake exceeds its requirement for maintenance and growth. A negative RFI means MEI < MER and that the animal either requires less energy than what is estimated or is eating less to produce the same weight gain. The concept of residual feed intake has been used to identify efficient test station bulls and a genetic basis for RFI has been identified with the heritability of the trait estimated to be between 0.16 and 0.46 (Fan et al. 1995; Liu et al. 1998). This suggests that RFI can be improved through selection much like average daily gain. The concept of RFI to measure efficiency of beef production needs to receive more attention as it has the potential to recognize genotypes or individual animals whose requirement equals metabolizable energy intake, ME intake is greater than requirement, and those whose ME intake is less than requirement.

The Practice

The increase in weight of a group of cattle over period of time is measured and modeled by linear regression. This normalizes each animal's growth curve to avoid short-term effects of morbidity or nutritional restrictions. Initial weight, ADG, mid-point weight (MIDWT) and final weight are calculated from the regression coefficients of each animal's growth curve. Daily feed intake is converted to total feed intake of each animal during the feeding period and then to total energy intake by multiplying total DM intake by metabolizable energy of the diet fed determined by indirect calorimetry. Total energy intake is then divided by 10 to give total DM intake standardized to an energy density of 10 MJ ME kg^{-1} DM. Total standardized feed intake (SFI) is then divided by the number of days on test to give average standardized daily feed intake (SFI, kg d^{-1}). To calculate expected feed intake (EFI, kg d^{-1}), measures of ADG (kg d^{-1}) and metabolic MIDWT ($kg^{0.75}$) are used to model daily EFI (Archer et al. 1998; Arthur et al. 2001). The model fitted is basically of the form: $Yi = a_0 + b_1 ADG_i + b_2$ metabolic $MIDWT_i + e_i$, where Y_i = daily EFI for animal i, a_0 = regression intercept, b_1 = partial regression coefficient of EFI on average daily gain, b_2 = partial regression coefficient of EFI on metabolic mid-weight, and e_i = residual error in EFI of animal i.

Residual feed intake is then calculated as deviations of SFI from EFI such that RFI = SFI - EFI. Thus, animals with low or negative RFI values are more efficient than those with positive RFI values.

Relationship between Residual Feed Intake and Feed Efficiency

Figure 3 summarises work done by Basarab et al. (2003). Over a finishing period ranging from 71 to 183 days steers from five genetic strains grew at 1.46 kg/day, had DMI of 10.9 kg/day and a RFI of 0.00 (SD=0.66) kg/day. The RFI of the steers varied from an efficient -1.49 kg/day to an inefficient 1.54 kg/day (Figure 3). With similar ADG some steers had DMI of 1.49 and 1.54 kg/day less and more than expected, respectively. Figure 3 also shows that RFI measures traits different from the traditional feed efficiency measured as feed to gain ratio. Basarab et al. (2003) reported that the relationship between FE and ADG on one hand and between RFI and ADG, on the other hand were r = -0.61 and -0.00, respectively, indicating that RFI may be an indicator of the animal's maintenance requirements rather than growth, size and/or appetite. Thus, from Figure 3 one can notice that some steers with similar FE have vastly different RFI. For example, steers numbered 16959197, 18221655 and 18221670 have similar feed to gain ratios (8.2 and 8.4:1) and similar ADG. However, their RFI values range from an efficient -1.26 to an inefficient 1.26 kg/d. Steers 116959197, 18221655 and 18221670 actually weighed 584, 514 and 430 kg, respectively, at harvest. Indeed, for similar DMI steer numbered 16959197 had an advantage of about 70 and 150 kg in body weight compared to steers 18221655 and 18221670. There are several possible reasons for these results. They include the following:1) differences in maintenance requirements of the efficient and inefficient steers, 2) steers which had low ME intakes tended to have low RFI intake values ($r=0.51$, $P<0.0001$), 3) Ferrell and Jenkins (1998) reported that the efficiency of ME use for retained energy was not constant, but decreased as ME intake increased, 4) a portion of non-linearity in the relationship of retained energy on ME intake is due to a depression in metabolizability of the diet at high levels of intake, 5) higher maintenance cost due to heavier organ weights of stomach complex, intestines, heart, lung, kidney and spleen, and/or 6) heat increment of feeding of certain steers all leading to higher heat production for the inefficient steers. We (Basarab, Okine and Moore 2004) elsewhere in this symposium elucidate in more detail the relationship between RFI and compositional traits of cattle.

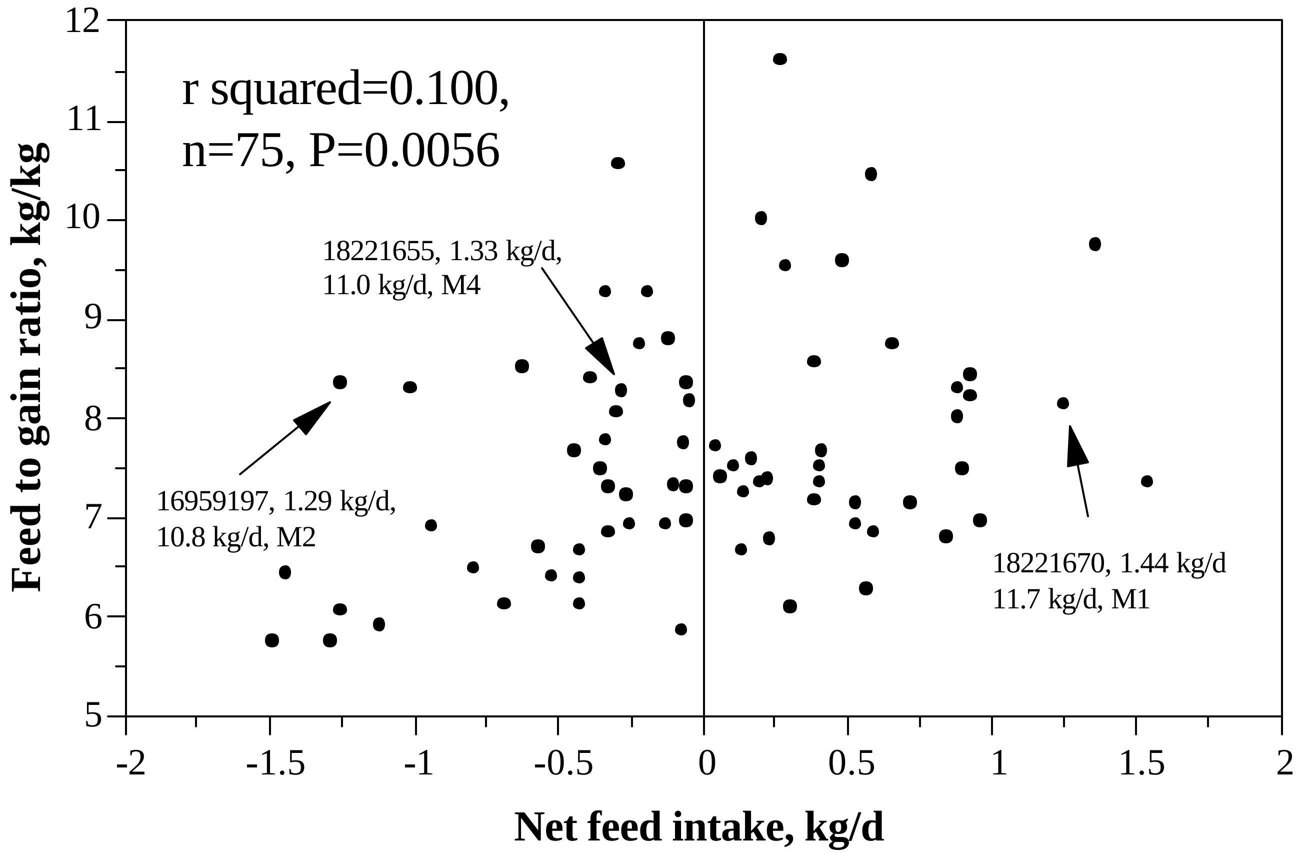

Figure 3. Relationship Between RFI and Feed Efficiency (Basarab et al. 2001a).

We have summarized differences between RFI and the traditional concepts of feed efficiency in Table 2.

Table 2. Genetic (above diagonal) and Phenotypic Correlations for RFI, Feed Efficiency, Body Size, Feed Intake and Average Daily Gain in Angus Cattle (Adapted from Arthur et al. 2001. J. Anim. Sci. 79:2805-2811).

Item	ADG	MMWT	FI	FE	RFI
ADG		0.53 ± 0.07	0.54 ± 0.06	-0.62 ± 0.06	-0.04 ± 0.08
MMWT	0.24		0.65 ± 0.03`	-0.01 ± 0.07	-0.06 ± 0.06
FI	0.41	0.63		0.31 ± 0.07	0.69 ± 0.03
FE	-0.74	0.16	0.23		0.66 ± 0.05
RFI	-0.06	0.02	0.72	0.53	

ADG = average daily gain; MMWT = metabolic mid-weight; FI = daily feed intake; FE = feed efficiency; RFI = residual feed intake.

The genetic and phenotypic correlations indicated in Table 2 show that feed efficiency is genetically (rg = 0.66) and phenotypically (rp = 0.53) correlated with RFI. The genetic and phenotypic correlations between FE and ADG were (rg = -0.62 and rp = -0.74). However, RFI is not correlated with ADG (rg = -0.04, rp = -0.06), indicating that genetic improvement in RFI will not result in a change in ADG. However, genetic improvement in RFI will result in a corresponding change in FE (rg = 0.66). Therefore unlike feed efficiency RFI is not correlated, either phenotypically or genetically, with ADG and metabolic mid weight. Indeed, improvements in RFI will lead to improvements in FE without the confounding effects of ADG.

Other Useful Extensions of the Concepts of Residual Feed Intake

Practical Differentiation of Nutritive Value of Different Feeds

Okine et al. (2001) hypothesized that when different diets with similar or different energy densities are fed to cattle the RFI, gross and net feed efficiency (GFE and NFE) analyses should be able to differentiate between the feeds. The differentiation between feeds should be demonstrable as: 1) the amount of feed consumed by the animal either above or below that required for maintenance and gain and/or 2) the amount of MEI relative to the gain achieved by the animal.

Sixty crossbred steers were individually penned and were allocated for a period of 105 days to one of six dietary treatments: 100% alfalfa silage; 85% alfalfa silage and 15% barley grain; 70% alfalfa silage and 30% barley grain; 100% fenugreek silage; 85% fenugreek silage and 15% barley grain; and 70% fenugreek silage and 30% barley grain on DM basis. Values for DMI, ADG, FGR and MER were not different ($P > 0.05$) between steers fed fenugreek and alfalfa silage. The MEI was 8% higher ($P < 0.01$) for steers fed alfalfa compared to fenugreek silage. However, ADG values were not different between the steers. Steers fed fenugreek silage had a negative RFI ($P< 0.01$) compared to those fed alfalfa. However, steers fed the 100% alfalfa silage diet showed positive RFI values. Okine et al. (2001) concluded that unlike RFI the normally accepted analyses of DMI, ADG and feed efficiency could not differentiate between the efficiency of production of steers fed alfalfa and fenugreek silage. We suggest that RFI could become a simple method of comparing observed efficiency of utilization of ME with the predicted efficiency of ME utilization of different feeds.

Methane and Manure Production

Methane (CH_4) emissions from ruminant animals range from 8 to 14% of the digestible energy intake and translates to average emissions of 28 L methane per kg of dry matter intake (20 g CH_4 /kg feed dry matter). This represents a substantial loss in efficiency of animal production, and contributes about 16 – 20% of the global atmospheric CH_4. Currently, there are no practical strategies to reduce methane emission from cattle without a reduction in cattle numbers. Herd et al. (2002) and Okine et al. (2003) hypothesized that cattle with low and/or negative RFI would produce less methane and manure than cattle with high and /or positive RFI. This deductive reasoning arises from the fact that cattle with negative RFI are expected to have reduced DMI but similar performance to cattle with high or positive RFI, since RFI is a trait that reflects the maintenance requirements of individual animals (Archer et al. 1998). We (Okine et al 2003) calculated that methane emission (g d^{-1}) was 5% lower for Low-RFI than High-RFI steers. Calculated manure production was different (2.4, 2.53 and 2.65 kg d^{-1}; P<0.0001) for Low, Medium and High-RFI steers, respectively. These results were similar to results from Herd et al (2002) and suggest that selection for Low-RFI in beef cattle is in theory accompanied by a significant reduction in methane and manure due to reduction in DMI feed intake and more efficient use of feed without any compromise in growth performance. The implication for the Kyoto accord is enormous.

Conclusion

Two major concepts are now competing as the selection criteria for efficient cattle. They are the traditional feed efficiency (FE) and a newer concept called residual feed intake (RFI). Feed efficiency or efficiency of gain is usually, measured as the ratio of feed consumed to gain in weight. Feed efficiency is of great economic importance in beef cattle production because FE contributes about 70% towards the total cost of gain and has up to7 –8 times the economic impact as a similar increase in average weight gain of cattle. Feed to gain is highly correlated with growth rate and may be confounded with maturity patterns, body size, composition of gain and appetite (genetic correlations of –61 to –95%). Selection of cattle based on feed efficiency favors cattle of genetically larger size. The increased mature size is expressed in the parental animals which are expensive to feed and maintain leading to an antagonistic relationship between the faster growth rate of growing cattle versus the maintenance requirements and cost of maintaining the cattle population. Thus, selection for high growth rates inevitably leads to a population of cattle with increased maintenance requirements, higher feed requirements and intake, with attendant higher manure, methane and carbon dioxide production and consequently higher feed and environmental costs. Unlike feed efficiency RFI is not correlated with growth rate and is not confounded with maturity patterns, body size, composition of gain or appetite. Residual feed intake is the difference between the metabolizable energy intake and metabolizable energy required for maintenance and gain and is largely independent of growth and maturity patterns. Use of the concept of RFI enables selection of animals based on gain and feed intake without the attendant increase in size and maintenance. In addition, RFI, unlike the normally accepted analyses of DMI, ADG and feed efficiency could be used to differentiate between the efficiency of production of cattle on different rations and feedstuffs. Finally, selection for RFI in beef cattle is in theory accompanied by a significant reduction in methane and manure due to reduction in daily feed intake and efficient use of feed without any compromise in growth performance.

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