

Limit feeding as a strategy to increase energy efficiency in intensified cow–calf production systems¹

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ABSTRACT: Two experiments were conducted to measure efficiency of energy use in limit-fed cows. In Exp. 1, 32 pregnant, crossbred cows were used to examine the effects of dietary energy concentration and intake level on energy utilization and digestion. In a 2 × 2 factorial treatment arrangement, cows received diets formulated at either 1.54 Mcal NE_m/kg high energy (H) or 1.08 Mcal NE_m/kg low energy (L); amounts of each diet were fed at amounts to achieve either 80% (80) or 120% (120) of maintenance energy requirements. Fecal grab samples were collected on days 14, 28, 42, and 56 for determination of energy digestion and metabolizable energy (ME) intake. Acid detergent insoluble ash and bomb calorimetry were used to estimate fecal energy production. Cow body weight and 12th rib fat thickness were used to estimate body energy, using 8 different methods, at the beginning and end of a 56-d feeding period. Energy retention (RE) was calculated as the difference in body energy on days 0 and 56. Heat energy (HE) was calculated as the difference in ME intake and RE. Energy digestion increased ($P = 0.04$) with intake restriction. Cows consuming H tended to have greater ($P = 0.08$) empty

body weight (EBW) gain than cows consuming L, but no difference was observed ($P = 0.12$) between cows fed 120 compared with cows fed 80. Estimates of HE were greater for L than H ($P < 0.01$) and greater for 120 than 80 ($P < 0.01$), such that estimated fasting heat production of H (57.2 kcal/kg EBW^{0.75}) was lower than that of L (73.3 kcal/kg EBW^{0.75}). In Exp. 2, 16 ruminally cannulated, crossbred steers were used to examine the effects of dietary energy concentration and intake level on energy digestion. Treatment arrangement and laboratory methods were replicated from Exp. 1. Following a 14-d adaptation period, fecal samples were collected, such that samples were represented in 2-h intervals post-feeding across 24 h. Diet × intake interactions were observed for nutrient digestibility. Energy digestibility was greater in steers fed H than in steers fed L ($P < 0.01$); however, digestibility of each nutrient increased by approximately 10% in steers fed H80 vs. those fed H120 ($P \leq 0.03$); nutrient digestibility was similar among levels of intake in steers fed L ($P = 0.54$). These results suggest that intake restriction may increase diet utilization and that the magnitude of change may be related to diet energy density.

Key words: beef cattle, intake, energy efficiency, heat production, limit-feeding, maintenance requirement

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INTRODUCTION

Intensification of livestock production systems has been proposed as a sustainable solution for meeting global protein needs in the face of decreased land availability for food production (FAO, 2011). Sustainability of intensified cow-calf systems will depend on control of variable costs; particularly, feed costs associated with cow maintenance. Cow maintenance energy requirements decrease following periods of feed restriction (Koong et al., 1985; Jenkins and Ferrell, 1997; Freetly and Nienaber, 1998); reducing maintenance needs by managing intake may provide an opportunity to reduce costs in intensified systems.

Increasing diet energy density may further reduce variable input costs. Increasing energy density of a total mixed ration (TMR) has been shown to increase energy utilization efficiency and/or efficiency of gain (gain:feed) in lambs (Sainz et al., 1995; McLeod and Baldwin, 2000), heifers (Reynolds et al., 1991), compensating beef cows (Swingle et al., 1979; Sawyer et al., 2004), and dairy cows (Wagner and Loosli, 1967; Tyrrell and Moe, 1975). We hypothesize that effects of intake restriction and dietary energy density are additive, such that restricting energy intake and increasing dietary energy density will improve efficiency of energy utilization in beef cows.

Our experimental objectives were to 1) measure effects of manipulating energy intake and dietary energy density on diet utilization and total heat production and 2) estimate change in maintenance requirements (NE_m) as a function of dietary energy density.

MATERIALS AND METHODS

All animal procedures were approved by the Agricultural Animal Care and Use Committee of Texas A&M AgriLife Research and followed guidelines stated in the Guide for the Care and Use of Agriculture Animals in Research and Teaching (Federation of Animal Science Societies, 2010).

Experiment 1: Energy utilization in beef cows

Thirty-two pregnant, crossbred cows ($\frac{3}{4}$ Angus \times $\frac{1}{4}$ Nellore) either 3 ($n = 27$) or 4 ($n = 5$) years of age were used in an experiment designed to examine the effects of dietary energy concentration and intake level on energy utilization. Cows in midgestation (approximately day 155) were stratified by estimated day of gestation (based on palpation) and BW (assessed 35 d prior to the experiment)

and randomly assigned to 1 of 8 concrete-surfaced pens, each containing 4 animals and fitted with 4 Calan-Broadbent feeders (American Calan, Northwood, NH) and automatic waterers in a covered, open-sided barn.

Within each pen, cows were randomly assigned to 1 of 4 dietary treatments in a 2×2 factorial treatment arrangement. The factorial consisted of 2 levels of dietary energy density [high energy (H; 1.54 Mcal NE_m /kg) or low-energy (L; 1.08 Mcal NE_m /kg)] and 2 levels of intake [80% (80) or 120% (120) of maintenance energy requirements; Table 1].

Body weight (day -35) and estimated day of gestation were used to calculate energy requirements as per National Academies of Sciences, Engineering, and Medicine (NASEM, 2016) recommendations and to determine the amount of each diet to provide daily, with respect to treatment (Table 2). Total requirements were calculated as the sum of maintenance and gestation requirements. Maintenance requirements (NE_m , Mcal/d) were calculated using the equation:

$$NE_m = 0.077 \times EBW^{0.75}$$

$$EBW = SBW \times 0.891$$

$$SBW = BW \times 0.96$$

where EBW = empty body weight, kg; SBW = shrunk body weight, kg; and BW = body weight, kg.

Requirements for gestation (NE_g , equivalents, Mcal/d) were calculated using the equation:

Table 1. Formulated ingredient and nutrient composition of treatment diets¹

Ingredient	High energy	Low energy
	% As fed	
Wheat straw	34.52	64.08
Corn	29.46	0.00
Distillers' grain	27.46	27.36
Urea	1.10	1.10
Molasses	5.00	5.00
Mineral	2.46	2.46
Diet components ²	DM basis ³	
CP, %	16.3	14.4
TDN, %	68.0	54.0
ME, Mcal/kg	2.45	1.94
NE_m , Mcal/kg	1.54	1.08
NE_g , Mcal/kg	0.95	0.53

¹According to NASEM (2016) model estimates.

²CP = crude protein; TDN = total digestible nutrients; ME = metabolizable energy; NE_m = net energy for maintenance; NE_g = net energy for gain.

³Dry matter content: high energy, 83.4%; low energy, 83.1%.

$$NE_y = [CBW \times (0.4504 - 0.000766t) \times e^{(0.03233 - 0.0000275t)t}] / 1,000 * k_m$$

$$k_m = NE_m / ME$$

where CBW = calf birth weight, 36 kg; t = days in gestation, d; NE_m = diet NE_m concentration, Mcal/kg; ME = diet metabolizable energy concentration, Mcal/kg

Cows were individually fed once daily at 0730 h; feed refusals, if present, were removed from feed bunks once weekly. At the beginning and end of the feeding period (days 0 and 56), animals were subjected to a series of measurements including: BW, hip height, and ultrasound assessments of rib fat thickness (between 12th and 13th rib), hip fat thickness, intramuscular fat (IMF), and ribeye area (REA). Measurements were used for direct comparison and as input variables for approximation of body energy reserves via selected regression models (Table 3).

Samples of the diets were collected daily and were composited by week on an equal weight basis for subsequent analyses. Two fecal grab samples were

collected from each cow (each separated by 12 h) and immediately frozen on days 14, 28, 42, and 56 for determination of diet digestibility. Acid detergent insoluble ash (ADIA) was used as an internal marker to estimate fecal production for digestion calculations.

Laboratory Analysis

Feed and fecal samples were processed for laboratory analyses using common procedures. Samples were dried in a forced-air oven for 96 h at 55 °C, allowed to air equilibrate, and weighed for determination of partial dry matter (DM). Samples were subsequently ground through a 1-mm screen using a Wiley mill (Thomas Scientific, Swedesboro, NJ) and dried for 24 h at 105 °C for determination of DM. Organic matter (OM) was determined as the loss in dry weight upon combustion in a muffle furnace for 8 h at 450 °C. Acid detergent fiber (ADF) analysis was performed using an Ankom Fiber Analyzer (Ankom Technology Corp., Macedon, NY), and ADIA was determined as the remaining DM upon combustion of ADF residue in a muffle furnace at 450 °C. Gross energy (GE; Mcal/kg DM) values were determined by direct calorimetry using a Parr 6300 Calorimeter (Parr Instrument Company, Moline, IL).

Digestion coefficients were calculated using the formula $[1 - (\text{fecal output of nutrient}/\text{intake of nutrient})] \times 100$. Fecal production was calculated by dividing dietary ADIA intake by fecal ADIA concentration. Digestible energy (DE; Mcal/kg DM) was calculated by multiplying observed coefficient of energy digestibility (%) by GE (Mcal/kg DM) of each diet. Metabolizable energy was estimated for each diet by multiplying DE by 0.82 (NASEM, 2016).

A calculated measure of body condition score was estimated at both the beginning and end of the

Table 2. Targeted intake of treatment diets and estimates of requirements as per NASEM (2016)

	High-energy diet		Low-energy diet	
	80	120	80	120
Daily intake				
As fed, kg	4.40	6.39	6.49	9.52
Dry matter, kg	3.91	5.68	5.79	8.49
DE, ¹ Mcal	11.68	16.97	13.70	20.09
ME, Mcal	9.58	13.92	11.23	16.47
NE_m , Mcal	6.02	8.74	6.25	9.17
Requirements, Mcal NE_m /d	7.53	7.28	7.81	7.64

¹DE = digestible energy; ME = metabolizable energy; NE_m = net energy for maintenance.

Table 3. Multiple regression coefficients of selected models used for estimating energy¹ contained in the empty body or carcass of beef cows

Model	Type	β_0	Independent variables ²									R^2	
			BW	BF_c	BF_m	BF_m^2	HH	WH	WT:HH	BCS	EBW		
Ferrell and Jenkins (1984, 1)	Empty Body	73.3	2.9	422.0				-2.7					0.87
Ferrell and Jenkins (1984, 2)	Empty Body	-333.0										4.6	0.69
Gresham et al. (1986)	Carcass	-733.7	1.8		77.7	-1.8		2.5					0.87
Wagner et al. (1988, 1)	Carcass	-487.2	1.3								78.4		0.90
Wagner et al. (1988, 2)	Carcass	-661.5	2.7										0.81
Wagner et al. (1988, 3)	Carcass	-756.7								361.5			0.83
Wagner et al. (1988, 4)	Carcass	-221.5									128.2		0.85

¹Mcal.

²BW = live body weight (kg); BF_c = back fat (cm); BF_m = back fat (mm); HH = hip height (cm); WH = wither height (cm, estimated as HH - 5); BCS = body condition score (1 to 9 scale, 1 = emaciated and 9 = very obese); WT:HH = ratio of WT:HH, kg:cm; EBW = empty body weight (kg).

trial using a regression equation (rBCS; $R^2 = 0.996$) developed from observations of fat thickness corresponding to observed body condition score (Herd and Sprott, 1998):

$$\text{rBCS} = -1.2927x^2 + 6.0916x + 2.2114$$

where x = rib fat thickness (cm) determined by ultrasound.

Equations published in NASEM (2016) were used, in addition to the previously mentioned regression models, to calculate empty body energy.

Body energy (BE) was calculated as:

$$\text{BE, Mcal} = 9.4 \times \text{TF} + 5.7 \times \text{TP}$$

where TF = total fat, kg; TP = total protein, kg.

Body components were calculated as follows:

$$\text{TF} = \text{AF} \times \text{EBW}$$

$$\text{TP} = \text{AP} \times \text{EBW}$$

where AF = proportion of empty body fat; AP = proportion of empty body protein.

Body composition was estimated using the following equations:

$$\text{AF} = 3.768 \times \text{rBCS}$$

$$\text{AP} = 20.09 - 0.668 \times \text{rBCS}$$

Previously published equations were selected to complement NASEM (2016) estimates of BE. Equations presented by Ferrell and Jenkins (1984) estimated energy content of the empty body of mature beef cows, which is consistent with estimates based on NASEM equations. Alternatively, equations from articles by Gresham et al. (1986) and Wagner et al. (1988) estimated energy in the carcass of mature beef cows; however, estimates of empty body energy and carcass energy were used synonymously as proxies for BE in our calculations. Because cows were stratified by days of gestation, and growth and energy content of the gravid uterus during midgestation is probably minimal (Ferrell et al., 1976), they were not explicitly calculated; rather, energy changes related to growth of the gravid uterus and conceptus are implicit in the estimates of the change in BE.

Total retained energy (RE_{total}) and total heat energy (HE_{total}) were calculated as follows:

$$\text{RE}_{\text{total}, \text{Mcal}} = \text{BE}_f - \text{BE}_i$$

$$\text{HE}_{\text{total}, \text{Mcal}} = \text{MEI}_{\text{total}} - \text{RE}_{\text{total}}$$

where BE_f = total body energy on day 56, Mcal; BE_i = total body energy on day 0, Mcal; $\text{MEI}_{\text{total}}$ = total metabolizable energy intake (56 d), Mcal.

Daily RE, HE, and MEI were calculated by dividing RE_{total} , HE_{total} , and $\text{MEI}_{\text{total}}$ by 56 d. Results for RE, HE, and MEI are reported in kcal/kg $\text{EBW}^{0.75}$. Average $\text{EBW}^{0.75}$ was calculated as $[(\text{initial EBW} + \text{final EBW})/2]^{0.75}$.

Maintenance level of intake of metabolizable energy (ME_m) was estimated for both H and L using a linear regression of the means of RE on MEI. The estimated regression equations representing each diet were solved for RE = zero; the solution of which represented ME_m for the respective diet.

Fasting heat production (FHP) was estimated for cows consuming H and L using the linear regression of the means of log (HE) on MEI. The linear functions were solved for MEI = zero; the solution represents the estimate of FHP for cows consuming the respective diet.

Statistical Analysis

All data analyses were analyzed using PROC MIXED procedures in SAS 9.3 (SAS Inst. Inc., Cary, NC) for a completely randomized design with a 2×2 factorial treatment arrangement. The model effects included diet, intake, and diet \times intake interactions.

Experiment 2: Intake and Digestion

Sixteen Angus \times Hereford steers (BW = 287 ± 21 kg) fitted with ruminal cannulas were used in an experiment designed to examine the effects of dietary energy concentration and intake level on diet utilization, ruminal pH, volatile fatty acid (VFA) concentrations, and gut fill. A 2×2 factorial treatment arrangement was utilized to replicate the treatments administered in Exp. 1. The diet was provided using mean intake levels from Exp. 1 ($\text{g}/\text{EBW}^{0.75}$). Intake in Exp. 2 was assigned according to individual $\text{EBW}^{0.75}$. Steers were housed in individual stalls within an enclosed, continuously lighted barn, and provided ad libitum access to fresh water throughout the experiment. Steers were fed at 0700 h and feed refusals (if present) were collected daily.

Experimental procedures (Fig. 2) were conducted as follows: 1) 14 d for adaptation to treatments, 2) 4 d for measurement of intake and digestion, 3) 1 d for determination of ruminal pH and VFA concentrations, and 4) 1 d for measurement of ruminal fill.

Calculations of intake were based on observations from day 14 through day 18. Representative diet samples and feed refusals were obtained daily on days 14 through 17 and frozen at -20°C to correspond with fecal samples collected on

day 15 through day 18 and immediately frozen at -20°C for determination of digestions. Fecal samples were collected every 8 h, with the sampling time advanced by 2 h each d, such that samples were represented in 2-h intervals post-feeding across 24 h.

On day 19 ruminal fermentation was characterized. A suction strainer (Raun and Burroughs, 1962; 19 mm diameter, 1.5 mm mesh) was used to collect ruminal fluid samples prior to feeding (0 h) and at 2, 4, 6, 9, 12, and 16 h after feeding. A portable pH meter with a combined electrode (VWR SympHony, Radnor, PA) was used to measure the pH of each sample at the time of sampling. Subsamples of ruminal fluid were prepared and frozen at -20°C for subsequent determinations of VFA concentrations. Prior to freezing, 8 mL of rumen fluid was combined with 2 mL of 25% *m*-phosphoric acid for sample preservation. Samples of ruminal fluid were thawed and centrifuged at $20,000 \times g$ for 20 min. Volatile fatty acid concentrations were measured using gas chromatography as described by Vanzant and Cochran (1994).

On day 20, ruminal fill was measured via ruminal evacuation immediately prior to and 4 h post-feeding. Fill is defined in this study as the average of these 2 measurements.

Diets, feed refusals, and fecal samples were processed and assessed using the same procedures as described in Exp. 1 for determination of partial DM, DM, OM, ADF, ADIA, and gross energy.

Calculations

Digestion coefficients were calculated using the following formula: $[1 - (\text{fecal output of nutrient} / \text{intake of nutrient})] \times 100$. Fecal production was calculated by dividing fecal ADIA output by the concentration of ADIA in the diet.

Statistical Analysis

All data analyses were analyzed using PROC MIXED procedures in SAS 9.2 (SAS Inst. Inc., Cary, NC). Model for analysis of fill, intake, and digestion responses included diet, intake, and diet \times intake as effects. Responses associated with ruminal fluid (VFA, pH) were analyzed as repeated measures using the same effects, but with the addition of time and its interaction with other model effects. Steer served as the subject of repeated measures and an autoregressive covariance structure was utilized.

RESULTS

Experiment 1: Energy Utilization in Beef Cows

One cow from L120 was removed from the experiment and subsequent statistical analysis due to illness unrelated to treatment.

Intakes of DM, DE, ME, and NE_m were greater in cows fed L than in H ($P < 0.01$) and greater ($P < 0.01$) in cows fed 120 than in cows fed 80 (Table 4; $P < 0.01$). There were no interactions between energy density and intake level for estimates of digestibility or dietary energy availability ($P \geq 0.33$). Digestibility of DM, OM, and GE was greater in cows fed H than in L ($P < 0.01$), but ADF digestibility was greater in L (56.84%) than in H (52.10%; $P < 0.01$). Digestibility of DM, OM, and GE was greater for cows fed 80 compared with 120% of NASEM requirements ($P < 0.04$), but digestibility of ADF was not affected by level of energy intake ($P \geq 0.45$). By design, observed concentrations of DE, ME, and NE_m per unit of dietary DM were greater in cows fed H than in those fed L ($P < 0.01$). Observed levels of NE_m availability (Mcal/kg) were similar to predicted values for H but were greater than predicted values for L. Due to the effect of intake on GE digestibility, observed concentrations of DE, and thus ME and NE_m , were greater in cows fed at 80 compared with those fed at 120% of requirements ($P = 0.03$). Observed NE_m intake relative to estimated requirements was lower than predicted in cows fed H ($P < 0.05$) and greater than expected in cows fed L ($P > 0.05$).

No interactions between diet energy density and level of intake were observed for BW or ultrasound measurements at any time-point ($P \geq 0.12$; Table 5). However, BW, $\text{EBW}^{0.75}$, hip fat, and rib fat were greater ($P \leq 0.05$) and ribeye area tended to be greater ($P = 0.08$) in cows fed L than in H prior to the start of the experiment. No interactions were observed for changes in these measures ($P \geq 0.26$). Empty BW change was not different than zero for L80 ($P = 0.21$), but was positive for all other treatments ($P \leq 0.05$). Cows consuming H tended to have greater EBW gain than cows consuming L ($P = 0.08$), but it was not measurably greater ($P = 0.12$) in cows fed 120 compared with 80.

Changes in hip fat, rib fat, IMF, or REA were not different between H-fed and L-fed fed cows ($P \geq 0.48$). Change in hip fat tended to be more negative for cows fed 80 (-1.25 cm) than for those fed 120 (-0.45 cm; $P = 0.06$), but change in rib fat, IMF, and REA were minimally affected by level of intake ($P \geq 0.15$).

Table 4. Apparent nutrient digestibility and energy availability of high- and low-energy density diets fed to beef cows in confinement at 80% or 120% of NASEM (2016) predicted energy requirement¹

Item ³	High-energy diet ²		Low-energy diet		SEM	Probability		
	80	120	80	120		Diet	Intake	Diet × intake
DMI, kg/d	3.74	5.43	5.49	7.84	0.101	<0.01	<0.01	<0.01
DMI, g/kg EBW ^{0.75}	44.62	63.98	63.09	87.78	1.33	< 0.01	<0.01	0.05
Digestibility, %								
DM	65.9	62.8	58.9	57.2	1.44	<0.01	<0.01	0.40
OM	69.1	66.5	63.8	62.4	1.45	<0.01	0.01	0.43
ADF	49.9	52.8	58.1	57.7	2.25	<0.01	0.45	0.33
GE	68.3	65.9	63.	61.5	1.63	<0.01	0.04	0.74
Energy availability, Mcal/kg								
GE	4.30		4.26					
DE	2.94	2.83	2.69	2.62	0.062	<0.01	0.03	0.74
ME	2.41	2.32	2.21	2.15	0.051	<0.01	0.03	0.74
NE _m	1.53	1.45	1.35	1.29	0.032	<0.01	0.03	0.74
Energy intake, kcal/kg EBW ^{0.75}								
DE	131.23	181.42	170.34	230.27	3.604	<0.01	<0.01	0.16
ME	107.61	148.76	139.68	188.83	2.955	<0.01	<0.01	0.29
NE _m	68.21	92.86	85.21	113.50	1.805	<0.01	<0.01	0.39
NE _m intake, % requirement	75.83	108.24	94.88	132.70				

¹Observed via feed and fecal nutrient analysis.

²Formulated NE_m concentrations for high- and low-energy diets were 1.54 and 1.08 Mcal/kg, respectively.

³DMI = dry matter intake; DM = dry matter; OM = organic matter; ADF = acid detergent fiber; GE = gross energy; DE = digestible energy; ME = metabolizable energy; NE_m = net energy for maintenance; EBW = empty body weight.

Table 5. Body measurements of beef cows in confinement fed high- and low-energy density diets at 80% or 120% of NASEM (2016) predicted energy requirement

Item	High-energy diet ¹		Low-energy diet		SEM	Probability		
	80	120	80	120		Diet	Intake	Diet × intake
Initial measurements								
EBW ² , kg	370	358	388	393	9.2	<0.01	0.65	0.34
EBW ^{0.75} , kg	84.44	82.31	87.49	88.25	1.563	<0.01	0.74	0.37
Hip fat, mm	4.19	3.24	6.19	5.27	1.067	0.05	0.34	0.99
Rib fat, mm	2.64	3.05	4.79	5.27	0.976	0.02	0.62	0.97
Intramuscular fat, %	2.91	2.47	2.94	2.90	0.262	0.35	0.33	0.43
Ribeye area, cm ²	57.44	64.52	64.52	67.58	3.570	0.08	0.08	0.48
Final measurements								
EBW, kg	387	393	401	408	11.4	0.19	0.54	0.91
EBW ^{0.75} , kg	87.30	88.21	89.54	90.84	1.900	0.17	0.48	0.96
Hip fat, mm	2.79	3.18	5.08	4.89	0.931	0.03	0.91	0.75
Rib fat, mm	2.48	2.98	4.16	5.21	1.029	0.04	0.39	0.76
Intramuscular fat, %	2.92	2.54	2.70	3.05	0.246	0.52	0.93	0.12
Ribeye area, cm ²	57.67	66.37	62.82	67.11	3.483	0.32	0.04	0.45
Change in measurements								
EBW, kg	17	35	12*	15	6.9	0.08	0.12	0.27
EBW ^{0.75} , kg	2.86	5.90	2.05	2.59	1.164	0.07	0.11	0.26
Hip fat, mm	-1.40	-0.06*	-1.11*	-0.39*	0.580	0.97	0.06	0.56
Rib fat, mm	-0.16*	-0.06*	-0.06*	-0.02*	0.356	0.48	0.25	0.39
Intramuscular fat, %	0.02*	0.07*	-0.24*	-0.14*	0.150	0.55	0.15	0.26
Ribeye area, cm ²	-3.44*	1.85*	-1.69*	-1.20*	2.215	0.77	0.20	0.29

¹Formulated NE_m concentrations for high- and low-energy diets were 1.54 and 1.08 Mcal/kg, respectively.

²EBW = empty body weight.

*Means are not different from zero ($P > 0.05$).

Retained energy was estimated using several different equations, each based on different combinations of estimators (Table 6). Regardless of equation used to estimate RE, no interactions between diet energy density and level of energy intake were observed ($P \geq 0.37$), nor did diet affect estimates of RE ($P \geq 0.15$). One equation (Ferrell and Jenkins, 1984; Eq. 1) estimated greater RE for cows fed 120 than those fed 80 ($P = 0.03$), whereas other equations (Ferrell and Jenkins, 1984; Eq. 2; Gresham et al., 1986; Wagner et al., 1988) used to estimate RE resulted in a tendency for cows fed 120 to have greater estimates of RE than those fed 80 ($P < 0.10$). One equation from Wagner et al. (1988; Eq. 4) estimated no differences in RE due to diet or intake effects ($P > 0.42$). The only predictor in this equation is body condition score; based on results for the change in rib fat due to treatment, and our use of rib fat thickness as the predictor of rBCS, the results of this equation are explicable.

There were no significant interactions observed between diet energy density and level of intake for HE, regardless of the equation used for estimating

RE ($P \geq 0.17$; Table 7). All estimated HE values were greater for L than H ($P < 0.01$) and greater for 120 than 80 ($P < 0.01$).

Experiment 2: Intake and Digestion

Intakes of DM, ADF, GE, DE, and ME were greater in L than H ($P < 0.01$) and greater in 120 than in 80 ($P < 0.01$; Table 8). Intake of NE_m was not different between diets ($P = 0.20$) but was greater in 120 than in 80 ($P < 0.01$).

Diet \times intake interactions were observed for nutrient digestibility. Digestibility of DM, OM, and GE was greater in steers fed H than in L ($P < 0.01$); however, digestibility of each nutrient increased by approximately 10% in steers fed H80 vs. those fed H120 ($P \leq 0.03$) but was similar for both levels of intake in steers fed L ($P = 0.54$). Digestibility of ADF was lower in steers fed H120 than those fed H80, but was not affected by intake of L (diet \times intake, $P = 0.08$).

A diet \times intake interaction was observed for ruminal pH ($P = 0.08$; Fig. 1). Mean pH was lower

Table 6. Estimates of retained energy¹ (RE) in confined beef cows fed high- and low-energy density diets at 80% or 120% of NASEM (2016) predicted energy requirement

Model	High-energy diet ²		Low-energy diet		SEM	Probability		
	80	120	80	120		Diet	Intake	Diet \times intake
NASEM	-1.77	8.13	-8.02	0.55	5.28	0.17	0.07	0.89
Ferrell and Jenkins (1984, 1)	4.57	17.10	-0.52	8.04	5.09	0.15	0.03	0.68
Ferrell and Jenkins (1984, 2)	7.92	24.08	6.69	12.37	6.06	0.27	0.06	0.37
Gresham et al. (1986)	1.70	10.15	-4.18	3.17	5.01	0.18	0.10	0.90
Wagner et al. (1988, 1)	1.41	7.38	-2.39	2.57	3.25	0.17	0.08	0.87
Wagner et al. (1988, 2)	5.48	16.67	4.63	8.56	4.20	0.27	0.06	0.37
Wagner et al. (1988, 3)	5.62	16.59	4.53	8.56	4.17	0.26	0.06	0.38
Wagner et al. (1988, 4)	-1.97	-0.92	-7.52	-2.47	4.68	0.43	0.49	0.65

¹kcal/d/EBW^{0.75}, calculated as RE/d/EBW^{0.75}, where d = 56 days.

²Formulated NE_m concentrations for high- and low-energy diets were 1.54 and 1.08 Mcal/kg, respectively.

Table 7. Estimates of heat production¹ (HE) in confined beef cows fed high- and low-energy density diets at 80% or 120% of NRC (2016) predicted energy requirement

Model	High-energy diet ²		Low-energy diet		SEM	Probability		
	80	120	80	120		Diet	Intake	Diet \times intake
NASEM	109.39	140.63	147.69	188.28	5.48	<0.01	<0.01	0.37
Ferrell and Jenkins (1984, 1)	103.04	131.66	140.20	180.79	5.81	<0.01	<0.01	0.28
Ferrell and Jenkins (1984, 2)	99.70	124.68	132.99	176.46	7.39	<0.01	<0.01	0.20
Gresham et al. (1986)	105.91	138.61	143.86	185.66	5.11	<0.01	<0.01	0.35
Wagner et al. (1988, 1)	106.21	141.38	142.07	186.26	3.86	<0.01	<0.01	0.23
Wagner et al. (1988, 2)	102.13	132.09	135.05	180.26	5.72	<0.01	<0.01	0.17
Wagner et al. (1988, 3)	101.99	132.17	135.15	180.27	5.68	<0.01	<0.01	0.17
Wagner et al. (1988, 4)	109.58	149.68	147.20	191.29	4.29	<0.01	<0.01	0.62

¹kcal/d/EBW^{0.75}, calculated as (ME - RE)/d/EBW^{0.75}, where d = 52 days.

²Formulated NE_m concentrations for high- and low-energy diets were 1.54 and 1.08 Mcal/kg, respectively.

Table 8. Effect of diet energy density and level of intake on digestibility¹ and ruminal fill in ruminally cannulated steers

Item ²	High-energy diet		Low-energy diet		SEM	Probability		
	80	120	80	120		Diet	Intake	Diet × intake
DMI, kg/d	2.82 ^a	4.22 ^b	3.96 ^c	5.88 ^d	0.135	<0.01	<0.01	0.08
DMI, g/kg EBW ^{0.75}	44.18 ^a	66.64 ^c	59.74 ^b	75.10 ^d	1.622	<0.01	<0.01	0.04
Digestibility, %								
DM	68.1 ^a	60.5 ^b	57.5 ^b	59.1 ^b	1.6	<0.01	<0.01	0.01
OM	71.7 ^a	64.0 ^b	61.3 ^b	63.4 ^b	1.6	<0.01	<0.01	<0.01
ADF	49.7 ^a	44.0 ^b	50.9 ^a	52.3 ^a	1.8	<0.01	<0.01	0.08
GE	68.6 ^a	61.1 ^b	59.0 ^b	60.7 ^b	1.7	<0.01	<0.01	0.02
Energy availability, Mcal/kg								
GE	4.31		4.27					
DE	2.96 ^a	2.63 ^b	2.52 ^b	2.60 ^b	0.071	<0.01	0.11	0.01
ME	2.42 ^a	2.06 ^b	2.06 ^b	2.13 ^b	0.058	<0.01	0.11	0.01
NE _m	1.54 ^a	1.30 ^b	1.21 ^b	1.27 ^b	0.053	<0.01	0.11	0.01
Energy intake, Mcal/d								
GE	12.13	18.09	16.31	20.75	0.593	<0.01	<0.01	0.22
DE	8.34	11.09	9.63	12.60	0.512	0.02	<0.01	0.85
ME	6.84	9.10	7.89	10.34	0.420	0.02	<0.01	0.85
NE _m	4.34	5.48	4.64	6.18	0.305	0.20	<0.01	0.51
Ruminal DM fill, kg	3.39	4.57	4.41	4.92	0.276	0.02	0.01	0.24

^{a,b,c,d}Within a row, means without a common superscript letter differ ($P < 0.05$).

¹Observed via feed and fecal analysis.

²DMI = dry matter intake; DM = dry matter; OM = organic matter; ADF = acid detergent fiber; GE = gross energy; DE = digestible energy; ME = metabolizable energy; NE_m = net energy for maintenance; EBW = empty body weight.

($P = 0.03$) in steers fed H120 than those fed L120 (6.30 and 6.41, respectively), but was not different ($P = 0.56$) between diets at low intake (L80 vs. H80). Prior to feeding, pH was greater in H than in L ($P < 0.01$) but was lower 6 to 12 h post-feeding ($P < 0.05$).

A diet × time interaction was observed for ruminal total VFA concentration ($P = 0.03$; Fig. 2). Prior to feeding until 2 h, steers fed L had greater total VFA concentration than those fed H ($P < 0.04$); however, at hour 12, total VFA concentration tended to be greater in H than in L ($P = 0.08$). A diet × intake interaction was also observed ($P = 0.03$). Total ruminal VFA concentration was greatest in L80 (66.5 mM) and lowest in H80 (60.8 mM). A diet × intake interaction was observed for acetate concentration ($P < 0.01$), with acetate increasing with greater intake of H (H80, 63.3; H120, 65.2 mM), but not differing between intakes of L (L80, 67.8; L120, 67.2 mM). Propionate concentration was greater in H than in L (21.0 and 19.5 mM, respectively; $P < 0.10$) and greater in 80 than 120 (20.9 and 19.7 mM, respectively; $P < 0.01$). No diet × intake or treatment × time interactions were observed for ruminal acetate:propionate ratio (A:P; Fig. 3). Ruminal A:P was greater in steers fed L than those fed H ($P < 0.01$), and greater in 120

than 80 ($P < 0.01$). Steers fed H80 had the lowest A:P from 6 to 16 h post-feeding ($P < 0.01$).

DISCUSSION

Experimental objectives were to quantify the effects of dietary energy density and intake level on efficiency of energy utilization in limit-fed beef cows and to evaluate potential sources of observed effects. Experiment 1 was primarily designed to measure energy utilization and to estimate RE/loss in the form of heat. Experiment 2 was intended to support and provide explanation for observed results from Exp. 1 for energy utilization and was designed to evaluate effects of treatments on ruminal digestion, fill (and by proxy, ruminal retention of ingesta), and fermentation parameters.

Diet utilization, which is largely driven by extent of ruminal digestion, was greater in H vs. L, by design. Restricting intake improved diet utilization, but this effect was more pronounced in H. Increases in digestibility with intake restriction, specifically in high-energy diets, have been reported extensively in the literature in dairy (Moe et al., 1965; Tyrrell and Moe, 1972; Colucci et al., 1982) and in beef cattle (Galyean et al., 1979; Loerch, 1990; Zinn et al., 1995). Observations from the dairy literature may be more applicable

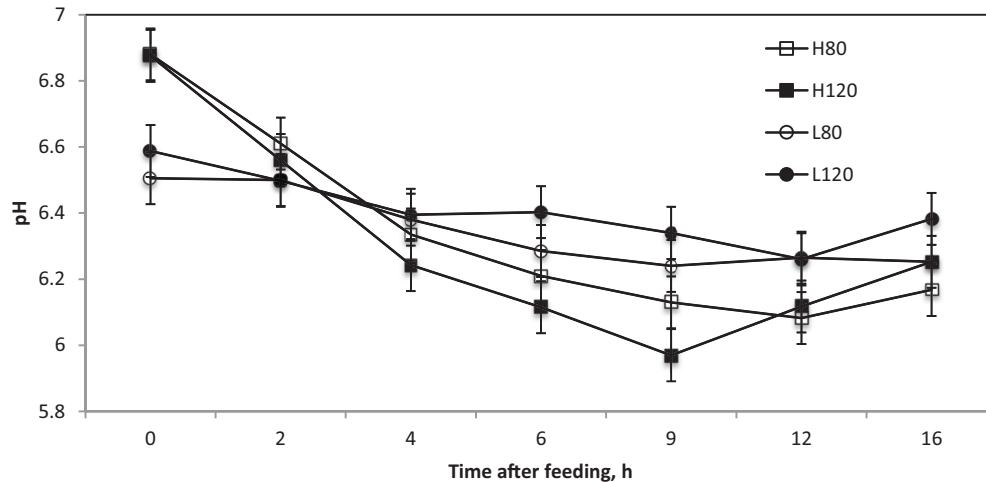


Figure 1. Ruminal pH of steers fed a high-energy diet (H) offered at 80% NE_m requirements (H80), H offered at 120% NE_m requirements (H120), a low-energy diet (L) offered at 80% NE_m requirements (L80), or L offered at 120% NE_m requirements (L120). Values are means \pm SEM (0.079); $n = 16$. A diet \times time interaction was observed for ruminal pH. Ruminal pH was greater in steers fed H than those fed L prior to feeding, but lower from 6 to 12 h after feeding. A diet \times intake interaction ($P = 0.09$) was also observed. Ruminal pH was lowest in H120 (6.30) and greatest in L120 (6.41).

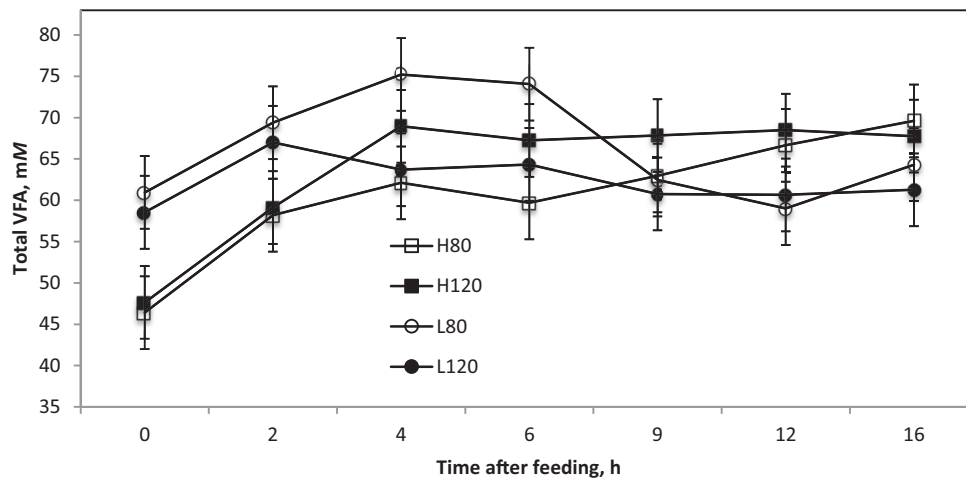


Figure 2. Ruminal VFA concentrations of steers fed a high-energy diet (H) offered at 80% NE_m requirements (H80), H offered at 120% NE_m requirements (H120), a low-energy diet (L) offered at 80% NE_m requirements (L80), or L offered at 120% NE_m requirements (L120). Values are means \pm SEM (4.400); $n = 16$. A diet \times time interaction was observed for ruminal total VFA concentration. Prior to feeding until 2 h, steers fed L had greater total VFA concentration ($P < 0.04$) than those fed H; -, at hour 12, total VFA concentration tended to be greater ($P = 0.08$) in H than in L. A diet \times intake interaction ($P = 0.03$) was also observed. Total ruminal VFA concentration was greatest in L80 (66.5 mM) and lowest in H80 (60.8 mM).

to the limit-fed cows in our study because effects on energy utilization were measured at similar degrees of intake restriction.

When intake is restricted, greater digestibility is often attributed to slower digesta passage rate (Mertens, 1987). Decreased rate of passage results in a slower decline in ruminal pH and improved fiber digestion (Mould et al., 1983). Dry matter intake as a percentage of ruminal DM fill decreased with intake restriction in both diets (92% to 83% in H; 120% to 90% in L) in Exp. 2, suggesting an increase in ruminal retention time with lower intake. The magnitude of this difference was greater in L than in H, which is consistent with the larger increase

in DM intake for the L diet necessary to achieve similar programmed energy intake. This effect may also explain the larger departure from expected values of digestibility and therefore energy availability for the L than the H diets. This difference, and the resulting underestimation of the energy value of the L diet, led to greater observed levels of NE_m intake relative to targets in L-fed cows compared with H-fed cows.

Although ruminal retention time may have increased to a greater degree in steers fed L compared with those fed H, digestibility was less affected by intake level of L in both experiments. Changes in passage rate caused by intake restriction could

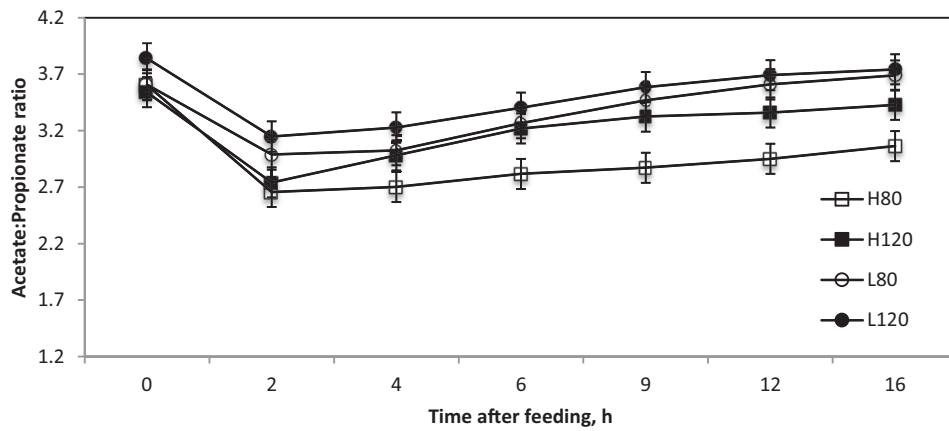


Figure 3. Ruminal acetate:propionate ratio (A:P) of steers fed a high-energy diet (H) offered at 80% NE_m requirements (H80), H offered at 120% NE_m requirements (H120), a low-energy diet (L) offered at 80% NE_m requirements (L80), or L offered at 120% NE_m requirements (L120). Values are means \pm SEM (0.133); $n = 16$. Ruminal A:P was greater in steers fed L than those fed H ($P < 0.01$) and greater in steers fed 120 than those fed 80 ($P < 0.01$).

have interacted with potential rate of degradation for each diet, resulting in pronounced changes in digestibility in H without a measurable change in L. It is also possible that maximal extent of digestion was approached in L, thus changes in passage rate would have more limited effects digestibility.

Effects on passage rate are not likely to be solely responsible for the changes in apparent energy availability observed in these studies. In Exp. 2, the rate of decline in ruminal pH from greater intake was more severe in H than in L, falling below 6.0 in H120. Additionally, ADF digestibility was reduced with greater intake of H in Exp. 2, supporting the conjecture that reduced fiber digestion accounts for a portion of the reduction in energy availability often observed with increasing intake (Mould et al., 1983). Intake restriction increased diet digestibility, with the magnitude of difference being greater in the high-energy diet than in the low-energy diet, which is consistent with the dairy literature (Brown, 1966; Tyrrell and Moe, 1974; Llamas-Lamas and Combs, 1991).

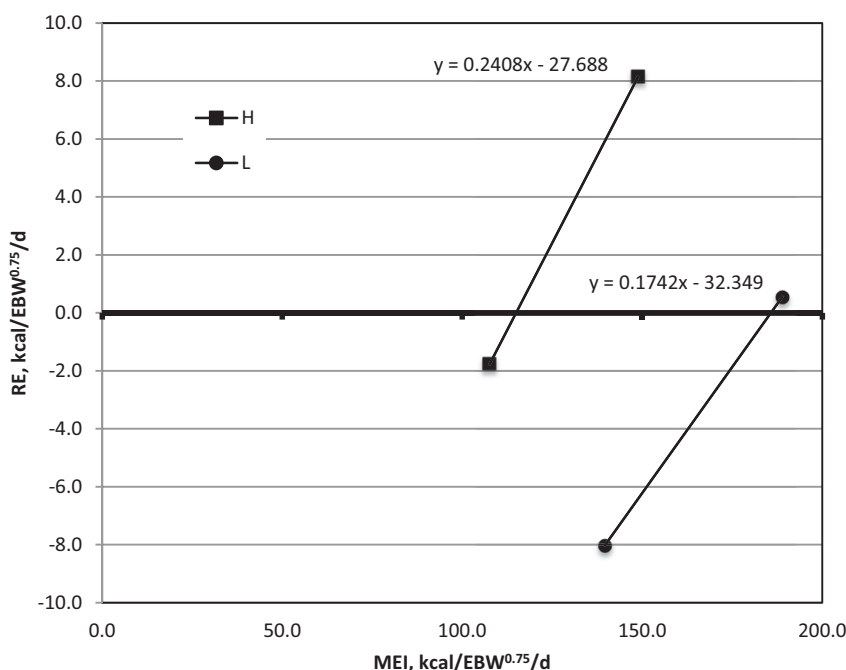
In cows fed H80, BW gain was positive, the observed changes in most measures of fat were not different from zero, and all estimates of RE were either positive or not different from zero. Differences in RE estimated from equations from the literature correspond to those calculated using NASEM (2016) equations, and the rank of treatment means is generally consistent across all equations (Table 9), suggesting that energy intake was sufficient to achieve maintenance, although energy intake was only 76% the recommended level (6.53 Mcal NE_m /d). Because changes in BW, measures of body fat, and thus estimates of RE were minimally affected by intake level, it is possible that energy

requirements were reduced due to a shift in equilibrium FHP, similar to that described by Freetly and Nienaber (1998). Energy restriction is known to decrease splanchnic tissue mass and subsequent heat production (McLeod and Baldwin, 2000; Camacho et al., 2014), increasing the efficiency of energy use (Freetly and Nienaber, 1998; Freetly et al., 2006, 2008) in sheep and mature cows. Similar effects of restricting intake have been demonstrated in growing cattle; Birkelo et al. (1991) observed a 7% reduction in FHP and a 14% reduction in ME_m with intake restriction from 2.2 to 1.2 times maintenance. Values for ME_m were estimated (Fig. 4) for each diet. Estimated ME_m for H (115 kcal/kg $EBW^{0.75}$) was lower than predicted values (141 kcal/kg $EBW^{0.75}$), but was greater than predicted (186 vs. 158 kcal/kg $EBW^{0.75}$) for L. The fact that ME_m is greater for L than H is reasonable, as the efficiency of ME use is known to be greater in high-energy diets than in low-energy diets (NASEM, 2016); however, the degree by which ME_m of H was shifted (18%), relative to NASEM (2016) estimates, is notable. This observation suggests an overestimation of ME_m requirements in cows consuming a high-energy diet by the NASEM (2016). Freetly and Nienaber (1998) reported a 22% decrease in ME_m requirements when intake was restricted by 65% in mature cows, which is similar to our observed decrease in H.

Order of HE estimates across treatments was similar across all equations, suggesting that the particular equation used for estimation of body energy is not necessarily of great importance; percent decrease in heat production from L to H (Table 10) ranged from 23.4% to 27.5%. Similarly, the percent reduction in heat energy associated with intake

Table 9. Effect of increasing dietary energy density and restricting intake on retained energy¹

	Factor means				Difference	
	H	L	80	120	Diet ²	Intake ³
NRC	3.18	-3.73	4.90	4.34	6.91	9.27
Ferrell and Jenkins (1984, 1)	10.84	3.76	2.02	12.57	7.08	10.55
Ferrell and Jenkins (1984, 2)	16.00	9.53	7.30	18.23	6.47	10.92
Gresham et al. (1986)	5.93	-0.51	-1.24	6.66	6.43	7.90
Wagner et al. (1988, 1)	4.39	0.09	-0.49	4.97	4.30	5.47
Wagner et al. (1988, 2)	11.08	6.60	5.06	12.62	4.48	7.56
Wagner et al. (1988, 3)	11.10	6.54	5.07	12.57	4.56	7.50
Wagner et al. (1988, 4)	-1.44	-4.99	-4.74	-1.69	3.55	3.05
Means	7.64	2.16	2.24	8.78	5.47	7.78

¹kcal/kg EBW^{0.75}.²Calculated as H - L³Calculated as 120 - 80.**Figure 4.** Means regression of retained energy on metabolizable energy intake of cows fed a high-energy diet (H) offered at 80% NE_m requirements (H80), H offered at 120% NE_m requirements (H120), a low-energy diet (L) offered at 80% NE_m requirements (L80), or L offered at 120% NE_m requirements (L120)

restriction is similar across equations (21.8% to 24.7%). The effects of dietary energy density and intake on heat production were additive, decreasing approximately 43% from L120 to H80 across all equations.

Heat production occurs in a nonlinear function of MEI; therefore, log transformation of heat production allows for a meaningful linear regression of HE on MEI (Garrett, 1987; Fig. 5). Estimated FHP of cows fed H (57.2 kcal/kg EBW^{0.75}) was lower than that of cows fed L (73.3 kcal/kg EBW^{0.75}), consistent with observations by Blaxter (1962), who found that FHP decreases as energy density

increases in the diet. Estimates of FHP in cows fed L or H were 35% and 17%, respectively, lower than NASEM (2016) estimates (88.3 kcal/kg EBW^{0.75}) for a midgestation cow and were also lower than the NASEM (2016) assumption of basal metabolism (77 kcal/kg EBW^{0.75}). Restricted intake and subsequently reduced metabolic load may have altered the size of metabolically active organs (Reynolds et al., 1991; McLeod and Baldwin, 2000), resulting in reduced energy requirements.

Using these estimates of FHP and ME_m, a graphic illustration of NE, following that of Garrett (1987), was produced (Fig. 6). This illustrates both

Table 10. Effect of increasing dietary energy density and restricting intake on daily heat production¹

	Factor means				Percentage change	
	H	L	80	120	Diet ²	Intake ³
NRC	125.0	168.0	128.5	164.5	-25.6	-21.8
Ferrell and Jenkins (1984, 1)	117.4	160.5	121.6	156.2	-26.9	-22.2
Ferrell and Jenkins (1984, 2)	112.2	154.7	116.3	150.6	-27.5	-22.7
Gresham et al. (1986)	122.3	164.8	124.9	162.1	-25.8	-23.0
Wagner et al. (1988, 1)	123.8	164.2	124.1	163.8	-24.6	-24.2
Wagner et al. (1988, 2)	117.1	157.7	118.6	156.2	-25.7	-24.1
Wagner et al. (1988, 3)	117.1	157.7	118.6	156.2	-25.8	-24.1
Wagner et al. (1988, 4)	129.6	169.2	128.4	170.5	-23.4	-24.7
Means	120.6	162.1	122.6	160.0	-25.7	-23.4

¹Mcal, 56 d.

²Calculated as $100\% \times [(H - L)/L]$.

³Calculated as $100\% \times [(80 - 120)/120]$.

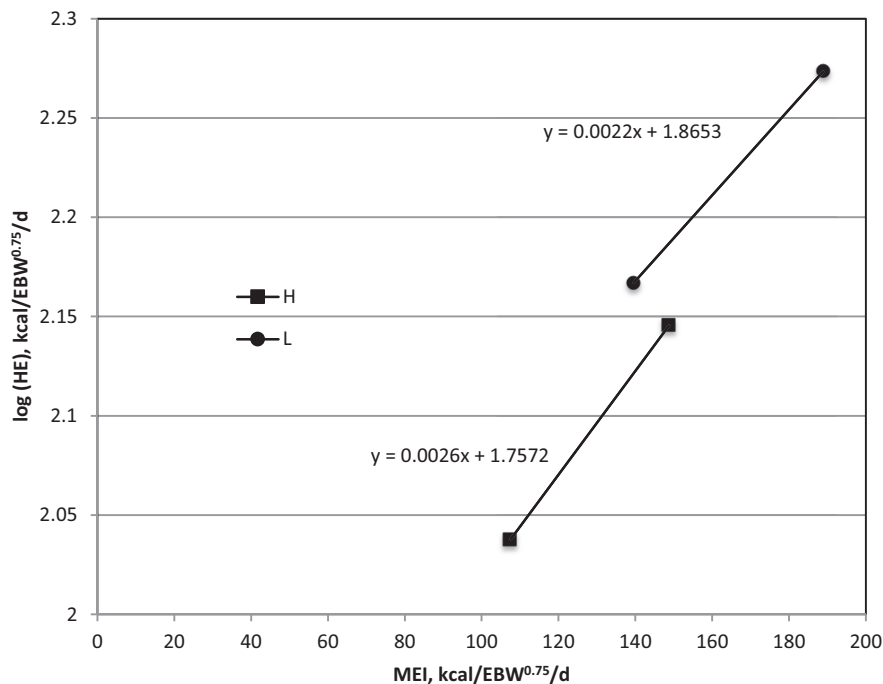


Figure 5. Means regression of heat production (logarithmic transformation) on metabolizable energy intake of cows fed a high-energy diet (H) offered at 80% NE_m requirements (H80), H offered at 120% NE_m requirements (H120), a low-energy diet (L) offered at 80% NE_m requirements (L80), or L offered at 120% NE_m requirements (L120).

the decrease in FHP and the increased efficiency with which ME is utilized in H relative to L. The slope of RE on MEI represents the efficiency of ME use for RE below (k_m) and above (k_g) maintenance intake.

Our estimates of ME intake were calculated by using the DE:ME conversion rate of 82% (NASSEM, 2016), which has been widely debated. Hales et al. (2012, 2013, 2014) observed DE:ME conversions much greater than 82% (89.3% to 95.0%) in growing cattle fed high-energy diets, which probably attributed to reduced methane production. If methane production was less than expected in cattle

fed H, then DE:ME was greater than estimated, causing ME intake and maintenance requirements to be underestimated. However, this conversion would need to be almost 102% to achieve maintenance in cows fed H80, which suggests that, even if DE:ME were underpredicted, the discrepancy is probably not adequate to provide the sole explanation of observed decreases in heat production. Mills et al. (2001) proposed that the proportion of ingested energy lost as methane actually increases with intake restriction, which would result in overestimated dietary ME (rather than underestimated) values in feed restricted animals. Furthermore,

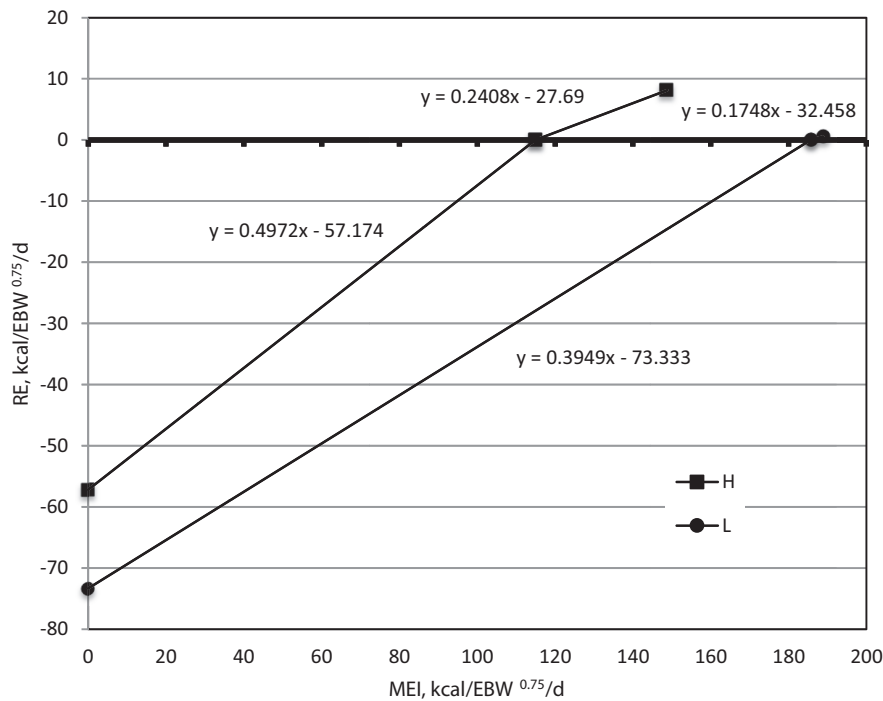


Figure 6. Estimated net energy delivery of treatment high (H)- and low (L)-energy diets.

Vermorel and Bickel (1980) suggested that methane losses are probably greater in mature animals than in young, growing animals. If DE:ME was lower than 82%, then our estimates of heat production would be overestimated, further supporting the hypothesis that maintenance requirements decrease with restricted intake of high-energy diets.

Overall, intake restriction can improve diet utilization, but the magnitude of change depends on diet energy density. This relationship should be quantified in diets fed at intake levels that are applicable to gestating beef cows. Diet had minimal effects on estimates of RE, but cows fed H had lower HE. Increasing intake increased RE; however, even in cows fed 80, RE was not negative. Increasing intake also increased HE, which is consistent with our hypothesis that restricting intake increases energy efficiency of diet utilization and reduces maintenance requirements. A model accommodating these dynamic adjustments will be necessary to the development of optimal feed delivery strategies, but these results suggest that opportunities exist to strategically enhance efficiencies in intensively managed systems.

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