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The effects of the forage-to-concentrate ratio on the conversion of digestible energy to metabolizable energy in growing beef steers

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Abstract

Metabolizable energy (**ME**) is calculated from digestible energy (**DE**) using a constant conversion factor of 0.82. Methane and urine energy losses vary across diets and dry matter intake (**DMI**), suggesting that a static conversion factor fails to describe the biology. To quantify the effects of the forage-to-concentrate ratio (**F:C**) on the efficiency of conversion of DE to ME, 10 Angus steers were used in a 5 × 5 replicated Latin square. Dry-rolled corn was included in experimental diets at 0%, 22.5%, 45.0%, 67.5%, and 83.8% on a dry matter (**DM**) basis, resulting in a high F:C (**HF:C**), intermediate F:C (**IF:C**), equal F:C (**EF:C**), low F:C (**LF:C**), and a very low F:C (**VLF:C**), respectively. Each experimental period consisted of a 23-d diet adaption followed by 5 d of total fecal and urine collections and a 24-h gas exchange collection. Contrasts were used to test the linear and quadratic effects of the F:C. There was a tendency ($P = 0.06$) for DMI to increase linearly as F:C decreased. As a result, gross energy intake (**GEI**) increased linearly ($P = 0.04$) as F:C decreased. Fecal energy loss expressed as Mcal/d ($P = 0.02$) or as a proportion of GEI ($P < 0.01$) decreased as F:C decreased, such that DE (Mcal/d and Mcal/kg) increased linearly ($P < 0.01$) as F:C decreased. As a proportion of GEI, urine energy decreased linearly ($P = 0.03$) as F:C decreased. Methane energy loss as a proportion of GEI responded quadratically ($P < 0.01$), increasing from HF:C to IF:C then decreasing thereafter. The efficiency of DE to ME conversion increased quadratically ($P < 0.01$) as F:C decreased, ranging from 0.86 to 0.92. Heat production (Mcal) increased linearly ($P < 0.04$) as F:C decreased but was not different as a proportion of GEI ($P \geq 0.22$). As a proportion of GEI, retained energy responded quadratically ($P = 0.03$), decreasing from HF:C to IF:C and increasing thereafter. DM, organic matter, and neutral detergent fiber digestibility increased linearly ($P < 0.01$) and starch digestibility decreased linearly ($P < 0.01$) as the F:C decreased. Total N retained tended to increase linearly as the proportion of concentrate increased in the diet ($P = 0.09$). In conclusion, the efficiency of conversion of DE to ME increased with decreasing F:C due to decreasing methane and urine energy loss. The relationship between DE and ME is not static, especially when differing F:C.

Key words: beef cattle, digestible energy, metabolizable energy

Abbreviations

ADF	acid detergent fiber
BW	body weight
CNES	California Net Energy System
CP	crude protein
DE	Digestible energy
DM	dry matter
DMI	dry matter intake
DRC	dry-rolled corn
F:C	forage-to-concentrate ratio
FE	fecal energy
GE	gross energy
GEI	gross energy intake
HP	heat production
MCP	microbial crude protein
ME	metabolizable energy
NASEM	National Academy of Sciences, Engineering, and Medicine
NDF	neutral detergent fiber
OM	organic matter
RE	retained energy
UE	urinary energy
VLF:C	very low forage-to-concentrate ratio

Introduction

Estimates of energy available from feeds are required for determining the quantity of a given feed needed to meet maintenance energy requirements and for growth models used to predict body weight (**BW**) gain. In beef cattle, gross energy (**GE**) obtained through feed consumed is lost via fecal and urinary excretion and through the production and loss of methane and heat. The amount of energy lost through a single route varies depending on diet type; however, the sum of these losses often represents a large proportion of the GE intake. For this reason, the California Net Energy System (**CNES**) was created and described by Lofgreen and Garrett (1968). The CNES was the first beef cattle feeding system to assign separate net energy values to feeds, either for maintenance or production, and is the predominate energy system used for beef cattle in the United States today.

Comparative slaughter studies were used to derive feed net energy values on a limited number of selected feeds during the development and refinement of the CNES. It is infeasible to directly quantify net energy by comparative slaughter or calorimetric techniques for each feedstuff available, or potentially available, for beef cattle. Therefore, most net energy values used today are derived from metabolizable energy (**ME**) using cubic equations established by Garrett (1980). Indeed, the National Academy of Sciences, Engineering, and Medicine (NASEM) (2016) utilizes these equations for the determination of the net energy values found in its standard feed library.

As an input into these equations, ME is estimated using a fixed efficiency of 0.82 of digestible energy (**DE**) (Agricultural Research Council [ARC], 1965; Garrett, 1980). However, methane and urinary energy (**UE**) losses vary across diets and dry matter intake (**DMI**), suggesting that the true relationship between DE and ME is not constant. The objective of this study was to quantify the effects of decreasing dietary forage and increasing concentrate on the efficiency of conversion of DE to ME.

Materials and Methods

The experimental protocol was approved by the U.S. Meat Animal Research Center (USMARC) Institutional Animal Care and Use Committee (approval number 51.1).

Ten purebred Angus yearling steers (365 ± 15.9 kg of initial BW) were used in a 5 × 5 replicated Latin square. Each of the five experimental periods consisted of a 23-d diet adaption followed by 5 d of total fecal and urine collections. Prior to the start of the first period, cattle were trained to metabolism stanchions, fecal bags, urine harnesses, and headbox respiration calorimeters in order to facilitate collection procedures. After adaptation to the metabolism facility, steers were stratified by BW and assigned to one of two Latin square replicates.

Dietary treatments were formulated to contain an increasing proportion of dry-rolled corn (**DRC**) with a concomitant decrease in forage supplied by corn silage and alfalfa hay (Table 1). DRC was included in the experimental diets at 0%, 22.5%, 45%, 67.5%, and 83.8% on a dry matter (**DM**) basis resulting in a high forage-to-concentrate ratio (**HF:C**), intermediate F:C (**IF:C**), equivalent F:C (**EF:C**), low F:C (**LF:C**), and a very low F:C (**VLF:C**), respectively. Based on past observations with similar corn hybrids grown and used at USMARC, we estimate the corn silage in the HF:C diet contained approximately 35% to 40% corn grain. Therefore, while the HF:C diet is predominantly forage, it does include some concentrate grain. Urea was added (0.20% DM) to the VLF:C treatment in order to compensate for the decreased dietary crude protein (**CP**) associated with the reduced inclusion of alfalfa hay.

Table 1. Ingredient and analyzed composition (DM basis) of experimental diets formulated to contain varying F:C fed to growing beef steers at ad libitum intake

	Treatment[1]				
Item	HF:C	IF:C	EF:C	LF:C	VLF:C
Ingredient, %					
DRC	—	22.50	45.00	67.50	83.80
Alfalfa hay	30.00	30.00	30.00	24.50	8.00
Corn silage	62.00	39.50	17.00	—	—
Soybean meal	5.00	5.00	5.00	5.00	5.00
Supplement[2]	3.00	3.00	3.00	3.00	3.00
Urea	—	—	—	—	0.20
Analyzed composition					
GE, Mcal/kg	4.24	4.22	4.27	4.22	4.29
DM, %	46.79	57.02	68.65	83.83	83.59
OM, %	91.37	90.99	91.81	92.60	94.35
CP, %	11.99	12.62	12.61	12.82	12.49
RDP[3], %	10.17	9.47	8.77	7.60	6.21
NDF, %	40.60	39.31	35.15	28.23	27.95
eNDF[3], %	33.44	25.61	17.77	9.74	3.41
ADF, %	25.16	23.30	21.06	14.29	9.30
Ether extract, %	3.73	3.37	3.15	3.02	2.90
Starch, %	21.10	24.20	26.72	36.46	45.26

RDP = rumen degradable protein
[1]DRC replaced corn silage and alfalfa hay at 0% (HF:C), 22.5% (IF:C), 45% (EF:C), 67.5% (LF:C), and 83.8% (VLF:C) of dietary DM.
[2]Formulated to contain Rumensin (Elanco Animal Health, Greenfield, IN) at 700 g/ton and vitamins and minerals to exceed NASEM (2016) requirements.
[3]Tabular values based on the NASEM (2016) requirements.

Formulated ingredient composition and analyzed nutrient content (DM basis) are presented in Table 1. Diets were formulated with increasing concentrations of DRC that replaced alfalfa hay, corn silage, or a combination of alfalfa hay and corn silage as the F:C ratio decreased. GE content ranged from 4.22 to 4.29 Mcal/kg and was formulated to be similar across diets. By design, the CP concentration was similar across diets—ranging from 12.0% to 12.8%. As expected, the neutral detergent fiber (**NDF**) and acid detergent fiber (**ADF**) content decreased as the F:C decreased. The VLF:C contained 53% more starch than the HF:C.

The corn silage was harvested from a single field after a majority of the kernels were dented and the milk line was visible. The DM at the time of harvest was 35.4%, and the silage was harvested over 2 d and packed into a silage bag using a pull-type bagger. We estimate that corn silage contained approximately 35% to 40% corn grain. The alfalfa hay was harvested from a single field on the second cutting, during mid-bloom at approximately 85% DM. The alfalfa hay used in the experiment was stored under a shed to preserve the quality.

During diet adaptation, the cattle were housed in a partially enclosed group pen and fed individually using Calan-Broadbent electronic head gates (American Calan, Inc., Northwood, NH). Cattle were adapted to the experimental diets by mixing the previous diet with the new diet for up to 7 d to prevent acidosis when transitioning from diets of less to more concentrate. All steers were on their final diet by day 8 of each adaption period. Throughout the experiment, steers were fed once daily at 0800 hours and were provided ad libitum access to feed and freshwater. On day 0 of each collection period, the steers were moved into the metabolism barn and housed in individual stanchions (87 × 214 cm), where urine and feces were collected for a total of 5 d.

During the collection period, orts were removed from the feed box 24 h after the initial diet offering, weighed, and a subsample was saved for subsequent lab analysis. A 100-g sample of each experimental diet was also collected daily and composited within period for later determination of DM, GE, organic matter (**OM**), CP, NDF, ADF, and starch. Total feces were collected into a canvas bag attached to a harness secured around the heart girth of each steer as described by Tolleson and Erlinger (1989). A custom rubber funnel was placed under the sheath, secured by an elastic strap over the back of the steer, and urine was collected into a polypropylene jug under vacuum. To prevent ammonia losses, 100 mL of 3.7 N HCl was added to each urine jug before daily collections to ensure the pH remained <5.0. Contents of the fecal bags and urine jugs were weighed each morning at approximately 0700 hours, thoroughly mixed, and a 3% aliquot of each was composited by steer and stored at –20 °C for subsequent analysis.

Gas exchange was measured over a 24-h period on day 2 for one-half of the experimental animals and on day 3 for the remaining animals. Each treatment was equally represented on each day of measurement. Liters of oxygen consumption, CH_4 production, and CO_2 production were determined using portable respiration calorimeters designed for indirect, open-circuit calorimetry. Portable headboxes were 0.76 × 0.76 × 1.78 m and contained a 0.76 × 117 cm opening on one side. Steers were given their daily feed allotment inside the calorimeter, which was equipped with an automatic water bowl. A vinyl hood was placed over the steer's neck and used to create a barrier between the inside of the box and outside air. Samples of gases entering and exhausting from each box were collected into polyethylene–aluminum–Mylar laminate bags and analyzed for O_2, CO_2, and CH_4 concentrations as described by Nienaber and Maddy (1985). Values for each of these variables along with urinary nitrogen were then used to calculate heat production (**HP**) using the Brouwer (1965) equation.

Diets, orts, and fecal samples were partially dried in a forced-air oven for 96 h at 55 °C, allowed to air-equilibrate, and then weighed for the determination of partial DM. Samples were then ground through a 1-mm screen using a Wiley mill (Thomas Scientific, Swedesboro, NJ) and further dried at 105 °C for 24 h for the determination of DM. OM was determined as the loss in weight following combustion in a muffle furnace for 8 h at 450 °C. Analysis for NDF and ADF was performed sequentially using an Ankom Fiber Analyzer (Ankom Technology Corp., Macedon, NY). Energy values for diet, ort, and fecal samples were determined on dry samples by bomb calorimetry using a Parr 6300 Calorimeter (Parr Instrument Co., Moline, IL). To analyze UE, cotton rounds were weighed and placed into bomb calorimeter crucibles; 4 mL of urine was added to the crucible, and differences in energy content were attributed to the urine. The difference of the urine and cotton rounds was divided by the milliliters of urine added to determine the calories per milliliters of urine. Diet, orts, fecal, and urine samples were sent to a commercial laboratory (SDK Labs, Hutchinson, KS) for analysis of CP (Kjeldahl procedure; method no. 951.01; AOAC, 2012) and starch content (not including urine).

One animal was removed from the experiment during period 3 due to unwillingness to cooperate with the collection procedures resulting in one steer for the given treatment for that period. An alternate animal was used for the remaining two periods. The alternate was previously adapted to the experimental procedures and the same dietary treatment assignments as the steer that was removed and had, therefore, received the same diet in each period.

Calculations

Methane and HP energy losses were calculated as follows:

$$CH_4,\ \text{megacalories (Mcal)} = (9.45 \times \text{L of } CH_4) \div 1000$$

$$\text{Heat production, Mcal} = \left(\begin{array}{l}(3.866 \times \text{L/d of } O_2) + (1.2 \times \text{L/d of } CO_2) \\ -(0.518 \times \text{L/d of } CH_4) - (1.413 \times \text{g/d of urinary N})\end{array}\right) \div 1000$$

where:

CH_4 = methane production (L/d)
O_2 = oxygen consumption (L/d)
CO_2 = carbon dioxide production (L/d)
N = urinary nitrogen excretion (g/d)

DE, ME, and retained energy (**RE**) were calculated as follows:

$$\text{DE, Mcal} = \text{GEI} - \text{fecal energy (FE)}$$

$$\text{ME, Mcal} = \text{DE} - (\text{urinary energy (UE)} + CH_4)$$

$$\text{ME : DE} = \text{ME, Mcal/ kg DM} \div \text{DE, Mcal/kg DM}$$

$$RE,\ \text{Mcal} = \text{ME} - \text{HP}$$

where:

GEI = DMI (g/d) × diet GE (Mcal/g DM)
FE = fecal production (kg DM/d) × fecal energy (Mcal/kg DM)
UE = urine production (kg/d) × urinary energy (Mcal/kg)
CH_4 = methane production (Mcal)
HP = heat production (Mcal)
Nitrogen (**N**) retained was calculated as follows:

$$\text{N retained (g)} = \text{N intake (g)} - \text{N excreted in feces (g)} - \text{N excreted in urine (g)}$$

Digestibility of DM, OM, NDF, ADF, and starch were calculated as follows:

$$\text{Digestibility, \%} = \left(\frac{\text{Intake} - \text{Fecal}}{\text{Intake}}\right) \times 100$$

where:

$$\text{Intake} = \text{DMI (kg/d)} \times \text{dietary nutrient concentration (\% DM)}$$

$$\text{Fecal} = \text{Fecal production (kg DM/d)} \times \text{fecal nutrient concentration (\% DM)}$$

Statistics

All data were analyzed as a replicated Latin square design using the mixed procedure of SAS (SAS Inst. Inc., Cary, NC). The model included fixed effects of period, dietary treatment, and the random effects of square and steer within square. Contrast statements were used to test the linear and quadratic effects of the F:C. The effects were considered significant at *P*-value of ≤0.05, with tendencies declared at *P*-values between 0.05 and 0.10. When both linear and quadratic contrasts had a *P*-value of < 0.05, the higher-order contrast (quadratic) was typically presented.

Results

DMI tended to increase linearly (Table 2; *P* = 0.06) as the F:C decreased. Consequently, GE intake (Mcal) also increased linearly (*P* = 0.04) as the concentration of DRC in the diet increased. Fecal energy (**FE**) loss expressed as Mcal (*P* = 0.02) or as a proportion of GE intake (*P* < 0.01) decreased linearly as F:C decreased. The DE of the diets expressed as Mcal or Mcal/kg increased linearly (*P* < 0.01). UE loss (Mcal or as % of GE or DE intake) decreased linearly (*P* ≤ 0.04) as the proportion of forage decreased and concentrate increased in the diet. Methane energy loss in Mcal (*P* = 0.01) and as a proportion of GE or DE intake responded quadratically (*P* < 0.01) increasing from HF:C to IF:C, then decreasing thereafter. As F:C decreased, ME intake (Mcal) increased linearly (*P* < 0.01), but ME density of the diet (Mcal/kg DM) responded quadratically, where ME concentration was similar for HF:C, IF:C, and EF:C but increased thereafter as F:C ratio decreased. Conversion efficiency of DE to ME increased quadratically (*P* < 0.01) as the F:C decreased, ranging from 85.8 to 91.9. HP (Mcal) increased linearly (*P* = 0.04) as F:C decreased in the diet but was not different as a proportion of GE intake (*P* = 0.22). Megacalories of RE increased linearly (*P* < 0.01) as F:C decreased, while RE as a proportion of GE intake responded quadratically (*P* = 0.03) in that it decreased from HF:C to IF:C and then increased at an increasing rate for each dietary treatment thereafter.

Intake of N increased linearly (*P* = 0.01; Table 3) as F:C decreased. Nitrogen excreted in the feces and total grams of N excreted responded quadratically (*P* < 0.01) increasing from HF:C to EF:C then decreasing thereafter, whereas N excreted in the urine increased linearly (*P* < 0.01) as F:C decreased. As a proportion of total N excretion, fecal N excretion linearly decreased (*P* < 0.01), whereas urine excretion linearly increased (*P* < 0.01) as F:C decreased. When expressed as a proportion of total N intake, fecal N excretion responded in a quadratic manner (*P* < 0.01), remaining constant from HF:C to EF:C, and decreasing for each dietary treatment thereafter. Conversely, the

Table 2. Energy partitioning in growing beef steers fed diets of varying F:C at ad libitum intake

	Treatment[1]						P-value	
Item	HF:C	IF:C	EF:C	LF:C	VLF:C	SEM[2]	Linear	Quadratic
DMI, g	7,543	8,045	8,649	7,777	8,522	423.3	0.06	0.25
GEI, Mcal	31.9	34.0	36.9	32.9	36.6	1.84	0.04	0.29
FE, Mcal	11.8	12.4	12.5	10.4	9.7	0.89	0.02	0.06
FE loss, % of GEI	36.3	36.2	34.0	30.8	26.8	1.72	<0.01	0.09
DE, Mcal	20.2	21.7	24.3	22.6	26.8	1.34	<0.01	0.81
DE, Mcal/kg	2.67	2.69	2.80	2.90	3.15	0.07	<0.01	0.07
UE, Mcal	0.90	0.88	0.90	0.82	0.78	0.052	0.04	0.54
UE loss, % of GEI	2.9	2.6	2.5	2.6	2.2	0.20	0.03	0.98
UE loss, % of DE	4.5	4.1	3.8	3.7	3.0	0.24	<0.01	0.63
Methane energy, Mcal	1.7	2.3	2.3	1.8	1.3	0.19	0.03	<0.01
Methane energy loss, % of GEI	5.2	6.5	6.3	5.2	3.7	0.44	<0.01	<0.01
Methane energy loss, % of DE	8.1	10.4	9.5	7.6	5.1	0.65	<0.01	<0.01
ME, Mcal	17.6	18.6	21.1	20.1	24.7	1.26	<0.01	0.24
ME, Mcal/kg	2.33	2.31	2.43	2.58	2.89	0.07	<0.01	<0.01
ME:DE	0.87	0.86	0.87	0.89	0.92	0.724	<0.01	<0.01
HP, Mcal	15.0	16.4	17.3	16.7	17.7	0.97	0.04	0.44
HP, % of GEI	46.9	47.4	48.6	51.1	49.2	2.51	0.22	0.80
RE, Mcal	2.7	2.5	3.6	3.5	6.8	1.02	<0.01	0.06
RE, % of GEI	8.4	7.2	8.4	10.2	18.0	2.75	<0.01	0.03

[1]DRC replaced corn silage and alfalfa hay at 0% (HF:C), 22.5% (IF:C), 45% (EF:C), 67.5% (LF:C), and 83.8% (VLF:C) of dietary DM.
[2]Pooled standard error of the least-squares mean (*n* = 10 except in period 3 *n* = 9).

proportion of N excretion in the urine was not different across treatments ($P \geq 0.27$). Apparent grams of N digested increased linearly as the proportion of DRC increased in the diet ($P < 0.01$), whereas apparent N digestibility responded quadratically ($P < 0.01$). Additionally, grams of N retained tended to increase linearly ($P = 0.09$) as the F:C decreased.

DM digestibility (Table 4) increased linearly as F:C decreased ($P < 0.01$). Intake of OM increased linearly, and fecal OM excretion decreased linearly ($P = 0.01$) as the F:C decreased ($P = 0.01$), such that grams of OM digested and OM digestibility as a proportion of OM intake increased linearly ($P < 0.01$). Intake of NDF responded quadratically in that it increased from HF:C to IF:C and then decreased for each treatment thereafter ($P = 0.01$). Fecal excretion of NDF linearly decreased ($P < 0.01$), and there was no difference in grams of NDF digested across treatments ($P = 0.44$). As a proportion of NDF intake, NDF digestibility increased linearly as F:C decreased ($P < 0.01$). Intake of ADF and fecal ADF excretion responded quadratically ($P \leq 0.03$), not differing from HF:C to EF:C but decreasing thereafter as F:C decreased. Grams of ADF digested and ADF digestibility as a proportion of ADF intake responded quadratically ($P < 0.01$) increasing from HF:C to EF:C, then decreasing thereafter. Starch intake responded quadratically ($P < 0.01$) with modest increases from HF:C to EF:C, but increasing from LF:C to VLF:C. Fecal excretion of starch

Table 3. Nitrogen balance in growing beef steers fed diets of varying F:C at ad libitum intake

	Treatment[1]						P-value	
Item	HF:C	IF:C	EF:C	LF:C	VLF:C	SEM[2]	Linear	Quadratic
N intake, g/d	146.1	163.1	174.7	160.4	170.7	8.84	0.01	0.06
N excretion, g/d								
Feces	67.7	73.7	80.8	64.1	58.4	4.13	<0.01	<0.01
Urine	65.9	80.3	83.0	82.7	83.7	5.56	0.01	0.09
Total	133.6	154.5	163.4	147.2	141.7	7.57	0.48	<0.01
N excretion, % of total N excretion								
Feces	53.2	48.8	49.6	44.9	41.3	2.71	<0.01	0.57
Urine	46.9	51.1	50.3	55.1	58.7	2.71	<0.01	0.57
N excretion, % of total N intake								
Feces	46.5	45.8	46.5	40.2	34.3	1.65	<0.01	<0.01
Urine	45.5	48.7	48.1	52.4	50.2	4.04	0.27	0.76
Apparent N digested, g/d	78.3	89.5	93.9	96.4	112.2	6.17	<0.01	0.62
Apparent N digested, % of N intake	53.6	54.8	53.7	60.1	65.7	1.63	0.03	<0.01
N retained, g/d	12.3	9.6	10.3	14.2	28.0	7.04	0.09	0.11

[1]DRC replaced corn silage and alfalfa hay at 0% (HF:C), 22.5% (IF:C), 45% (EF:C), 67.5% (LF:C), and 83.8% (VLF:C) of dietary DM.
[2]Pooled standard error of the least-squares mean ($n = 10$ except in period 3 $n = 9$).

Table 4. Diet digestibility in growing beef steers fed diets of varying F:C at ad libitum intake

	Treatment[1]						P-value	
Item	HF:C	IF:C	EF:C	LF:C	VLF:C	SEM[2]	Linear	Quadratic
Dry matter digestibility, %	61.8	62.7	65.3	69.3	73.6	1.54	<0.01	0.06
OM								
Intake, g/d	6,888.5	7,321.2	7,943.6	7,206.5	8,050.9	397.3	0.01	0.47
Fecal excretion, g/d	2,376.9	2,519.7	2,500.7	2,065.8	1,916.2	182.9	0.01	0.07
Digested, g/d	4,514.1	4,824.7	5,421.8	5,163.9	6,113.5	294.4	<0.01	0.55
Digestibility, % of intake	66.0	65.8	68.4	72.3	75.7	1.64	<0.01	0.08
NDF								
Intake, g/d	3,047.6	3,156.2	3,020.2	2,192.6	2,362.9	152.50	<0.01	0.01
Fecal excretion, g/d	1,856.6	1,699.8	1,524.8	1,098.3	890.1	91.05	<0.01	0.02
Digested, g/d	1,197.0	1,462.4	1,494.5	1,100.3	1,471.8	93.84	0.44	0.13
Digestibility, % of intake	40.0	46.0	49.9	50.2	62.7	1.88	<0.01	0.10
ADF								
Intake, g/d	1,890.3	1,866.6	1,815.8	1,104.7	794.5	91.93	<0.01	<0.01
Fecal excretion, g/d	1,260.5	1,118.3	952.6	679.0	494.5	56.97	<0.01	0.03
Digested, g/d	640.2	758.3	862.1	435.6	298.9	60.67	<0.01	<0.01
Digestibility, % of intake	33.3	40.0	47.1	38.9	35.3	2.94	0.58	<0.01
Starch								
Intake, g/d	1,568.0	1,976.7	2,287.3	2,863.4	3,852.5	194.99	<0.01	0.01
Fecal excretion, g/d	1.1	109.3	161.9	221.7	256.0	35.79	<0.01	0.40
Digested, g/d	1,564.6	1,867.5	2,123.3	2,641.8	3,594.3	190.19	<0.01	<0.01
Digestibility, % of intake	99.7	94.4	92.7	92.1	93.3	1.28	<0.01	<0.01

[1]DRC replaced corn silage and alfalfa hay at 0% (HF:C), 22.5% (IF:C), 45% (EF:C), 67.5% (LF:C), and 83.8% (VLF:C) of dietary DM.
[2]Pooled standard error of the least-squares mean ($n = 10$ except in period 3 $n = 9$).

increased linearly ($P < 0.01$) as F:C decreased, whereas grams of starch digested and digestibility as a proportion of starch intake responded quadratically ($P < 0.01$).

Discussion

Based on diet formulation, no difference in GE among the treatment diets was anticipated. Diets contained comparable proportions of protein and total carbohydrates, while the type of carbohydrates (namely starch and cellulose), although inconsequential to the GE content, varied. As corn silage and alfalfa hay were replaced with DRC to achieve different F:C ratios, NDF and ADF decreased, whilst starch increased.

It is generally accepted that decreasing the dietary roughage level decreases DMI in cattle fed high-concentrate diets (Galyean and Defoor, 2003), accordingly reductions in the intake of the LF:C and VLF:C treatments in the present experiment were expected. Gill et al. (1981) evaluated the effects of five roughage levels (8%, 12%, 16%, 20%, or 24% DM) in diets based on steam-flaked or high-moisture corn and found that decreasing roughage level decreased DMI, presumably because cattle eat to a constant energy intake and grain is more digestible and results in a lesser enteric CH_4 loss than forage. The study reported that adding roughage (alfalfa hay and corn silage) decreased the ME values of the diet by 0.35% for every 1 percent added roughage (Gill et al., 1981). Lovett et al. (2003) used individually fed heifers to evaluate the effects of three F:C (65:35, 40:60, or 10:90) on animal performance and reported that as F:C decreased, both DMI and GE intake increased quadratically such that DMI and GE intake increased up to the 40:60 treatment and then decreased thereafter. Arelovich et al. (2008) compiled published literature for dairy (18 experiments) and beef cattle (11 experiments) to evaluate the relationship between dietary NDF and DMI. Total dietary NDF for the dairy cattle database ranged from 22.5% to 45.8% and 7.5% to 35.3% for the beef database. It was reported that DMI increased as NDF concentration decreased in the dairy database, while in the beef database, DMI decreased with decreased dietary NDF. This disparity between the dairy and beef database is likely due to the differences in sources of NDF (e.g., NDF supplied by forages vs. NDF supplied by other ingredients) and the greater starch content, and thereby greater fermentability, of the beef diets. In the present study, DMI tended to increase linearly as the F:C ratio (and dietary NDF concentration) decreased. A possible explanation is an increase in passage rate as F:C decreased, up to our 45% concentrate treatment (EF:C); however, in the LF:C and VLF:C treatments, the intake was likely controlled by chemostatic factors and not physical fill (Galyean and DeFoor, 2003; Allen et al., 2009). For the HF:C, IF:C, and EF:C diets that ranged in forage concentration from 92% to 47% of DM, DMI was likely limited by gut fill. A linear increase in GE intake can be attributed to the DMI response, as GE of the diets were not different.

FE loss is driven by the digestibility of the diet. It is plausible that FE was derived primarily from fiber. The dietary concentration of ADF is correlated with digestibility (Van Soest et al., 1991). As F:C decreased, the amount of ADF in the diet, and thus in the feces, decreased, such that FE losses were reduced, even though ADF digestibility responded quadratically. Thus, the linear decrease in FE excretion was caused by the decreased concentration of fiber (NDF and ADF) in the feces as the F:C ratio decreased. Additionally, the decrease in FE loss as a proportion of GE intake is due to the increase in DM digestibility as the F:C decreased because, generally, concentrate is more digestible than forage. Hales et al. (2014) evaluated the effects of four levels of alfalfa hay inclusion (2%, 6%, 10%, or 14%) in DRC-based diets containing wet distillers' grains with solubles on energy balance and nutrient digestibility. It was noted that as a proportion of gross energy intake (**GEI**), as alfalfa hay increased FE loss increased (Hales et al., 2014). In that study, alfalfa hay replaced DRC, so the increase in FE resulted from alfalfa hay replacing starch in the diet. Zinn and Plascencia (1996) used four ruminally and duodenally cannulated Holstein steer calves in a 4 × 4 Latin square design to determine the effects of two supplemental fat levels and two forage levels (10% or 30% alfalfa hay) on characteristics of digestion. Decreasing forage (alfalfa) from 30% to 10% of diet DM reduced FE losses and, correspondingly, increased DE.

Decreasing F:C resulted in modest, but detectable, linear decreases in total UE loss (Mcal) and UE as a proportion of both GE and DE intake. UE is primarily derived from urinary N constituents, including urea, purine derivatives, creatine and creatinine, and hippuric acid (Dijkstra et al., 2013). Both N intake and N excreted in the urine (g/d) increased linearly as the F:C decreased in the diet. Increases in N intake resulted primarily from increases in DMI. However, urinary N excreted as a proportion of total N intake was not affected by F:C, such that UE losses expressed per unit of urinary N also decreased as F:C decreased. This changing ratio suggests that differences in UE losses may be due to changes in the relative proportion of N constituents as F:C decreased. Specifically, the proportion of hippuric acid excreted in the urine may have decreased as the F:C decreased. The formation of hippuric acid in the liver is driven by the dietary concentration of degradable phenolic acids, which would be higher in forages than concentrates (Spek et al., 2013). A decrease in hippuric acid excretion could result in a decrease in UE as the heat of combustion of hippuric acid is higher than that of urea (Blaxter et al., 1966). While these changes may be quantitatively small, UE accounts for approximately one-third to one-half of the energy losses from DE to ME. Variation in UE constituents of the magnitude observed in this study may account for differences in ME to DE of 0.02 units, that is, from 0.87 to 0.89.

In contrast to the results of the present study, Hales et al. (2014) reported no differences in UE loss as alfalfa hay decreased from 14% to 2% of the dietary DM in finishing beef steers; however, the metabolizable protein balance was greater in that study because all diets included 25% wet distillers' grains plus solubles. Additionally, in the present study, the range of forage inclusion varied from 92% to 8%; in the previous study, the response surface may not have been sufficient to detect an effect. Reynolds et al. (1991) fed diets containing either 75% alfalfa hay or 75% concentrate (primarily ground corn) and found that UE losses were lower when heifers were fed the 75% concentrate vs. the 75% alfalfa hay diet, supporting the observation that diet type may alter UE losses and thus affect the conversion of DE to ME.

Methane is produced as a byproduct of ruminal carbohydrate fermentation (Mitsumori and Sun, 2008; Hook et al., 2010). Methanogens utilize hydrogen, carbon dioxide, formate, and acetate to produce methane (Qiao et al., 2014). Fermentation of structural carbohydrates to acetate yields substrates for methane production. Reducing forage and increasing concentrate in the diet decrease the acetate-to-propionate ratio (not measured in the present experiment) and reducing the substrates available for methanogenesis (Yan et al., 2000; Mitsumori and Sun, 2008). Similarly, it is well established that low pH in the rumen depresses methanogenesis (Van Kessel and Russell, 1996), and the pH, although not measured, was likely lesser in the cattle fed diets greater in concentrate than forage.

In the present study, methane energy losses responded quadratically. Except for the HF:C treatment, methane energy losses per unit of GE intake decreased at an increasing rate as the F:C decreased. Lovett et al. (2003) fed three F:C ratios (65:35, 40:60, or 10:90) and reported a quadratic response in liters of methane emitted each day, which increased from the 65:35 to the 40:60 treatment and then decreased for the 10:90 treatment, which agrees with the results of the present study. Moss et al. (1995) using wethers determined the effects of the F:C ratio on methane production, with grass silage and rolled barley diets fed at 1.5-times maintenance. Diets represented four F:C ratios (100:0, 75:25, 50:50, or 25:75). They observed a linear decrease in OM intake and a quadratic response in the volume of methane produced, which increased from the 100:0 to the 75:25 F:C ratio and then decreased thereafter. As in the current study, decreasing F:C ratio had a quadratic effect on energy lost as methane, with initial concentrate additions increasing the methane production and subsequent additions reducing methane losses as a proportion of GEI. Lower DMI observed with the HF:C treatment in combination with the lower OM digestibility (and presumably ruminal fermentation rate) may have been sufficient to limit the methane production relative to other treatments, in spite of the higher forage content of that diet. Overall, these results suggest that the changes in methane energy losses across diets are sufficient to have a substantial impact on the conversion of DE to ME.

The quadratic response in dietary ME (Mcal/kg) with decreasing F:C is a result of the linear decrease in UE and the quadratic response in methane energy losses. Zinn and Plascencia (1996) also reported that decreasing forage level in the diet from 30% to 10% alfalfa hay (similar to the LF:C to VLF:C treatments in the present study) increased dietary ME in Mcal/kg of DM. In the present study, the observed ME in Mcal/kg is 5% to 12% greater than would be predicted by the equation ME = 0.82 DE. ME has been calculated from DE for many years using a factor of 0.82 and was reported in *The nutrient requirements of farm livestock no. 2 ruminants* (ARC, 1965). The studies used to derive the 0.82 factor were predominantly conducted near a maintenance level of DMI for cattle fed high-forage diets. Subsequently, DE × 0.82 was incorporated into the fifth, sixth, and seventh revised editions of the Nutrient Requirements of Beef Cattle (NRC, 1976, 1984, and 2000, respectively). The seventh revised edition of the NRC (2000) cautioned that the ratio can vary considerably depending on intake, age of the animal, and feed source. Likewise, in the eighth revised edition of the Nutrient Requirements of Beef Cattle (NASEM, 2016), the authors note that recent data indicate a variable relationship in ME:DE ranging from 0.82 to greater than 0.95 and is dependent on cattle age, intake level, and composition of the diet (Vermorel and Bickel, 1980; Hales et al., 2012, 2013, 2014, 2015a, 2015b, 2017).

Galyean et al. (2016) compiled data consisting of 87 treatment means from 23 published papers utilizing beef or dairy animals in which the direct measurements of fecal, urinary, and methane losses were made with respiration calorimetry. The linear regression equation developed by Galyean et al. (2016) was ME = 0.9611 × DE – 0.2999 (r^2 = 0.986).

In the present experiment, the quadratic response in the conversion of dietary DE to ME results from the quadratic response in methane energy loss as a percentage of both GE and DE intake. In combination with the linear decrease in urine energy loss as a percentage of GE or DE intake, these results support the hypothesis that the conversion of DE to ME is not constant across diets and is a function of dietary components.

While the current experiment supports previous research that the ME:DE ratio is non-constant, the authors recognize the difficulty in using a non-constant conversion factor, especially in calculating the net energy for maintenance and net energy for gain of feedstuffs from ME using cubic equations published by Garrett (1980). Future research is warranted to further develop an accurate prediction of ME from DE across a wide variety of diets, from high forage to high concentrate, fed to cattle today.

Monensin was used in the present experiment and other experiments where an ME:DE relationship > 0.82 was noted in cattle fed concentrate-based diets (Hales et al., 2012, 2013, 2014, 2015a, 2015b, 2017). While the ionophore monensin may decrease enteric methane production (Russell and Strobel, 1989), it is unlikely monensin contributes to an increased ME:DE ratio. Blaxter and Wainman (1964) used three mature wethers and three mature steers and fed mixtures of poor-quality hay and flaked maize that consisted of on a DM basis: 1) 100% hay, 2) 80% hay and 20% maize, 3) 60% hay and 40% maize, 4) 40% hay and 60% maize, 5) 20% hay and 80% maize, and 6) 100% maize. None of the diets used by Blaxter and Wainmann (1964) included monensin and the ME:DE ratio in the 100% flaked maize diet at two-times maintenance was 0.92. This result is similar to the ratio observed in the VLF:C diet in the present experiment and similar to other ME:DE ratios noted in high-concentrate diets including monensin (Hales et al., 2012, 2013, 2014, 2015a, 2015b, 2017).

Hales (2019) presented a quadratic equation for the prediction of ME from DE using 234 individual animal observations collected at Meat Animal Research Center during respiration calorimetry experiments where ME = –0.057 × DE^2 + 1.3764 × DE – 0.9483. The equation was reported to work well in high-concentrate diets but was not recommended for use in high-forage diets. A maximum biological threshold for the conversion of DE to ME was noted to be between 3.43 and 3.65 Mcal ME/kg of intake (Hales, 2019). The ME in the present experiment for all dietary treatments was below this range in values, even the VLF:C diet that contained the least forage and the most DRC. The lesser ME in the present experiment than previously reported when measured using respiration calorimetry (Hales et al., 2012, 2013, 2014, 2015a, 2015b) is likely because of decreased DM digestibility of the present diets, especially the HF:C, IF:C, and EF:C diets. Similarly, the ME noted in the VLF:C diet was lesser than ME measured in similar high-concentrate diets, likely because of the lack of added fat or the use of a lesser processed corn (dry rolled vs. steam flaked).

The ME:DE ratio in the VLF:C diet was 0.92, which is still less than the 0.94 or the theoretical maximum proposed by Hales (2019). Cattle fed high-concentrate diets eat to maintain constant energy intake, and the relationship between average daily gain and the gain:feed ratio is quadratic (Krehbiel et al., 2006). Additionally, gain:feed is maximized from 3.46 to 3.65 Mcal ME/kg of DMI. The dietary ME in the current experiment is less than Krehbiel et al. (2006) and Hales (2019) recommended to maximize gain:feed or the conversion of DE to ME, respectively.

HP increased linearly and mirrored GE intake, which is reasonable as CO_2 is the largest coefficient in the Brouwer (1965) equation used to estimate HP. DMI is generally correlated with the amount of enteric CO_2 produced as it is a byproduct of ruminal fermentation and basal metabolism. In fed animals, HP is comprised of basal metabolism, the heat of activity associated with obtaining feed, and heat increment (Lofgreen and Garrett, 1968; NASEM, 2016). Assuming that basal metabolism and heat of activity with obtaining feed were equivalent for all treatments, primarily because all cattle were in stanchions during the

collection periods, differences in heat increment would drive treatment differences in HP. The linear increase in RE followed the increase in ME above maintenance (i.e., heat energy), which was driven by the increase in DE resulting from increased DMI, decreased FE losses, and increased ME:DE conversion.

Differences in N intake were not anticipated as the experimental diets were formulated to have similar CP concentrations. Therefore, the increase in N intake as F:C decreased was because of the effects of the dietary treatments on DMI. The quadratic effect on grams of N excreted in the feces may be the collective result of increased apparent digestibility of the diets, a reduction in microbial crude protein (**MCP**) synthesis, and hindgut fermentation occurring specifically in the HF:C, IF:C, and EF:C treatments. Strobel and Russell (1986) demonstrated a significant decline in the efficiency of MCP synthesis at pH values less than 6.0 often observed when feeding high-concentrate diets. Cattle in the present experiment were adapted to the experimental diets for 23 d prior to the collection period, and the decline in fecal N for the LF:C and VLF:C treatments may be the result of depressed MCP synthesis as the proportions of grain in these diets would lead to a sustained pH level of 6.0 or less; however, pH was not measured in the present study. Additionally, the decrease in NDF and ADF intake coupled with the increase in starch intake as the F:C decreased reduced the amount of fermentable carbohydrate reaching the hindgut, lowering fecal N excretion specifically for the LF:C and VLF:C treatments. Furthermore, if MCP production was reduced due to low pH or production of ammonia from ruminal degradable protein exceeded microbial requirements, it is plausible that ammonia was absorbed across the rumen wall, converted to urea in the liver, and excreted in the urine causing the observed increase in urinary N excretion. Castillo et al. (2001) supplemented grass silage-based diets with concentrates of divergent starch degradability and found that N excreted in the urine (grams per day) was greatest for the high-degradable starch diet. The increase in apparent N digested is a result of the increase in N intake combined with the decrease in fecal N excreted.

It has been documented that different carbohydrate sources can cause variation in the distribution of excreted N between feces and urine. Bierman et al. (1999) evaluated the effect of level and source of dietary fiber on N and OM excretion. The formulated diets contained 28.4%, 13.6%, or 9.9% NDF either from wet corn gluten feed, corn silage and alfalfa hay, or DRC, respectively. These diets are most similar to the EF:C, LF:C, and VLF:C used in the present experiment. As in our study, when expressed as a proportion of total N excretion, fecal N excretion decreased, and urinary N excretion increased (numerically) as the proportion of fiber in the diet decreased.

In the present study, all experimental diets were of similar OM content; therefore, the increase in OM intake is a result of the dietary effects on DMI. As in our study, Reynolds et al. (1991) noted that DM, OM, and NDF total tract digestibility increased in heifers fed a 75% concentrate diet compared with a 75% alfalfa hay diet, which is because of a greater total digestible nutrient content of ground corn than alfalfa hay. Crawford et al. (2008) also noted an increase in NDF digestibility as alfalfa hay inclusion decreased from 13.5% to 4.5% of DM in high moisture and DRC-based diets. Conversely, Hales et al. (2014) noted no difference in NDF digestibility, as a percent of GE intake, when alfalfa hay was decreased in the diet from 14% to 2% of DM replacing DRC. Cole et al. (1976) reported that when NDF was increased in the diet in the form of dietary forage, cellulose digestion typically increased. The quadratic response in ADF total tract digestibility is likely a result of negative associative effects. It is generally accepted that as the proportion of concentrate in the diet increases, specifically to levels seen in the LF:C and VLF:C treatments, negative associative effects cause a decrease in fiber digestibility due to the effects of low pH levels on the fibrolytic bacterial population. Ruminal microorganisms on the higher forage diets (HF:C and IF:C) were most likely more fibrolytic bacteria, such as *Butyrivibrio fibrisolvens* and *Fibrobacter succinogenes*, which cannot tolerate a ruminal pH below 5.7 (Russell and Wilson, 1996). *Streptococcus bovis* and *Selenomonas ruminantium*, which are starch-utilizing bacteria, would have predominated in the VLF:C diets.

By design, starch intake increased linearly because DRC replaced forage in the diets. However, as the F:C ratio decreased, starch digestibility as a proportion of total starch intake decreased. A potential explanation for the decrease in starch digestibility could be a shift in the site of starch fermentation from the rumen to the small intestine. Shifts in the site of digestion to the small intestine are often accompanied by a decrease in the overall starch digestibility (Huntington et al., 2006). Another possibility for a decrease in starch digestibility as the F:C ratio decreased could be an increase in the rate of passage (not measured) as concentrate grain replaced forage.

In conclusion, many of the changes across the range of diets fed in the present experiment were caused by replacing moderately digestible substrates, corn silage and alfalfa hay, with a more digestible DRC. The decrease in the F:C ratio caused an increase in energy intake, a decrease in fecal and urine energy loss, and an increase in methane at a decreasing rate. Similarly, ME was increased as the F:C ratio decreased, and the ME:DE ratio also increased as DRC replaced corn silage and alfalfa hay.

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Conflict of interest statement

The authors have no conflict of interest.

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