Relationship between residual feed intake and digestibility for lactating Holstein cows fed high and low starch diets

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ABSTRACT

We determined if differences in digestibility among cows explained variation in residual feed intake (RFI) in 4 crossover design experiments. Lactating Holstein cows ($n = 109$; 120 ± 30 d in milk; mean $\pm$ SD) were fed diets high (HS) or low (LS) in starch. The HS diets were 30% ($\pm 1.8\%$) starch and 27% ($\pm 1.2\%$) neutral detergent fiber (NDF); LS diets were 14% ($\pm 2.2\%$) starch and 40% ($\pm 5.3\%$) NDF. Each experiment consisted of two 28-d treatment periods, with apparent total-tract digestibility measured using indigestible NDF as an internal marker during the last 5 d of each period. Individual cow dry matter (DM) intake and milk yield were recorded daily, body weight was measured 3 to 5 times per week, and milk components were analyzed 2 d/wk. Individual DM intake was regressed on milk energy output, metabolic body weight, body energy gain, and fixed effects of parity, experiment, cohort (a group of cows that received treatments in the same sequence) nested within experiment, and diet nested within cohort and experiment, with the residual being RFI. High RFI cows ate more than expected and were deemed less efficient. Residual feed intake correlated negatively with digestibility of starch for both HS ($r = -0.31$) and LS ($r = -0.23$) diets, and with digestibilities of DM ($r = -0.30$) and NDF ($r = -0.23$) for LS diets but was not correlated with DM or NDF digestibility for HS diets. For each cohort within an experiment, cows were classified as high RFI (HRFI; >0.5 SD), medium RFI (MRFI; ± 0.5 SD), and low RFI (LRFI; <-0.5 SD). Digestibility of DM was similar ($\sim 66\%$) among HRFI and LRFI for HS diets but greater for LRFI when fed LS diets (64 vs. 62%). For LS diets, digestibility of DM could account for up to 31% of the differences among HRFI and LRFI for apparent diet energy density, as determined from individual cow performance, indicating that digestibility explains some of the between-animal differences for the ability to convert gross energy into

net energy. Some of the differences in digestibility between HRFI and LRFI were expected because cows with high RFI eat at a greater multiple of maintenance, and greater intake is associated with increased passage rate and digestibility depression. Based on these data, we conclude that a cow's digestive ability explains none of the variation in RFI for cows eating high starch diets but 9 to 31% of the variation in RFI when cows are fed low starch diets. Perhaps differences in other metabolic processes, such as tissue turnover, heat production, or others related to maintenance, can account for more variation in RFI than digestibility.

Key words: digestibility depression, feed efficiency, dry matter intake

INTRODUCTION

Residual feed intake (RFI) has been used to assess feed efficiency in beef cattle (Richardson et al., 2004; Nkrumah et al., 2006; Lawrence et al., 2011), swine (Harris et al., 2012), poultry (Luiting et al., 1994; Mignon-Grasteau et al., 2004), and dairy cattle (Rius et al., 2012; Tempelman et al., 2015; VandeHaar et al., 2016). Residual feed intake is a tool used to evaluate feed efficiency and is the difference between what an animal consumes and what it is predicted to consume (Koch et al., 1963); it quantifies feed efficiency within a production level so it is independent of the dilution of maintenance as determined on a requirement basis. Within a given production level, cows with low RFI are deemed more efficient because they eat less than contemporaries. Low RFI cows are able to convert gross energy to net energy more efficiently because they have improved digestive and metabolic efficiencies, or have lower maintenance requirements than expected for a given BW.

The relative contributions of the specific biological mechanisms that explain differences in RFI among animals are not clear. For finishing beef steers, Richardson and Herd (2004) hypothesized that variation in RFI was due to feeding patterns (2%), activity level (10%), protein turnover and tissue metabolism (37%), body composition (5%), heat increment of feeding (9%),

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digestibility (10%), and other undefined metabolic processes (27%). Total-tract digestibility is a reflection of both diet digestibility and the digestive ability of the animal. Animals with greater digestive ability lose less energy in feces and are expected to be more energetically efficient than contemporaries consuming the same diet. Previous studies in dairy heifers (Rius et al., 2012) and beef steers (Richardson et al., 1996; Nkrumah et al., 2006) have demonstrated that animals classified as low RFI also had improved digestibility. Additionally, broilers selected divergently for digestive efficiency differed in RFI, with broilers of the high digestive efficiency line having lower RFI than birds of the low digestive efficiency line (Mignon-Grasteau et al., 2004).

Differences in digestibility between high and low RFI animals may be dependent on the type of diet the animal consumes. Rougière et al. (2009) studied lines of broilers selected for digestive efficiency, which were also divergent for RFI, and determined that feeding diets of coarse particle size that increased gut retention time resulted in improved digestibility for the low but not the high digestive efficiency line. Hernandez-Sanabria et al. (2012) showed that the proportion of *Eubacterium* sp. in rumen fluid samples differed between high and low RFI cattle when a 100% concentrate diet was fed, but not when an 80% concentrate diet was fed. In contrast, Carberry et al. (2012) observed stronger relationships between RFI and rumen microbial population proportions when cattle were fed a high forage (100%) compared with a low forage (30%) diet. Both of these studies suggest that the relationship between RFI and rumen microbial communities, and thus ruminal digestion, may be affected by the type of diet fed.

We hypothesized that (1) digestibility would account for some of the variation in RFI and that low RFI cows would have improved digestibility compared with high RFI cows, and (2) this relationship would differ for diets high compared with low in starch. Our objective in the present study was to determine if digestibility accounts for variation in RFI in lactating dairy cows fed high (**HS**) and low (**LS**) starch diets.

MATERIALS AND METHODS

Cows, Experimental Design, and Diets

Experimental procedures were approved by the Institutional Animal Care and Use Committee of Michigan State University. Data from 4 separate crossover experiments, described by Potts et al. (2015), were used to determine the relationship between RFI and digestibility. Lactating Holstein cows were fed diets that differed in starch concentration in experiments 1 ($n = 32$), 2 ($n = 25$), 3 ($n = 32$), and 4 ($n = 20$). Treat-

ment effects for experiments 1 and 3 are reported in separate publications (Boerman et al., 2015a,b). Cows ($n = 109$) averaged (mean $\pm$ SD) 120 ± 30 DIM, 42 ± 9 kg of milk/d, and 665 ± 77 kg of BW at the beginning of the experiments. Each experiment consisted of two 28-d treatment periods during which HS or LS diets were fed. Prior to the first treatment period in each experiment, cows were fed a common diet for 14, 5, 7, and 3 d for experiments 1, 2, 3, and 4, respectively. Cows were blocked based on pre-treatment-period milk yield and parity and randomly assigned to treatment sequence. Cows were housed in individual tie stalls and milked twice daily (0300 and 1430 h) in a milking parlor. Water was available ad libitum, and tie stalls were equipped with a double-cupped watering system to prevent contamination of feed with water and a front gate to prevent other cows from stealing feed during cow movements to and from the milking parlor.

During each experiment, cows were fed HS or LS diets (Table 1). On average, HS diets were 30% ($\pm 1.8\%$) starch and 27% ($\pm 1.2\%$) NDF, and contained 30 to 35% corn grain; LS diets were 14% ($\pm 2.2\%$) starch and 40% ($\pm 5.3\%$) NDF, with soybean hulls replacing a proportion of corn grain. In experiment 3, the LS diet also contained a fat supplement and more legume silage than HS. In experiments 2 and 4, LS diets contained less forage than HS. Diets were adjusted for changes in forage DM concentration twice weekly.

Data and Sample Collection

Cows were fed once daily at 1000 h (experiments 2 and 4) or 1200 h (experiments 1 and 3) for $>110\%$ of expected intake based on intake from the previous day, and orts were removed and weighed daily before feeding. Milk yield was recorded electronically at each milking and milk samples were obtained from 4 consecutive milkings per week. Milk samples were analyzed for fat, true protein, lactose, somatic cells, and milk urea nitrogen with infrared spectroscopy (AOAC, 1990; method 972.160) by Michigan DHIA (Universal Lab Services, Lansing, MI). Body weight for each cow was recorded 3 (experiments 2, 3, and 4) or 5 (experiment 1) times per week immediately after the morning milking. Body condition score was determined on a 5-point scale in 0.25-unit increments, where 1 = thin and 5 = fat, as described by Wildman et al. (1982), by 3 trained investigators and recorded for each cow at the beginning and end of each period.

Sampling procedures were the same for all 4 experiments. Samples of feces, orts, and feed ingredients were collected during the last 5 d of each treatment period to estimate nutrient digestibility. Samples of feces were collected every 15 h (2400, 0230, 0600, 0900, 1200, 1500,

Table 1. Composition of high (HS) and low (LS) starch diets fed during each experiment

Item	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	HS	LS	HS	LS	HS	LS	HS	LS
Ingredient, % of DM								
Corn silage	23.9	24.3	23.6	23.8	23.7	24.2	23.5	20.9
Legume silage	21.9	22.1	21.2	21.4	11.1	22.6	20.6	18.4
Wheat straw	4.97	5.04	5.19	—	3.79	1.94	4.82	—
Soybean hulls	—	28.9	—	30.5	—	10.6	—	32.1
Cottonseed, whole	—	—	—	—	7.45	9.07	—	9.22
Corn, ground	29.6	3.61	21.4	—	13.1	—	30.8	7.18
Corn, ground high moisture	—	—	8.28	8.16	21.5	11.0	—	—
Soybean meal, 48%	16.6	13.5	17.2	12.9	15.9	14.6	17.2	9.08
Fat supplement ¹	—	—	—	—	—	2.51	—	—
Vitamin and mineral ²	2.03	2.06	2.06	2.09	2.02	2.05	2.08	2.08
Limestone	0.50	—	0.50	—	0.75	0.76	0.52	—
Sodium bicarbonate	0.51	0.52	0.49	0.50	0.75	0.76	0.51	0.51
Dicalcium phosphate	—	0.25	0.18	0.50	—	—	—	0.51
Nutrient, ³ % of DM								
DM	53.9	53.6	55.9	55.7	55.8	51.7	49.5	52.2
NDF	27.2	43.9	25.9	39.4	25.1	32.8	27.6	44.2
Forage NDF	23.6	23.9	21.9	17.9	17.6	20.2	23.5	17.4
Starch	30.1	12.2	30.3	15.5	32.5	16.1	28.2	11.8
NFC ⁴	47.9	32.2	48.6	35.4	48.7	35.9	47.0	30.7
Soluble fiber ⁵	12.8	15.5	13.6	15.8	12.3	15.1	14.0	14.8
Sugar ⁶	1.08	0.57	0.92	0.24	1.06	0.79	1.09	0.81
CP	16.4	15.9	16.6	16.0	17.0	18.3	16.9	15.2
Ash	5.9	6.4	6.5	7.3	5.4	6.8	6.1	6.5
Ether extract	2.52	1.90	2.15	1.95	3.24	5.61	2.30	3.41
Organic acid ⁶	3.88	3.93	3.79	3.84	2.90	3.97	3.74	3.33
NDF:starch	0.90	3.60	0.85	2.54	0.77	2.04	0.98	3.75
NE _L , ⁷ Mcal/kg	1.62	1.56	1.68	1.62	1.80	1.75	1.72	1.62
GE, ⁸ Mcal/kg	4.20	4.16	4.16	4.11	4.26	4.34	4.19	4.21

¹Fat: 85% palmitic acid enriched free fatty acid supplement (BergaFat F-100, Berg and Schmidt America LLC, Libertyville, IL).

²Vitamin and mineral mix contained 34.1% dry ground shell corn, 25.6% white salt, 21.8% calcium carbonate, 9.1% Biofos (The Mosaic Co., Plymouth, MN), 3.9% magnesium oxide, 2% soybean oil, and <1% of each of the following: manganese sulfate, zinc sulfate, ferrous sulfate, copper sulfate, iodine, cobalt carbonate, vitamin E, vitamin A, vitamin D, and selenium.

³Nutrient composition was determined from feed ingredients sampled during the last 5 d of each 28-d experimental period.

⁴NFC calculated as $100 - (\text{NDF}\% + \text{CP}\% + \text{ash}\% + \text{fatty acid}\%)$ according to NRC (2001).

⁵Soluble fiber calculated as $\text{NFC}\% - (\text{starch}\% + \text{organic acid}\% + \text{sugar}\%)$.

⁶Estimated from Spartan Dairy Ration Evaluator (version 3.0, Michigan State University, East Lansing).

⁷Mean apparent net energy concentration of diets, based on average cow performance. For each diet, $\text{DietNE}_L = \frac{\text{MilkE} + 0.08 \times \text{MBW} + \Delta\text{BodyE}}{\text{DMI}}$ for all cows on the diet, where MilkE = milk energy output, MBW = metabolic BW, and ΔBodyE = body energy change.

⁸Gross energy concentration, calculated from nutrient profile of individual feed ingredients: 4.20 kcal/g of carbohydrate, 5.65 kcal/g of CP, 9.50 kcal/g of fatty acid (estimated as ether extract - 1; NRC, 2001), 3.95 kcal/g of sugar (Merrill and Watt, 1973).

1800, 2100 h) to obtain 8 samples per cow to represent every 3 h of a day to account for diurnal variation. Samples of diet ingredients (~0.5 kg) and orts from each cow (12.5% of the amount) were obtained each day during the 5-d collection periods. All samples were stored at -20°C until analysis.

Sample Analysis

Sample analyses were the same for all 4 experiments. For each experiment, diet ingredient and orts samples were composited by period. Diet ingredients, orts, and feces were dried in a forced-air oven (55°C for 72 h) before grinding through a Wiley mill (1-mm screen, Ar-

thur H. Thomas Co., Philadelphia, PA). Feces obtained from a cow during a period were composited on an equal DM basis. Samples of diet ingredients, orts, and feces were analyzed for CP, starch, NDF, indigestible NDF, and ash. Diet ingredients were also analyzed for ether extract, which was determined using a modified Soxhlet apparatus (AOAC, 1990). Crude protein was determined according to Hach et al. (1987). Starch was analyzed by an enzymatic method after gelatinization with sodium hydroxide (Karkalas, 1985). Subsequently, glucose concentration was determined via glucose oxidase method (Glucose kit #510, Sigma Chemical Co., St. Louis, MO) and absorbance was measured with a micro-plate reader (SpectraMax 190, Molecular De-

vices Corp., Sunnyvale, CA). Neutral detergent fiber and indigestible NDF were determined according to Mertens (2002) and Goering and Van Soest (1970), respectively. Indigestible NDF, which was used as an internal marker to estimate fecal output and nutrient digestibility (Cochran et al., 1986), was estimated as NDF residue after 240 h of in vitro fermentation (Goering and VanSoest, 1970); flasks were re-inoculated at 120 h to ensure a viable microbial population. Rumen fluid for the in vitro incubations was collected from a nonpregnant dry cow fed only dry hay. Ash was determined after 5 h combustion at 500°C. Concentrations of nutrients are expressed as a percentage of DM.

Calculations

Milk energy output (**MilkE**; Mcal/d) for a cow was estimated according to NRC (2001; Equation 2-15) with the adjusted coefficient for true protein instead of CP:

$$\text{MilkE} = 9.29 \times \text{fat (kg)} + 5.63 \times \text{true protein (kg)} + 3.95 \times \text{lactose (kg)},$$

where each component is based on the average output of a cow during a 28-d treatment period. Metabolic BW for a cow (**MBW**; kg^{0.75}) was estimated as $\text{BW}^{0.75}$, where BW is the mean BW for the cow during a specified treatment period. Body weight change (**ΔBW**; kg/d) was calculated for individual cows within a period by regressing BW (20 records per cow per period in experiment 1 and 12 records per cow per period in experiments 2, 3, and 4) against time. For each cow, BW records that were >3.5 SD from this regression line were identified as outliers and removed; this process was repeated twice. The slope of the third regression for each individual cow within a period was used to define her ΔBW within that period. In total, 2, 2, 8, and 3 BW measurements (all from different cows) were removed during this process for experiments 1, 2, 3, and 4, respectively. Energy for body tissue gain (**ΔBodyE**; Mcal/d) was estimated by an equation derived from NRC (2001; Table 2-5):

$$\Delta\text{BodyE} = (2.88 + 1.036 \times \text{BCS}) \times \Delta\text{BW},$$

where BCS is the average BCS for a cow during a 28-d treatment period.

The milk:feed ratio for a cow during a period was determined as the average daily ECM yield {ECM = [0.327 × milk (kg) + 12.95 × fat (kg) + 7.20 × protein (kg)]; Tyrrell and Reid, 1965} over the average daily DMI. Gross efficiency, or the percent of consumed energy captured in milk and body tissue gain, was cal-

culated as the sum of the average MilkE and ΔBodyE divided by the average gross energy intake during a 28-d treatment period. Individual feed nutrient analyses were used to calculate diet gross energy content, with sugar and organic acid content of feeds being estimated from Spartan Dairy Ration Evaluator (version 3.0, Michigan State University, East Lansing, MI). Energy values for each nutrient were assigned according to Merrill and Watt (1973): 4.20 kcal/g of carbohydrate, 5.65 kcal/g of CP, 9.50 kcal/g of fat (estimated as ether extract - 1; NRC, 2001), 3.95 kcal/g of sugar, and 3.62 kcal/g of fermented acid. Apparent diet energy density (**DietNE_L**; Mcal/kg) was calculated for each cow when fed each diet as

$$\text{DietNE}_L = (\text{MilkE} + 0.08 \times \text{MBW} + \Delta\text{BodyE})/\text{DMI}.$$

Multiple of maintenance (**MM**) was calculated 2 ways: (1) based on NRC (2001) requirements for observed production and (2) based on observed intake and the NRC (2001) maintenance requirement. Multiple of maintenance based on NRC (2001) requirements for observed production (**MM_R**) was calculated as

$$\text{MM}_R = (\text{MilkE} + 0.08 \times \text{MBW} + \Delta\text{BodyE}) / (0.08 \times \text{MBW}).$$

Multiple of maintenance based on observed intake (**MM_I**) was calculated as

$$\text{MM}_I = (\text{DMI} \times \text{mean DietNE}_L) / (0.08 \times \text{MBW}),$$

where mean DietNE_L was either 1.7 or 1.6 Mcal of NE_L/kg, which was the average apparent DietNE_L for HS and LS across all 4 experiments, respectively (Table 1).

Statistical Analysis

Data from all 4 experiments were compiled for analysis. Two cows from experiment 3 were not included in the analysis due to a displaced abomasum and severe mastitis infection during the 5-d collection of periods 1 and 2, respectively. Dry matter intake for an individual cow during each 28-d treatment period was regressed as a function of major energy sinks using GLM Procedure in SAS (version 9.3, SAS Institute Inc., Cary, NC). To define RFI, DMI was modeled as

$$\begin{aligned} \text{DMI}_i = & \beta_0 + \beta_1 \times \text{MilkE}_i \\ & + \beta_2 \times \text{MBW}_i + \beta_3 \times \Delta\text{BodyE}_i + \text{parity} \\ & + \text{experiment} + \text{cohort}(\text{experiment}) \\ & + \text{diet}(\text{cohort} \times \text{experiment}) + \varepsilon_i, \end{aligned} \quad [1]$$

where DMI_i is the mean DMI observed or the i th cow; β_0 is the intercept; and β_1 , β_2 , and β_3 are the coefficients associated with the mean $MilkE_i$, MBW_i , and $\Delta BodyE_i$ observed for the i th cow, respectively. Parity (1 or 2+), experiment (1, 2, 3, or 4), cohort (1 or 2) within experiment, and diet (HS or LS) within cohort and experiment were fixed effects, where a cohort was defined as a group of cows that received treatments in the same sequence (i.e., HS then LS or LS then HS). The error term in the model was used to define RFI. To determine if DM digestibility could account for some of the residual in model 1, we also regressed DMI as in model 1 with the addition of DM digestibility and the interaction of DM digestibility and diet (HS or LS) as covariates:

$$\begin{aligned} DMI_i = & \beta_0 + \beta_1 \times MilkE_i + \beta_2 \times MBW_i \\ & + \beta_3 \times \Delta BodyE_i + \text{parity} + \text{experiment} \\ & + \text{cohort}(\text{experiment}) + \text{diet}(\text{cohort} \times \text{experiment}) \\ & + \text{DM digestibility} + \text{DM digestibility} \times \text{diet} + \epsilon_i. \quad [2] \end{aligned}$$

The interaction between DM digestibility and diet was included to determine if the effect of DM digestibility varied by diet. For our analysis, RFI was determined using model 1.

Cows were grouped based on RFI status and classified as high RFI (**HRFI**), low RFI (**LRFI**), or medium RFI (**MRFI**). Cows with RFI >0.5 SD of the mean RFI for a cohort within an experiment were considered HRFI, those <-0.5 SD of the mean were considered LRFI, and those within ± 0.5 SD of the mean were considered MRFI. The effect of RFI group (HRFI, MRFI, or LRFI) was determined using the MIXED Procedure of SAS according to a model that included the fixed effects of RFI group (HRFI, MRFI, or LRFI) and experiment (1, 2, 3, or 4), their interaction, and the random effect of cow nested within experiment. Additionally, to account for differences in feed intake as a multiple of maintenance (MM_I) among RFI groups, nutrient digestibilities were analyzed according to a mixed model that included the fixed effects of RFI group (HRFI, MRFI, or LRFI) and experiment (1, 2, 3, or 4), MM_I as a covariate, all 2- and 3-way interactions, and the random effect of cow nested within experiment. For both mixed models, Tukey's test was used to investigate differences of least squares means. Prior to analysis, the cohort mean nutrient digestibilities were adjusted to the overall mean nutrient digestibilities for HS or LS across all 4 experiments. The REG Procedure was used to determine regression equations, and Pearson correlations were obtained using the CORR Procedure of SAS. For relationships among nutrient digestibilities

and RFI, partial correlations, which accounted for effects of parity, cohort, and experiment, were obtained using the PARTIAL option of the CORR Procedure.

Production, efficiency (milk:feed, gross efficiency, and RFI), and digestibility responses to HS and LS diets were analyzed using a mixed model that included the fixed effects of experiment (1, 2, 3, or 4), diet (HS or LS), period (1 or 2) nested within experiment, parity (1 or 2+), all interactions of fixed effects, and the random effect of cow nested within parity and experiment. Main effects and correlations were considered significant at $P < 0.05$ and trends at $P < 0.10$. Interactions were considered significant at $P < 0.10$ and trends at $P < 0.15$.

RESULTS AND DISCUSSION

Performance

Feeding HS and LS diets resulted in significant variation in feed intake level as indicated by greater MM_I and MM_R for HS diets ($P < 0.01$; Table 2). Estimated GE intake was similar (~ 107 Mcal/d; $P = 0.16$), but NE_L intake was increased for HS than LS (44 vs. 42 Mcal/d; $P < 0.01$), which reflects the greater digestibility of HS. The HS diets increased gross efficiency (31 vs. 29%; $P < 0.01$), but milk:feed was not affected by diet type ($P = 0.87$). Gross efficiency is different from milk:feed because it accounts for energy partitioned to both milk and body reserves. That gross efficiency, but not milk:feed, was different between HS and LS suggests that cows partitioned a greater proportion of consumed energy toward body tissue when fed HS. This is supported by a greater body energy change (3.74 vs. 2.16 Mcal/d; $P < 0.01$), but similar MilkE (29.6 vs. 29 Mcal/d; $P = 0.34$) such that total energy captured as milk output plus body tissue gain was greater ($P < 0.01$) for HS compared with LS. Residual feed intake was not different between HS and LS diets, as expected, because diet was included in the regression model for calculating RFI.

Digestibilities of starch and DM were greater for HS diets ($P < 0.01$), but NDF digestibility was greater for LS diets ($P < 0.01$); the latter was expected because LS diets contained more digestible NDF sources than HS diets. Others have also observed greater NDF digestibility when nonforage fiber sources, such as beet pulp or soyhulls, replaced ground or high moisture corn in the diet (Voelker and Allen, 2003; Gencoglu et al., 2010). Similar to our results for DM digestibility, Beckman and Weiss (2005) observed a significant linear increase in DM digestibility as the diet NDF:starch ratio was reduced. Although our NDF:starch ratios for LS diets are larger on average (2.98) than that of the lowest starch

diet tested in that study (1.27), our NDF:starch ratios for HS were similar (0.88) to those of the high and medium starch diets studied by Beckman and Weiss (0.74 and 0.95; Beckman and Weiss, 2005). For our study, differences in DMI as a multiple of maintenance, energy partitioning, and nutrient digestibilities among HS and LS verify that our diets were distinctly different in their utilization by high producing cows.

Nutrient digestibilities were moderately repeatable across HS and LS diets, as shown in Figure 1. Starch and DM digestibilities when cows were fed LS diets were correlated with starch and DM digestibilities when cows were fed HS diets ($r = 0.31$, $r = 0.28$; both $P < 0.01$). These results indicate that cows that had greater digestive abilities on HS also had greater digestive abilities for LS diets. Thus, it appears that cows that have superior digestive ability for a given diet will also likely have greater digestive ability when fed other types of diets. Digestibilities of NDF ($r = 0.23$; $P = 0.02$) and CP ($r = 0.22$; $P = 0.02$; data not shown) were less repeatable across HS and LS, which reflects the fact that the ability of the cow to digest of each of these nutrients is more dependent on diet rather than individual cow characteristics.

The HRFI and LRFI cows had similar MilkE, MBW, and Δ BodyE, but LRFI cows had significantly lower

DMI and significantly greater milk:feed, gross efficiency, and apparent DietNE_L than HRFI cows for both diets (Table 3). Multiple of maintenance based on observed intake (MM_I) correlated positively with RFI (Figure 2) when cows were fed HS ($r = 0.49$; $P < 0.01$) and LS diets ($r = 0.52$; $P < 0.01$), which was not surprising, because low RFI cows (more efficient) have lower DMI than high RFI cows (less efficient), and MM_I is based on observed DMI. In contrast, MM_R was not related to RFI for either diet, as was expected because RFI should not be related to MilkE, MBW, or Δ BodyE, which are the determinants of MM_R ($P > 0.30$; Figure 2).

Digestibility and RFI

The relationships between RFI and digestibilities of DM, starch, NDF, and CP are illustrated in Figure 3. Partial correlation coefficients, which represent relationships after correction for effects of experiment, cohort, and parity, are reported throughout the text but were similar to Pearson correlation coefficients. Digestibility of DM correlated negatively with RFI ($r = -0.30$; $P < 0.01$) for LS diets, but not for HS diets ($r = -0.01$; $P = 0.90$); thus, DM digestibility accounted for 9% of the variation in RFI when cows were fed LS but not HS diets. Furthermore, the LRFI cows had greater DM

Table 2. Production, efficiency, and digestibility for cows ($n = 107$) fed high (HS) and low (LS) starch diets

Item	Diet			<i>P</i> -value ¹				
	HS	LS	SEM	Diet	Period(Exp)	Parity	Exp	Diet $\times$ Exp
Intake and performance ²								
DMI, kg/d	25.8	25.2	0.24	0.11	0.78	<0.01	<0.01	0.26
GE intake, Mcal/d	108	106	1.00	0.16	0.78	<0.01	<0.01	0.31
NE _L intake, Mcal/d	43.8	41.6	0.53	<0.01	<0.01	<0.01	<0.01	0.80
MM, based on intake	4.18	3.87	0.04	<0.01	0.77	<0.01	<0.01	0.25
MM, based on requirements	4.20	3.99	0.05	<0.01	<0.01	<0.01	<0.01	0.83
MilkE, Mcal/d	29.6	29.0	0.45	0.34	0.17	<0.01	<0.01	0.32
Δ BodyE, Mcal/d	3.74	2.16	0.31	<0.01	<0.01	0.51	0.26	0.20
MBW, kg ^{0.75}	131	130	0.94	0.78	0.88	<0.01	0.02	1.00
Efficiency								
NE captured in milk and body tissue, ³ Mcal/d	33.4	31.2	0.52	<0.01	<0.01	<0.01	<0.01	0.79
Gross efficiency, ⁴ %	31.0	29.3	0.39	<0.01	<0.01	0.55	<0.01	0.98
Milk:feed	1.66	1.65	0.02	0.87	<0.01	0.06	<0.01	0.04
RFI, kg of DM/d	0.00	0.04	0.15	0.87	0.99	0.92	0.99	0.99
Digestibility, %								
DM	66.8	63.4	0.26	<0.01	1.00	<0.01	0.81	1.00
Starch	95.3	94.7	0.15	<0.01	0.90	0.06	0.77	0.97
NDF	36.7	48.6	0.45	<0.01	0.91	<0.01	0.58	0.92
CP	66.1	64.9	0.31	0.01	1.00	0.99	0.98	0.99

¹*P*-value associated with fixed effects of diet, period nested within experiment, parity, experiment (exp), and the interaction of diet and experiment.

²GE intake = gross energy intake; NE_L intake = apparent NE_L intake based on performance; MM = multiple of maintenance (estimated from requirements for performance or determined from observed intake); MilkE = milk energy output; Δ BodyE = body energy change; MBW = metabolic BW.

³NE captured in milk and body tissue = MilkE + Δ BodyE.

⁴Gross efficiency = (MilkE + Δ BodyE)/GE intake.

Figure 1. Relationship between nutrient digestibilities when cows ($n = 107$) were fed high (HS) and low (LS) starch diets. Each point indicates an individual cow and her performance when she was fed each diet. Correlation coefficients were significant for DM ($r = 0.28$; $P < 0.01$), starch ($r = 0.31$; $P < 0.01$), and NDF ($r = 0.23$; $P = 0.02$) digestibilities. Open squares represent cows that received HS and then LS during an experiment; closed triangles represent cows that received LS and then HS during an experiment. These relationships indicate that a cow with low digestibility for one diet also had low digestibility for the other diet.

digestibility than HRFI cows for LS (64.2 vs. 62.4%; $P < 0.05$; Table 3). For beef steers fed an 85% concentrate diet, Richardson and Herd (2004) estimated that 10% of the variation in RFI was due to digestibility, which is similar to our results for DM digestibility when cows were fed LS. However, this relationship was not apparent when cows were fed HS diets as DM digestibility was similar between LRFI and HRFI cows for HS. This disparity suggests that the relationship between RFI and a cow's digestive ability is dependent on diet type. Similar to our findings for LS diets, others have reported that DM digestibility is greater for low RFI dairy heifers (Rius et al., 2012), beef cattle (Richardson et al., 1996; Nkrumah et al., 2006), and swine (Harris et al., 2012). In contrast, some studies have not shown significant relationships between RFI and DM digest-

ibility in beef cattle (Richardson et al., 2004; Lawrence et al., 2011), which is similar to our findings for HS. Discrepancies in this relationship among studies could partially be accounted for by differences in the type of diets fed, as well as physiological state of the animals studied.

Starch digestibility correlated negatively with RFI when cows were fed both HS and LS ($r = -0.31$ and $r = -0.23$; $P < 0.01$ and $P = 0.02$, respectively; Figure 3), suggesting that low RFI cows had a greater ability to digest starch irrespective of diet type. However, in contrast to the correlation analysis, starch digestibility was not significantly different among HRFI, MRFI, and LRFI groups (Table 3) for LS diets ($P = 0.17$), but tended to be different among RFI groups for HS diets ($P = 0.07$). Digestibilities of NDF and CP correlated

Table 3. Performance, efficiency, and apparent total-tract digestibility of cows (mean $\pm$ SE; $n = 107$) fed high and low starch diets by residual feed intake (RFI) grouping¹

Item	High starch diet			Low starch diet		
	HRFI	MRFI	LRFI	HRFI	MRFI	LRFI
n	33	40	34	32	39	36
Performance ²						
DMI, kg/d	28.7 $\pm$ 0.56 ^a	25.6 $\pm$ 0.56 ^b	25.2 $\pm$ 0.55 ^b	27.4 $\pm$ 0.64 ^a	25.1 $\pm$ 0.59 ^b	24.4 $\pm$ 0.60 ^b
MM _R	4.29 $\pm$ 0.08	4.11 $\pm$ 0.08	4.26 $\pm$ 0.08	4.12 $\pm$ 0.10	3.96 $\pm$ 0.10	3.93 $\pm$ 0.10
MM _I	4.54 $\pm$ 0.06 ^a	4.17 $\pm$ 0.06 ^b	4.02 $\pm$ 0.06 ^b	4.20 $\pm$ 0.07 ^a	3.84 $\pm$ 0.06 ^b	3.67 $\pm$ 0.06 ^c
MilkE, Mcal/d	31.5 $\pm$ 0.95	29.4 $\pm$ 0.95	30.5 $\pm$ 0.94	30.2 $\pm$ 1.06	28.3 $\pm$ 0.98	29.8 $\pm$ 1.01
Δ BodyE, Mcal/d	3.5 $\pm$ 0.6	3.0 $\pm$ 0.6	4.3 $\pm$ 0.6	2.36 $\pm$ 0.5	2.57 $\pm$ 0.5	1.38 $\pm$ 0.5
MBW, kg ^{0.75}	134 $\pm$ 1.9	130 $\pm$ 1.9	133 $\pm$ 1.9	130 $\pm$ 2.1	131 $\pm$ 1.9	133 $\pm$ 1.9
DietNE _L , Mcal/kg	1.60 $\pm$ 0.03 ^b	1.67 $\pm$ 0.03 ^b	1.80 $\pm$ 0.03 ^a	1.57 $\pm$ 0.03 ^c	1.64 $\pm$ 0.02 ^b	1.71 $\pm$ 0.02 ^a
Efficiency						
Milk:feed	1.59 $\pm$ 0.03 ^b	1.66 $\pm$ 0.03 ^{ab}	1.74 $\pm$ 0.03 ^a	1.59 $\pm$ 0.03 ^b	1.62 $\pm$ 0.03 ^b	1.75 $\pm$ 0.03 ^a
Gross efficiency, ³ %	29.3 $\pm$ 0.68 ^b	30.1 $\pm$ 0.68 ^b	32.9 $\pm$ 0.67 ^a	28.2 $\pm$ 0.69	29.0 $\pm$ 0.63	30.3 $\pm$ 0.65
RFI, kg of DM/d	1.60 $\pm$ 0.12 ^a	-0.01 $\pm$ 0.12 ^b	-1.46 $\pm$ 0.12 ^c	1.65 $\pm$ 0.12 ^a	-0.06 $\pm$ 0.11 ^b	-1.40 $\pm$ 0.12 ^c
Digestibility, %						
DM	66.6 $\pm$ 0.44	67.1 $\pm$ 0.44	65.9 $\pm$ 0.44	62.4 $\pm$ 0.45 ^b	63.1 $\pm$ 0.42 ^{ab}	64.2 $\pm$ 0.43 ^a
Starch	94.9 $\pm$ 0.26	95.4 $\pm$ 0.26	95.7 $\pm$ 0.26	94.4 $\pm$ 0.25	94.7 $\pm$ 0.23	95.1 $\pm$ 0.24
NDF	36.8 $\pm$ 0.95	37.1 $\pm$ 0.95	34.0 $\pm$ 0.94	47.3 $\pm$ 0.71	48.0 $\pm$ 0.66	49.6 $\pm$ 0.67
CP	65.9 $\pm$ 0.52	66.6 $\pm$ 0.52	65.2 $\pm$ 0.51	64.2 $\pm$ 0.50	64.8 $\pm$ 0.46	65.5 $\pm$ 0.47

^{a-c}Least squares means within a row and diet with different superscripts are significantly different ($P < 0.05$).

¹HRFI = high RFI cows (>0.5 SD), MRFI = medium RFI cows (± 0.5 SD), LRFI = low RFI cows (<-0.5 SD).

²MM_R = multiple of maintenance estimated from requirements for performance; MM_I = multiple of maintenance based on observed intake; MilkE = milk energy output; Δ BodyE = body energy change; MBW = metabolic BW; DietNE_L = apparent energy density of the diet, calculated from mean cow performance for each diet, as (MilkE + Δ BodyE + $0.08 \times$ MBW)/DMI for each cow.

³Gross efficiency = (MilkE + Δ BodyE)/GE intake.

negatively with RFI for LS diets ($r = -0.23$ and $r = -0.23$; both $P = 0.02$, respectively), but not HS diets ($P > 0.30$; Figure 3). When HRFI and LRFI groups of cows were compared, digestibility of NDF, but not CP, tended to be significantly greater for the LRFI group fed LS diets (49.6 vs. 47.3%; $P = 0.05$; Table 3). In contrast to our findings for NDF and CP digestibilities, Nkrumah et al. (2006) observed significantly greater CP digestibility, but not NDF digestibility, for low RFI beef cattle compared with high RFI cattle. Additionally, lactating dairy cattle identified as low RFI heifers had significantly greater nitrogen digestibility, but similar NDF digestibility when compared with high RFI cohorts (Rius et al., 2012).

To determine RFI, DMI was modeled as a function of major energy sinks (model 1); coefficients for MilkE, MBW, and Δ BodyE were 0.35 ($P < 0.01$), 0.09 ($P < 0.01$), and 0.04 ($P = 0.14$) and the model R^2 and root mean square error were 0.86 and 1.45, respectively. This model also included effects of parity, experiment, cohort(experiment) and diet(cohort $\times$ experiment), which were also significant ($P \leq 0.01$). When DM digestibility and its interaction with diet were added as covariates (model 2), we obtained similar coefficients for MilkE, MBW, and Δ BodyE (0.33, 0.09, and 0.04; $P < 0.01$, $P < 0.01$, and $P = 0.28$, respectively). For that model, coefficients for DM digestibility and DM digest-

ibility $\times$ diet were significant (-0.17 for DM digestibility, $P = 0.04$; 0.17 for DM digestibility for HS diet, $P = 0.03$) and the R^2 and root mean square error were 0.86 and 1.43, respectively. Because both DM digestibility and DM digestibility $\times$ diet were significant, and MSE decreased when these covariates were added to the model used to predict DMI (and therefore, derive RFI), these results provide further support for the hypothesis that a cow's digestive ability could contribute to RFI.

We observed that apparent DietNE_L, which was calculated from individual production requirements according to NRC (2001), was greater for the LRFI group for HS (1.80 vs. 1.60 Mcal/kg; $P < 0.05$) and LS diets (1.71 vs. 1.57 Mcal/kg; $P < 0.05$; Table 3). Because apparent DietNE_L was 8.91% greater and DM digestibility was 2.75% greater (64.2 vs. 62.4%; Table 3) for LRFI cows fed LS diets, up to 31% of the differences (2.75%/8.91%) in apparent DietNE_L could have been due to differences in DM digestibility. This suggests that differences in digestive ability may partially explain why some animals have a superior ability to extract net energy from their feed. Because digestive ability may account for a portion of the between-animal differences for apparent DietNE_L, it may also account for differences in RFI. Residual feed intake is essentially an estimate of the efficiency by which cows convert gross energy into net energy, though we realize that

there are errors associated with determining RFI. For example, it is assumed that the coefficient for calculating maintenance energy requirements from MBW is 0.08 for every cow; however, this coefficient probably varies greatly among cows, which contributes to RFI.

Variation among HS and LS diets for the relationships between RFI and nutrient digestibilities could be reflective of true differences between animals for digestibility and the ability of some animals to use certain

types of feed more efficiently than others. In their study of broilers selected for high or low digestive efficiency, Rougière et al. (2009) observed that digestive efficiency of the least efficient birds increased when they were presented with a coarse diet that promoted gut retention time. For our study, feeding LS diets resulted in greater differences in digestibility among HRFI and LRFI groups, which might have resulted from LRFI cows having a greater capacity for digestion of low starch, high fiber diets than HRFI cows. Perhaps both groups of cows have similar digestive abilities for high starch diets, which are more readily digestible than high NDF diets. Although we did not characterize the rumen microbial communities of HRFI and LRFI cows, potential differences could account for a portion of the greater NDF digestibility observed for LRFI and not HRFI for LS diets via their influence on ruminal fiber digestion. These differences might be less important for HS diets because postruminal starch digestion compensates for changes in ruminal starch digestion such that apparent total-tract digestibility of starch remains fairly constant (Allen, 2000).

Digestibility Depression as Related to Multiple of Maintenance

We observed similar relationships of digestibility with MM_I and DMI as a percentage of MBW for HS and LS so only the relationships of digestibility with MM_I will be presented and discussed. Multiple of maintenance based on observed DMI (MM_I) correlated negatively with digestibilities of DM ($r = -0.47$; $P < 0.01$), starch ($r = -0.25$; $P = 0.01$), and NDF ($r = -0.43$; $P < 0.01$) when cows were fed LS diets (Figure 4). However, when cows were fed HS diets, MM_I was not related to DM or NDF digestibilities ($P > 0.20$), but correlated negatively with starch digestibility ($r = -0.35$; $P < 0.01$). As MM_I increased, digestibility of NDF and DM decreased 4.0 and 2.8 units per MM_I ($P < 0.01$) for LS diets, respectively, but depression in NDF and DM digestibilities associated with MM_I was not significant for the HS diets (0.34 and 0.69 unit decrease per MM_I , respectively; $P = 0.79$ and $P = 0.23$, respectively). As MM_I increased, starch digestibility decreased 1.2 and 0.8 percentage units per MM_I ($P < 0.01$ and $P = 0.01$, respectively) when cows were fed HS and LS diets, respectively. Thus, each unit increase in MM_I resulted in a ~ 3 unit reduction in DM digestibility for LS diets in our study. This was not surprising because it is well established that digestibility decreases as DMI as a multiple of maintenance increases (Tyrell and Moe, 1975). Our results for LS diets correspond to the assumption that each increase in intake as a multiple of maintenance decreases DM digestibility by ~ 4

Figure 2. Relationship between residual feed intake (RFI) and (A) multiple of maintenance based on intake (high starch, HS: open circles, dashed line: $\text{kg/d} = 1.66x - 7.01$; intercept SE = 1.2; intercept $P < 0.01$; slope SE = 0.29; slope $P < 0.01$; $R^2 = 0.24$; low starch, LS: closed circles, solid line: $\text{kg/d} = 1.70x - 6.58$; intercept SE = 1.0; intercept $P < 0.01$; slope SE = 1.7; slope $P < 0.01$; $R^2 = 0.28$) and (B) multiple of maintenance based on requirements (HS: $\text{kg/d} = -0.23x + 0.98$; intercept SE = 1.1; intercept $P = 0.37$; slope SE = 0.25; slope $P = 0.37$; $R^2 = 0.01$; LS: $\text{kg/d} = 0.22x - 0.88$; intercept SE = 0.87; intercept $P = 0.31$; slope SE = 0.22; slope $P = 0.30$; $R^2 = 0.01$) for cows ($n = 107$) fed high (HS) and low (LS) starch diets.

Figure 3. Relationship between residual feed intake (RFI) and digestibility of (A) DM (high starch, HS, open circles, dashed line: $\% = 0.0054x - 0.34$; intercept SE = 3.7; intercept $P = 0.93$; slope SE = 0.056; slope $P = 0.92$; $R^2 < 0.01$; low starch, LS, closed circles, solid line: $\% = -0.15x + 9.8$; intercept SE = 3.3; intercept $P < 0.01$; slope SE = 0.051; slope $P < 0.01$; $R^2 = 0.09$), (B) starch (HS: $\% = -0.30x + 29$; intercept SE = 8.4; intercept $P < 0.01$; slope SE = 0.088; slope $P < 0.01$; $R^2 = 0.10$; LS: $\% = -0.22x + 21$; intercept SE = 9.0; intercept $P = 0.02$; slope SE = 0.095; slope $P = 0.02$; $R^2 = 0.05$), (C) NDF (HS: $\% = 0.023x - 0.81$; intercept SE = 0.93; intercept $P = 0.38$; slope SE = 0.025; slope $P = 0.37$; $R^2 = 0.01$; LS: $\% = -0.075x + 3.6$; intercept SE = 1.6; intercept $P = 0.03$; slope SE = 0.034; slope $P = 0.03$; $R^2 = 0.04$), and (D) CP (HS: $\% = 0.017x - 1.1$; intercept SE = 3.1; intercept $P = 0.73$; slope SE = 0.047; slope $P = 0.73$; $R^2 < 0.01$; LS: $\% = -0.12x + 7.7$; intercept SE = 3.2; intercept $P = 0.02$; slope SE = 0.049; slope $P = 0.02$; $R^2 = 0.05$) when cows ($n = 107$) were fed high (HS) and low (LS) starch diets. For HS, partial correlations for DM, starch, NDF, and CP digestibilities after corrections for experiment, cohort, and parity were 0.01 ($P = 0.90$), -0.32 ($P < 0.01$), 0.09 ($P > 0.30$), and 0.03 ($P > 0.30$), respectively. For LS, partial correlations for DM, starch, NDF, and CP digestibilities after corrections for experiment, cohort, and parity were -0.30 ($P < 0.01$), -0.23 ($P = 0.02$), -0.23 ($P = 0.02$), and -0.23 ($P = 0.02$), respectively.

percentage units (NRC, 2001). Although we expected that digestibility would be depressed by greater levels of DMI due to increased passage rate (Colucci et al., 1982), it was surprising that the depression in digestibility was only significant for the LS diets. The NRC (2001) suggests that the digestibility of diets that are

more digestible at $1\times$ maintenance intake are depressed more per unit increase in MMI than that of diets that are less digestible at $1\times$ maintenance intake. Based on this idea, we expected to see greater digestibility depression per increase in MMI for HS than for LS diets because corn grain, the predominant concentrate

in HS diets, contains more TDN at 1× maintenance (89%) than concentrate ingredients used to replace it to formulate LS diets [soybean hulls (67%), whole cottonseed (77%), and corn and legume silages (69% and 57%, respectively)]; however, this was not the case in our study. The greater digestibility depression for LS diets could be related to the smaller particle size of soybean hulls compared with other NDF sources, and greater feed intake could have reduced their ruminal retention time, enabling a greater proportion to travel out of the gastrointestinal tract undigested (Firkins, 1997). This hypothesis might account for the reduction in both NDF and DM digestibilities that were observed as MM_I increased for LS diets.

In contrast to MM_I , multiple of maintenance based on production requirements (MM_R) was not related to digestibility of starch for HS and LS diets ($P = 0.21$; data not shown). However, MM_R correlated negatively with NDF and DM digestibilities ($r = -0.31$ and $r = -0.33$; $P < 0.01$; data not shown) for LS diets, with NDF and DM digestibilities decreasing 1.97 and 1.32 units ($P < 0.01$; data not shown) per unit increase in MM_R , respectively.

Digestibility Depression and RFI

Feed intake correlated positively with RFI for both diets, as shown in Figure 2 using intake as a multiple of maintenance. This is to be expected because RFI is the error in the observed versus predicted intake. Because greater intake depresses nutrient digestibility (NRC, 2001, and shown in Figure 4), one thus can expect that RFI will be negatively correlated with digestibility. Digestibilities were modeled as a function of RFI group and experiment plus the effect of MM_I as a covariate to account for possible effects of intake level on digestibility. Significance of MM_I but not RFI group in this regression would indicate that differences in digestibility among RFI groups were accounted for by the observed DMI differences. For LS diets, the effect of MM_I was significant for NDF and DM digestibilities ($P < 0.01$), but the effect of RFI group was not (Table 4), suggesting that the previously observed differences between HRFI and LRFI groups fed LS for NDF and DM digestibilities (Table 3) could be due to differences in intake level.

The relationship between DM digestibility and MM_I by RFI group for HS and LS diets is illustrated in Figure 5. For HS diets, DM digestibility decreased 0.39 ($P = 0.82$) and 1.34 units ($P = 0.16$) for each unit increase in MM_I for LRFI and HRFI cows, respectively, indicating that digestibility depression associated MM_I was not significantly different from zero for either RFI group. For LS diets, DM digestibility decreased 1.08 (P

Figure 4. Relationships between multiple of maintenance determined from observed DMI and digestibility of (A) DM (high starch, HS, open circles, dashed line: $\% = -0.69x + 70$; intercept SE = 2.4; intercept $P < 0.01$; slope SE = 0.58; slope $P = 0.23$; $R^2 = 0.01$; low starch, LS, closed circles, solid line: $\% = -2.76x + 74$; intercept SE = 2.0; intercept $P < 0.01$; slope SE = 0.51; slope $P < 0.01$; $R^2 = 0.22$), (B) starch (HS: $\% = -1.24x + 101$; intercept SE = 1.4; intercept $P < 0.01$; slope SE = 0.33; slope $P < 0.01$; $R^2 = 0.12$; LS: $\% = -0.80x + 98$; intercept SE = 1.2; intercept $P < 0.01$; slope SE = 0.31; slope $P = 0.01$; $R^2 = 0.06$), and (C) NDF (HS: $\% = -0.34x + 38$; intercept SE = 5.3; intercept $P < 0.01$; slope SE = 1.3; slope $P = 0.79$; $R^2 < 0.01$; LS: $\% = -3.96x + 67$; intercept SE = 3.1; intercept $P < 0.01$; slope SE = 0.8; slope $P < 0.01$; $R^2 = 0.19$) for cows ($n = 107$) fed high (HS) and low (LS) starch diets.

Table 4. Apparent total-tract digestibility of low and high starch diets by cows (mean ± SE; n = 107) classified by residual feed intake (RFI) grouping¹ using DMI as a multiple of maintenance as a covariate

Item	High starch diet					Low starch diet				
	<i>P</i> -value ²					<i>P</i> -value				
	HRFI	MRFI	LRFI	RFI group	MM _I	HRFI	MRFI	LRFI	RFI group	MM _I
n	33	40	34			32	39	36		
Digestibility, %										
DM	67.7 ± 0.84	66.9 ± 0.50	66.5 ± 0.71	0.16	0.70	63.7 ± 0.61	63.0 ± 0.40	64.1 ± 0.54	0.44	<0.01
Starch	95.4 ± 0.48	95.3 ± 0.29	95.7 ± 0.41	0.51	0.11	94.7 ± 0.38	94.6 ± 0.25	95.0 ± 0.34	0.82	0.18
NDF	38.8 ± 1.81	36.9 ± 1.08	35.6 ± 1.53	0.18	0.98	49.2 ± 0.98	47.8 ± 0.65	49.7 ± 0.87	0.28	<0.01
CP	66.5 ± 0.96	66.4 ± 0.57	66.2 ± 0.82	0.24	0.38	64.5 ± 0.73	64.8 ± 0.48	65.7 ± 0.64	0.68	0.43

¹HRFI = high RFI cows (>0.5 SD), MRFI = medium RFI cows (±0.5 SD), LRFI = low RFI cows (<-0.5 SD).
²*P*-values associated with the effects of RFI grouping (HRFI, MRFI, or LRFI) and multiple of maintenance based on observed feed intake (MM_I).

Figure 5. Relationship between DM digestibility and intake on (A) high-starch (HS) and (B) low-starch (LS) diets for cows ranked for RFI as high (HRFI; >0.5 SD of the cohort mean), medium (MRFI; ±0.5 SD of the cohort mean), and low (LRFI; <0.5 SD of the cohort mean). Intake is as a multiple of maintenance calculated from observed feed intake. HRFI cows are shown as closed squares and the solid black lines for both HS (% = -1.34x + 73; intercept SE = 4.2; intercept *P* < 0.01; slope SE = 0.93; slope *P* = 0.16; R² = 0.06; n = 33) and LS (% = -2.75x + 74; intercept SE = 4.4; intercept *P* < 0.01; slope SE = 1.0; slope *P* = 0.01; R² = 0.19; n = 32). LRFI cows are shown as open triangles and solid gray line for both HS (% = -0.39x + 68; intercept SE = 7.0; intercept *P* < 0.01; slope SE = 1.7; slope *P* = 0.82; R² = <0.01; n = 34) and LS (% = -1.08x + 68; intercept SE = 4.1; intercept *P* < 0.01; slope SE = 1.1; slope *P* = 0.34; R² = 0.03; n = 36). MRFI cows are shown by X symbols. For both A and B, the black dotted and gray dashed lines show the 95% confidence limits for the mean of HRFI and LRFI cows, respectively.

= 0.34) and 2.75 units (*P* = 0.01) for each unit increase in MM_I for LRFI and HRFI cows, respectively, indicating that the degree of digestibility depression per unit increase in MM_I was more severe for HRFI than LRFI

cows for LS diets. However, the 95% confidence intervals for the mean response of HRFI and LRFI groups reveal substantial overlap for both diets (Figure 5).

CONCLUSIONS

We explored the relationship between RFI and digestibility in lactating dairy cows 4 ways: (1) based on digestibility results for RFI groups with feed intake as a covariate; (2) based on the regression of digestibility on intake as a multiple of maintenance for the 3 RFI groups fed each diet; (3) based on apparent NE_L values of the diets calculated from animal performance; and (4) based on the inclusion of DM digestibility as a covariate in the regression model to determine RFI (model 2). We conclude that digestibility accounts for at least 9 and up to 31% of the variation in RFI for mid-lactation cows fed LS diets, but none of the variation when fed HS diets. Increased digestive ability would enable a cow to eat less to maintain the same production and thus have a low RFI (efficient phenotype). However, we recognize that this relationship is not necessarily causative. More work is needed to understand this relationship.

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