Improving Ruminal Digestibility

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Summary

Level of DM intake has the most profound effect on digestible nutrient intake in ruminant animals. Unfortunately, increasing DM intake takes a toll on the digestibility coefficient of most nutrients because of the resulting reduced ruminal residence time. Furthermore, substrate specific physiochemical effects are another large source of variation that will limit availability of nutrients to microbial and enzymatic digestion. Nonetheless, modifying the diet to manipulate a few key nutrient parameters may provide incremental improvement in nutrient digestibility, potentially compensating for some of the digestibility loss from reduced ruminal residence time or ingredient substrate limitations. This short dissertation will discuss dietary effects on digestibility of neutral detergent fiber **(NDF)**, starch, and feed protein in the rumen. While relatively small in individual impact, such dietary modifications, taken collectively, may offer an opportunity to improve feed efficiency, apart from the influences of intake or ingredient quality.

Introduction

Any discussion of improving ruminal digestibility first requires a consideration of the elements involved, along with their responsiveness and potential interactions. Previous excellent reviews (Huntington, 1997; Weimer, 1998; Firkins, 2002) have considered elements such as intake levels (and associated passage rates), ruminal pH, ruminal ammonia concentrations, substrate availability, rates of ruminal digestibility of fiber and starch, dietary fat levels, additives (microbial and non-microbial), and more. For a narrative of the effects of additives, a number of very good reviews are available (Hutjens, 2007; Adesogan, 2009) and will not be discussed here. Furthermore, the impact of substrate availability from processing, particularly with regards to starch processing, has also been well reviewed (Firkins et al., 2001; Owens, 2009) and will not be discussed either. Rather, this discussion will concentrate primarily on nutrient effects on digestibility in the rumen across a broad variety of diets and intakes. The ruminal digestibility coefficients focused upon will be ruminal digestibility of starch, NDF, and feed protein.

Nutrient Sources of Variation in Ruminal Digestibility

Data collected from 671 Holstein steers (400 to 1100 lb), fitted with duodenal and ileal open-gutter T-cannulas, were used to relate nutrient intake effects on the ruminal digestibility of starch, NDF, and feed crude protein **(CP)**. Data were obtained from 44 experiments, conducted by the authors at the Purina Animal Nutrition Center (formerly, the Purina Research Center), at Gray Summit, MO, from 1984 until 2009, encompassing 172 different treatments. In all studies, chromic oxide was used as the indigestibility marker and microbial purines were used as the microbial marker. Dry matter intakes ranged from 2.5 to 3.8%

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of body weight **(BW)**. A 4 x 4 Latin Square designed was used in all experiments.

Ranges in nutrient content across all diets are shown in Table 1. For the purpose of this dissertation, the approach taken was to relate the amount of NDF, starch, and feed protein digested in the rumen (expressed as a percent of DM intake), as well as ruminal pH and ammonia concentration, and fat level in the diet to the subsequent ruminal digestibility coefficient for NDF, starch, and feed protein (expressed as a percent of nutrient). Independent and dependent variables are shown in Table 2. Where they existed, linear and quadratic relationships were identified, along with their significance (P values) and their coefficient of determination (R^2; also referred to as the correlation coefficient squared). The R^2 was calculated as the fraction of the sum of squares accounted for by the regression model. Where the P value for the quadratic term was greater than 0.05, the R^2 is from the linear model; if the quadratic P value was less than 0.05, the R^2 is from the quadratic model which contains the linear and squared terms for the X variable. These relationships were incorporated into Table 2 as directional representations between the independent variables and the 3 dependent digestibility coefficients. The R^2 values were understandably small, as substrate specific factors affecting digestibility in these studies were relatively much greater. However, where noted, these relationships were significant ($P \leq 0.05$).

Dry matter intake effects on ruminal digestion

Ruminal digestibility coefficients for DM, starch, NDF and feed protein (after subtracting out the microbial contributions to the duodenal protein flow) were depressed as DMI increased (Figure 1). The energy value for feeds as represented by equation 2-3 in the Nutrient Requirements of Dairy Cattle (2001), assumes an 8% reduction in digestibility at 3X maintenance. However, all ruminal digestibility coefficients in Figure 1, with the exception of starch, were depressed in a quadratic fashion ($P \leq 0.04$), suggesting that the depression in ruminal digestion diminishes as intake increases, rather than merely decreasing in a linear fashion.

Ruminal NDF digestibility

When looking at the wide distribution of data in Figure 2, it becomes apparent there can be a 7 to 10 fold range in ruminal NDF digestibility coefficients. This may imply opportunities to manipulate diets in ways to profoundly improve digestibility of NDF in the rumen. Figure 3 shows that while there was a positive relationship between the amount of ruminal feed protein digestion and ruminal NDF digestibility ($P \leq 0.05$), no such relationship existed between ruminal ammonia concentrations and ruminal NDF digestibility. This would suggest that ruminal ammonia was not limiting for the ruminal microbes responsible for digesting NDF, at least within the range of 4.8 to 26 mM observed in this database. This observation would be consistent with those of Schaefer et al. (1980), suggesting that ammonia requirements of selected bacteria in pure culture are actually quite low. Nevertheless, the relationship with ruminal feed protein digestion would be consistent with the conclusion (Argyle and Baldwin, 1989) that some ruminal microorganisms may have a requirement for preformed amino acids and/or peptides for maximum growth and activity.

The negative relationship (Figure 4) between the amount of ruminal starch digestion and ruminal NDF digestibility ($P \leq 0.01$) would be consistent with the positive relationship between ruminal pH and ruminal NDF digestibility ($P \leq 0.01$). Both observations are indicative of the competition between starch and fiber digesting bacteria in the rumen and the preference for higher ruminal pH to support the growth and optimal enzyme activity of fiber digesting bacteria (Mertens, 1979). The inflection point above which ruminal NDF digestibility decreases more rapidly appears to be

in excess of 15% of DMI as rumen digestible starch. Furthermore, ruminal NDF digestibility appears to increase more rapidly at ruminal pH levels in excess of 6.0.

A negative quadratic relationship ($P \leq 0.01$) existed between fat percentage in the diet (by acid hydrolysis; **FatAH**) and ruminal NDF digestibility (Figure 5). However, the negative effect appeared to be greater at lower dietary FatAH concentrations and was greatly diminished at levels greater than 6% FatAH. However, much of this may have been an artifact of the dataset being more heavily weighted at the lower end of the fat intake range, resulting in a poorer distribution of the data and an inappropriate regression analysis.

The ruminal digestibility coefficient of most nutrients is a result of the competing functions of rate of digestion and rate of passage (Mertens and Ely, 1982). This relationship is especially true for NDF digestibility and was observed in a recent study (DCM #145) conducted by the authors at the Purina Animal Nutrition Center, where 3 corn silage hybrids were fed in diets containing 40% corn silage with and without 3% wheat straw. While adding wheat straw reduced the formulated diet energy density, subsequent measures of in vivo digestibility of DM were increased by 3% ($P \leq 0.05$) across all 3 hybrids (Table 3). In particular, NDF digestibility was improved ($P \leq 0.04$) on the straw containing diets (Table 3). Both observations were presumably due to increased residence time of the diet in the rumen when straw was included, despite DMI not being significantly affected.

This would suggest that there may be an optimum mass of digesting NDF, above which intake is limited by bulk fill and below which intake can increase, but possibly at the expense of reduced digestion, and subsequently, feed efficiency. This is in line with the NDF-Energy Intake System recently revisited by D.R. Mertens (2009), where he

suggests that there is a unique solution for dietary NDF at each milk production level where the fill limitation and energy demand curves intersect. Each solution defines the NDF level that maximizes both DMI and maximum NDF (and forage) in the diet. Mertens (2010) further mentions that while the optimum NDF level can be fine-tuned for differences in NDF digestibility, the effect from changing crude NDF is 2 to 3 times greater than changing the digestibility of the NDF. However, one could argue that in practical situations where dietary NDF has reached maximum fill potential in high producing cows, the digestibility of the NDF can take on relatively greater importance.

Ruminal starch digestibility

When looking at the distribution of data in Figure 6, it becomes apparent there was a 3 to 4 fold range in ruminal starch digestibility coefficients. This may suggest some opportunities to modify diets in ways to manipulate digestibility of starch in the rumen, but perhaps of not the same magnitude of improvement as one might achieve with NDF digestion. Figure 7 shows that while there was a positive relationship between the amount of ruminal feed protein digestion and ruminal starch digestibility ($P \leq 0.01$), no such relationship existed between ruminal ammonia concentrations and ruminal starch digestibility. As with ruminal NDF digestion (discussed above), this would suggest that ruminal ammonia was not limiting for the ruminal microbes responsible for digesting starch, at least within the range of 4.8 to 26 mM observed in this database.

Interestingly, there was a positive relationship ($P \leq 0.01$) between the amount of NDF digested ruminally and ruminal starch digestibility (Figure 8). Even though the amount of starch present in the diet was presumably displaced and reduced as the amount of NDF digested ruminally increased, the resulting rumen environment appeared to be more conducive for starch digestibility. Neither rumen pH nor FatAH level in

the diet had any relationship with ruminal starch digestibility (Figure 9), suggesting neither had an effect on the microbes responsible for starch digestion or their enzymes.

Ruminal feed protein digestibility

With the rising cost of feed proteins, anything that can reduce ruminal digestion of protein should improve efficiency of utilization since potential urinary losses can result from deaminated ammonia not assimilated into microbial protein. When looking at the distribution of data in Figure 10, the 3 to 4 fold range in ruminal feed protein digestibility coefficients is surprising wide. This may imply opportunities to modify diets in ways to reduce digestibility of feed protein in the rumen, thus improving the metabolizable protein supply and subsequent efficiency of conversion into milk and/or tissue protein.

There was a relatively stronger positive effect (Figure 11) from the amount of NDF digested in the rumen (P $\leq$ 0.03; R^2 = 0.09) than there was from the amount of starch digested in the rumen (P $\leq$ 0.01; R^2 = 0.04) on ruminal feed protein digestibility. Both would be indicative of greater overall rumen microbial activity, leading to an associated increase in ruminal feed protein breakdown. The stronger positive effect from the amount of NDF digested in the rumen may relate to the observation by others of greater proteolysis in the rumen on higher forage diets (Stewart, 1977). This would be consistent with the increased digestibility of feed protein in the rumen as pH increased in the rumen (P $\leq$ 0.01; Figure 12). One promising relationship that could be leveraged to reduce feed protein digestion in the rumen, thus increasing the rumen undegraded protein content of the metabolizable protein supply, was the negative impact of FatAH level in the diet on feed protein digestibility in the rumen (P $\leq$ 0.01; Figure 12). This may imply direct negative effects by fat in the rumen on proteolytic microorganisms or indirect negative effects on fiber digesting microorganisms, affecting access by microorganisms to cell wall bound protein.

Conclusions

While the various relationships discussed above between digestible nutrient intake and ruminal digestibility coefficients for NDF, starch, and feed protein were significant, the R^2 values were relatively small. Obviously, level of DMI and substrate specific factors affecting digestion have the most profound effect on digestible nutrient intake. Unfortunately, increasing DMI takes a toll on the digestibility coefficient of most nutrients because of the resulting reduced ruminal residence time. These data, however, suggested that the depression in ruminal digestion (with the exception of starch) diminishes as intake increases, rather than merely decreasing in a linear fashion. Nonetheless, modifying the diet to manipulate a few key nutrient parameters, taken collectively, may provide opportunities for incremental improvement in nutrient digestibility.

Higher ruminal NDF digestibility appeared to be associated with greater amounts of feed protein digested in the rumen and lower amounts of starch digested in the rumen, as well as a higher ruminal pH and lower dietary fat level. Ruminal starch digestibility appeared relatively unaffected by digestible nutrient intake or rumen environment (pH and ammonia). Strategies to limit availability of starch, either through processing, preservation method, or starch source selection, would be a more reliable method of manipulating starch digestion in the rumen. While decreasing the amounts of starch and NDF digested in the rumen was associated with reduced feed protein digestion in the rumen, increasing dietary fat levels may be a more practical method to improve rumen undegraded protein content of the diet. Taken collectively, these methods may marginally manipulate digestibility. However, substrate specific manipulations like processing,

ingredient quality and starch source selection should be a more effective and predictable means to manipulate ruminal digestibility.

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Table 1. Dietary nutrient ranges from 44 experiments with 671 Holstein steers (fitted with duodenal and ileal cannulas), conducted by the authors at the Purina Animal Nutrition Center (formerly, the Purina Research Center), at Gray Summit, MO, from 1984 until 2009, encompassing 172 different treatments.

	Mean	Minimum	Maximum
DM intake, lb/day[1]	18.8	8.9	34.1
Protein,% of DMI	17.9	12.9	21.3
Fat, %	4.53	2.76	8.72
NDF, %	37.7	23.0	53.8
Starch, %	26.1	11.5	37.9

[1]Dry matter intakes ranged from 2.5 to 3.8% of body weight.

Table 2. Relationships between the amount of NDF, starch, and feed protein digested in the rumen (expressed as a percent of DM intake), as well as ruminal pH and ammonia concentration, and fat level in the diet and the subsequent ruminal digestibility coefficient of NDF, starch, and feed protein (expressed as a percent of nutrient).

	DM Intake, lb/day[2]	Ruminal Feed Protein Dig., % of DM	Ruminal Ammonia mM	Ruminal NDF Dig., % of DM	Ruminal Starch Dig., % of DM	Ruminal pH	Fat, % of DM Intake
NDF, % of NDF	⇓⇑	⇑⇒	O	X	⇒⇓	⇒⇑	⇓⇒
Starch, % of starch	⇓	⇑	O	⇑	X	O	O
Feed protein, % of protein	⇓⇒	X	⇑	⇑⇒	⇑	⇑	⇓⇒

[1]In all studies, chromic oxide was used as the indigestibility marker and microbial purines were used as the microbial marker. A 4 x 4 Latin Square designed was used in all experiments. [2]Where they existed, linear and quadratic relationships were identified between the independent variables (column headings) and dependent variables (row headings). Block arrows signify directional relationships between the independent variables and the 3 dependent digestibility coefficients where $P \leq 0.05$ for the linear term and $P > 0.05$ for the quadratic term is shown as a single arrow, or where $P \leq 0.05$ for the quadratic term is shown as two arrows. "0" represents no significant relationship and "X" represents potential autocorrelation.

Table 3. Three corn silage hybrids were fed to lactating cows in diets containing 40% corn silage with and without 3% wheat straw. While adding wheat straw reduced the formulated diet energy density, subsequent measures of in vivo digestibility of dry matter were increased by 3% across all three hybrids (P ≤ 0.05; DCM #145).

Wheat Straw, %	0	0	0	3	3	3	
Corn Silage Hybrid[1]	6818	6100	6831	6818	6100	6831	SE
DMI, lb/day	46.3	41.6	44.1	44.7	47.8	42.7	2.2
DM Digested, % of intake[2]	64.0[a]	65.5[ab]	65.3[ab]	66.6[ab]	68.0[b]	66.1[ab]	1.2
NDF Digested, % of intake[3]	32.9[a]	38.7[ab]	34.7[a]	38.1[a]	46.5[b]	36.4[a]	2.8

[1]Croplan Genetics, Winfield Solutions, Shoreview, MN.
[2]Dry Matter Digested; significant (P ≤ 0.05) effect by straw level. Means not followed by a common letter differ (P ≤ 0.05) using the Least Significant Difference **(LSD)** procedure.
[3]Neutral Detergent Fiber Digested; significant effect by straw level (P ≤ 0.04) and hybrid (P ≤ 0.03). Means not followed by a common letter differ (P ≤ 0.05) using LSD procedure.
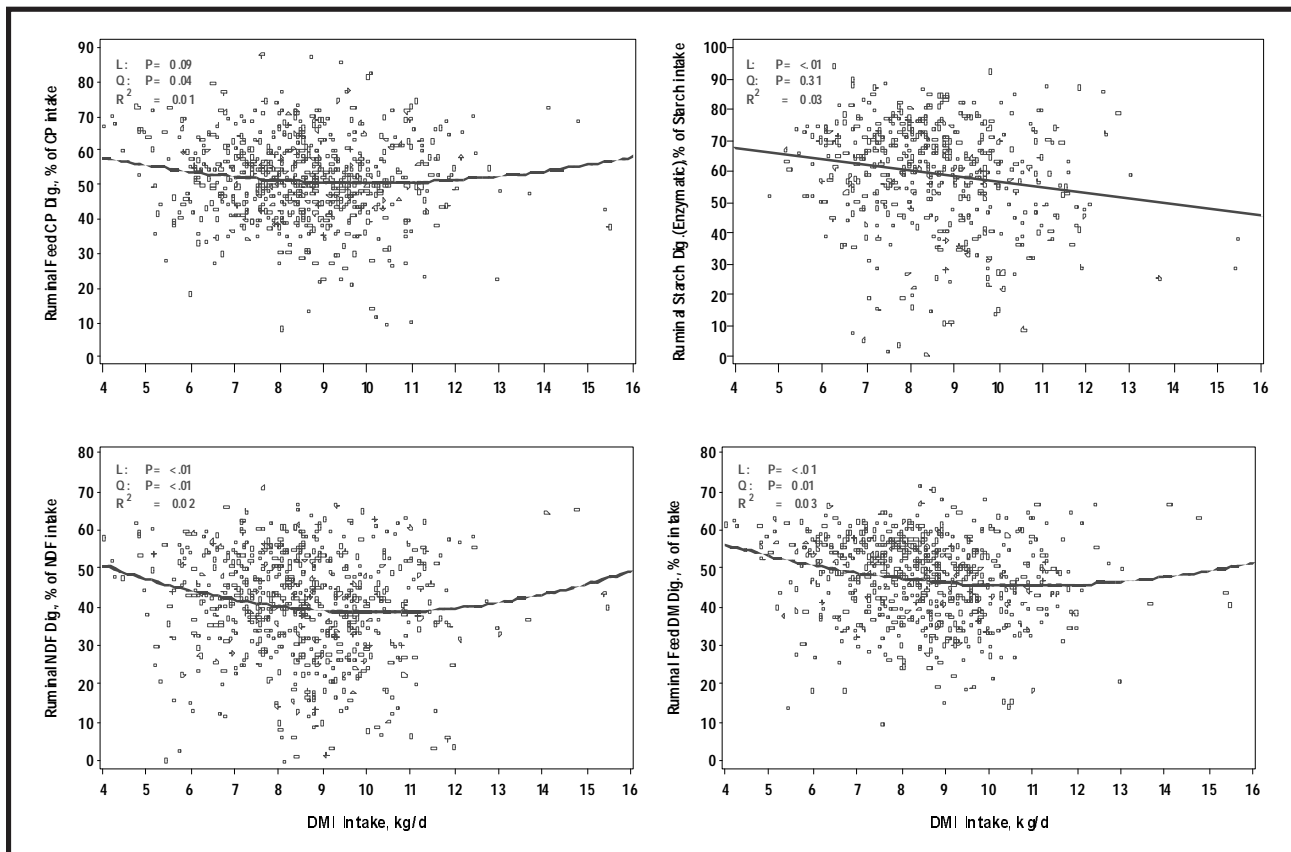
Figure 1. Ruminal digestibility coefficients for dry matter (**DM**), starch, NDF and feed protein (after subtracting out the microbial contributions to the duodenal protein flow) were depressed as dry matter intake (**DMI**) increased.

Data from 44 experiments with 671 Holstein steers (fitted with duodenal and ileal cannulas), conducted by the authors at the Purina Animal Nutrition Center (formerly, the Purina Research Center), at Gray Summit, MO, from 1984 until 2009, encompassing 172 different treatments. Where they existed, linear and quadratic relationships were identified, along with their significance (P values) and their coefficient of determination (R^2).
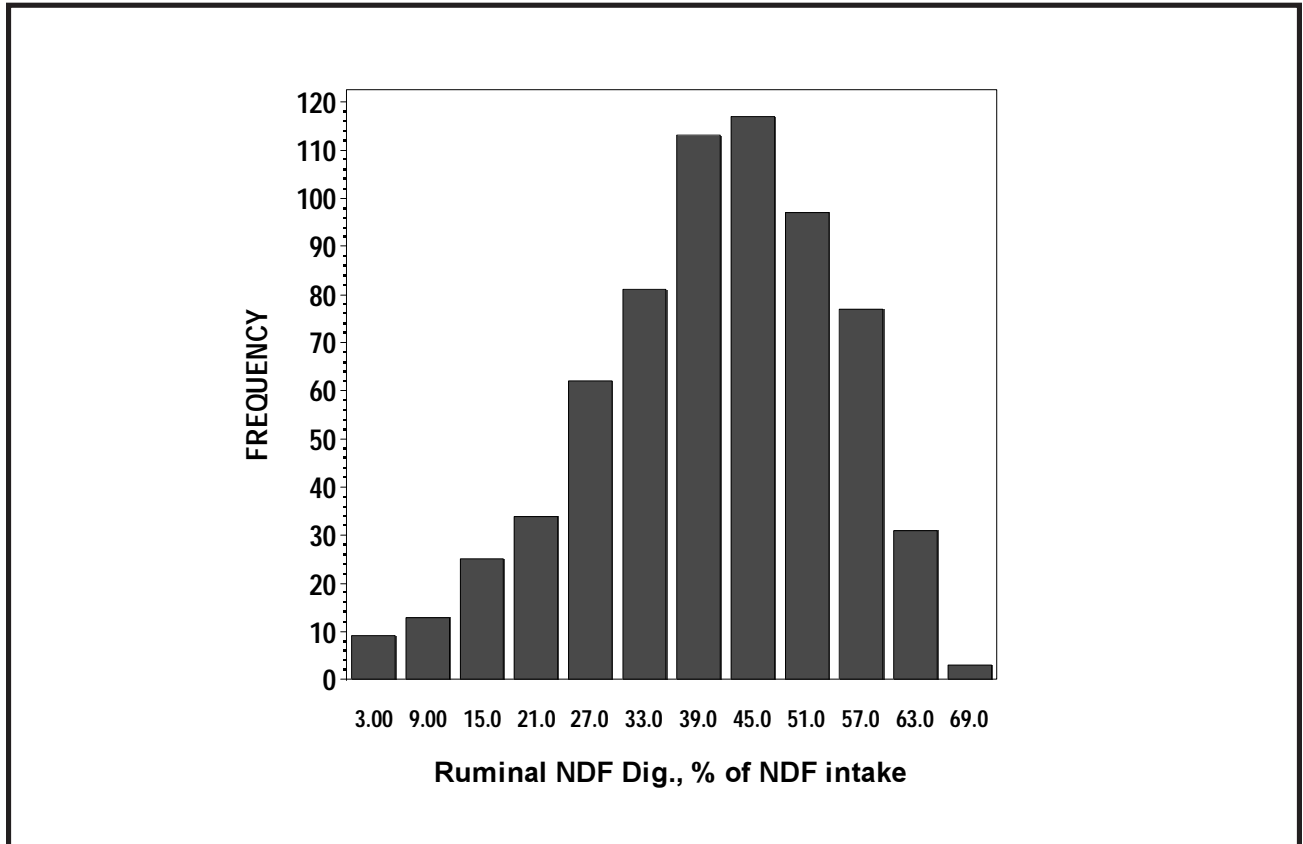
Figure 2. From the wide distribution of data, it becomes apparent there can be a 7 to 10 fold range in ruminal NDF digestibility coefficients.

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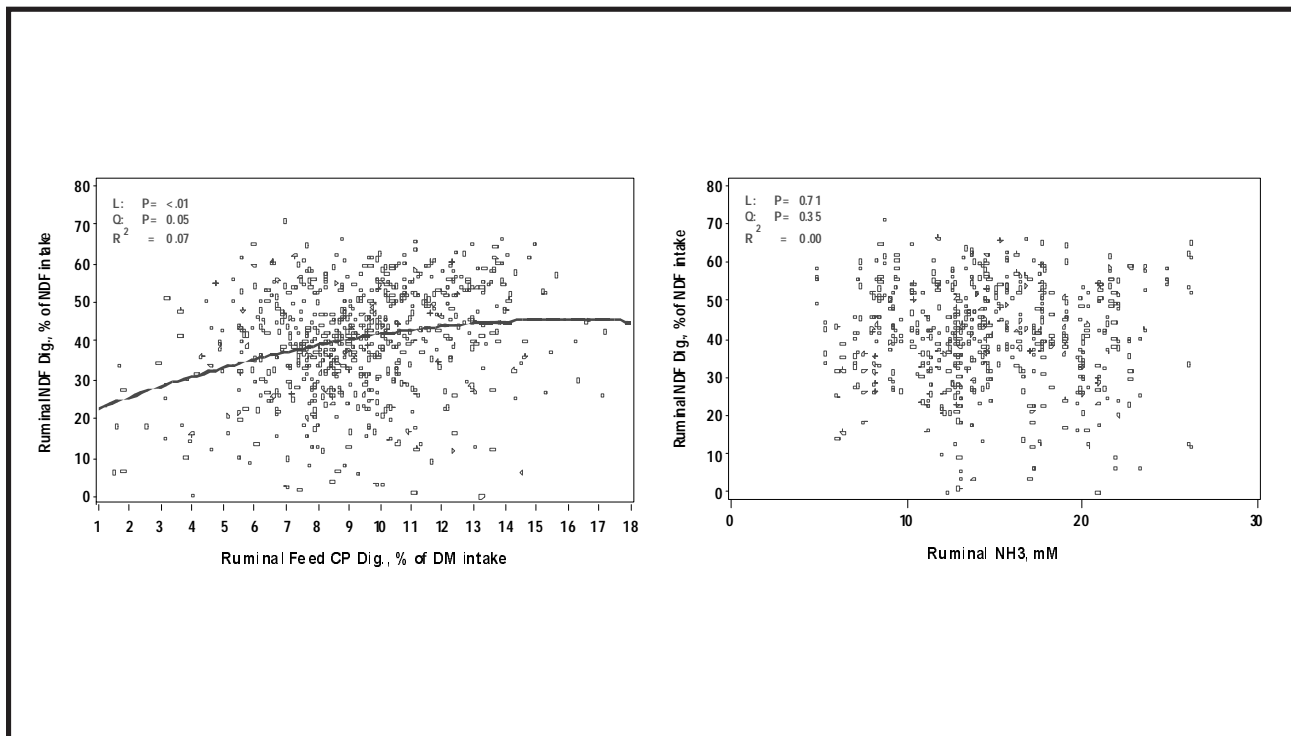
Figure 3. While there was a positive relationship between the amount of ruminal feed protein digestion and ruminal NDF digestibility (P ≤ 0.05), no such relationship existed between ruminal ammonia concentrations and ruminal NDF digestibility.

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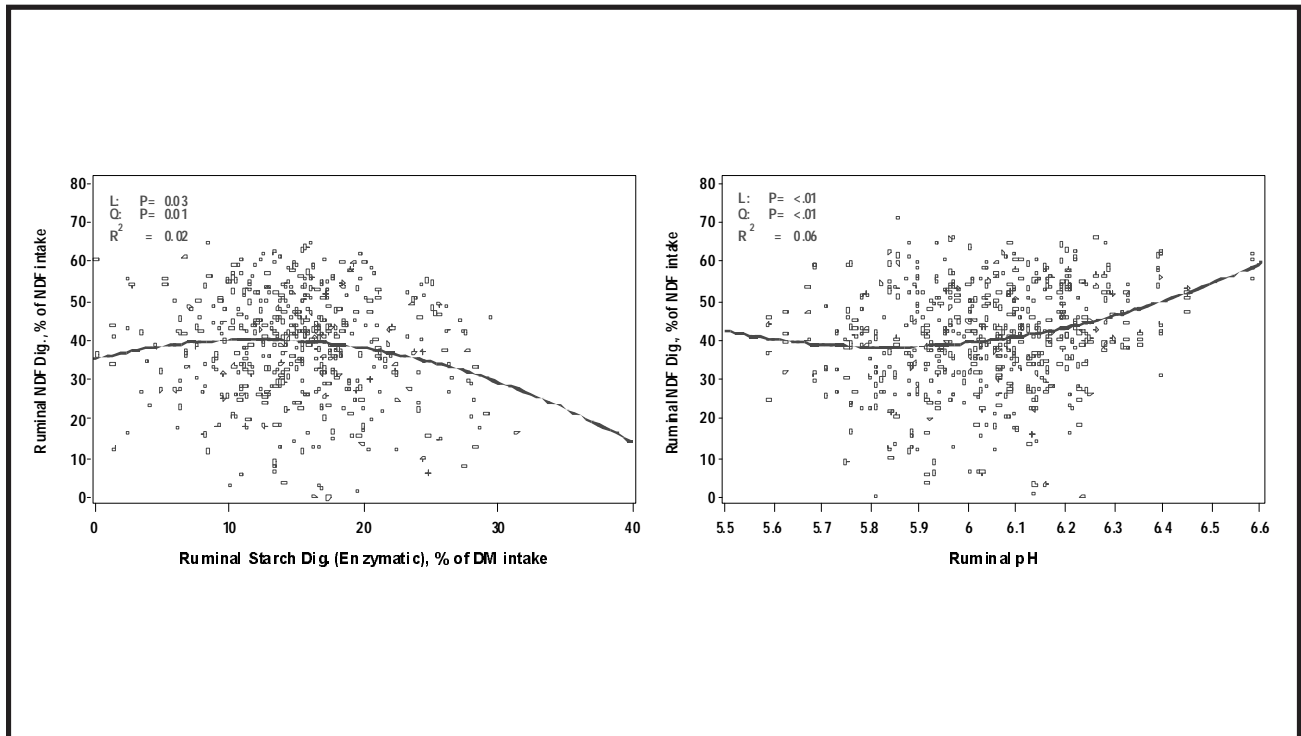
Figure 4. The negative relationship between the amount of ruminal starch digestion and ruminal NDF digestibility ($P \leq 0.01$) would be consistent with the positive relationship between ruminal pH and ruminal NDF digestibility ($P \leq 0.01$).

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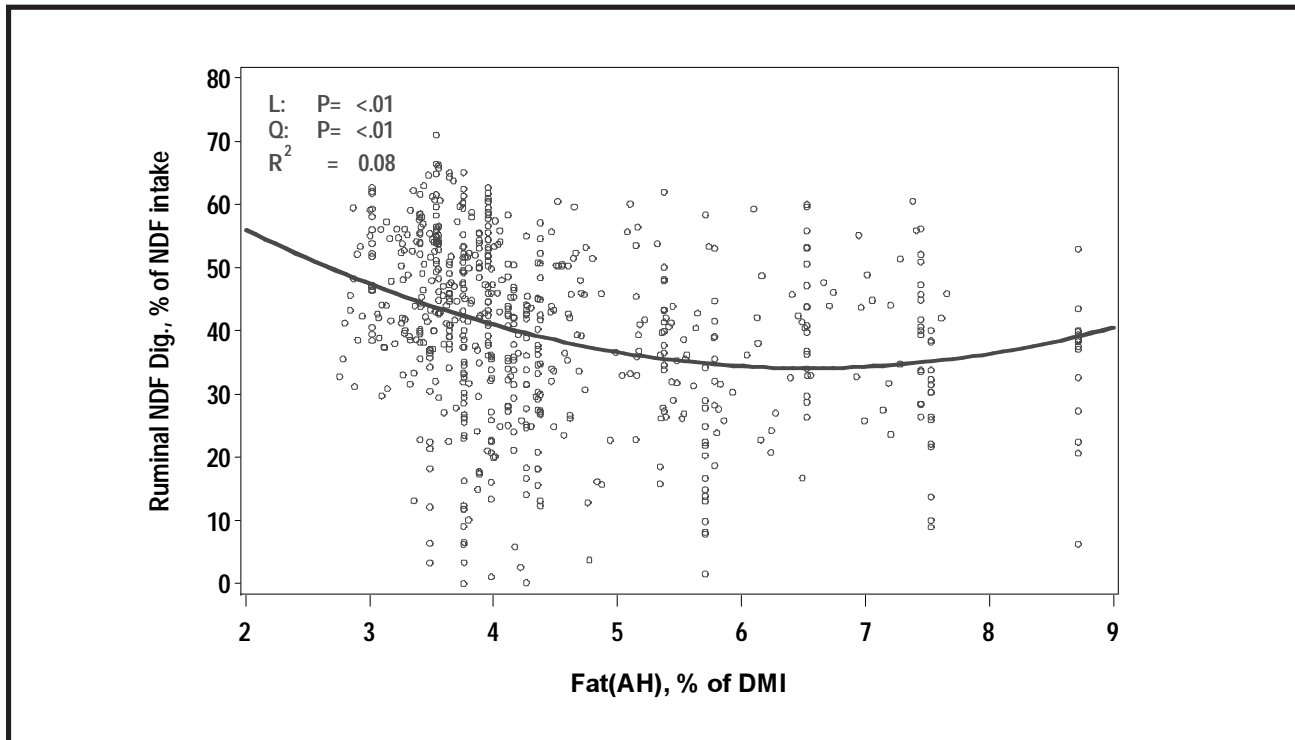
Figure 5. A negative quadratic relationship (P ≤ 0.01) existed between fat percentage in the diet (by acid hydrolysis; FatAH) and ruminal NDF digestibility.

Data from 44 experiments with 671 Holstein steers (fitted with duodenal and ileal cannulas), conducted by the authors at the Purina Animal Nutrition Center (formerly, the Purina Research Center), at Gray Summit, MO, fr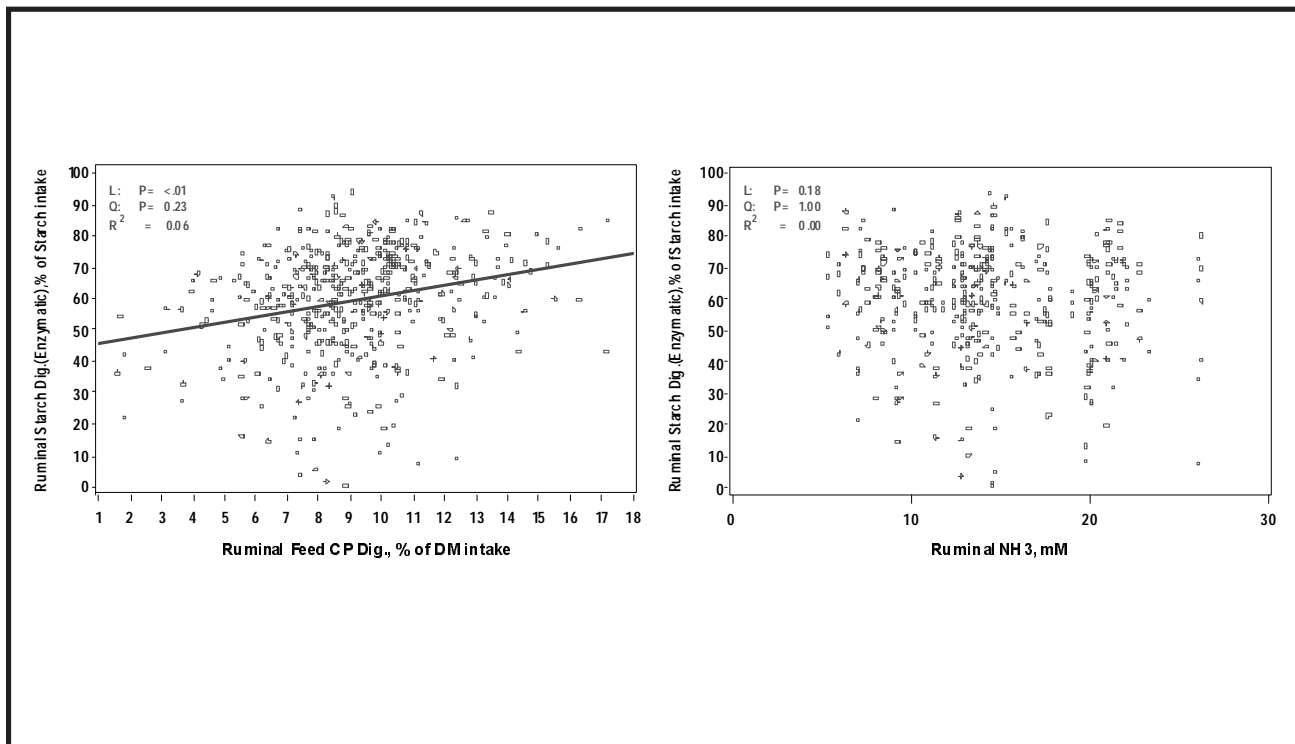om 1984 until 2009, encompassing 172 different treatments. Where they existed, linear and quadratic relationships were identified, along with their significance (P values) and their coefficient of determination (R^2).
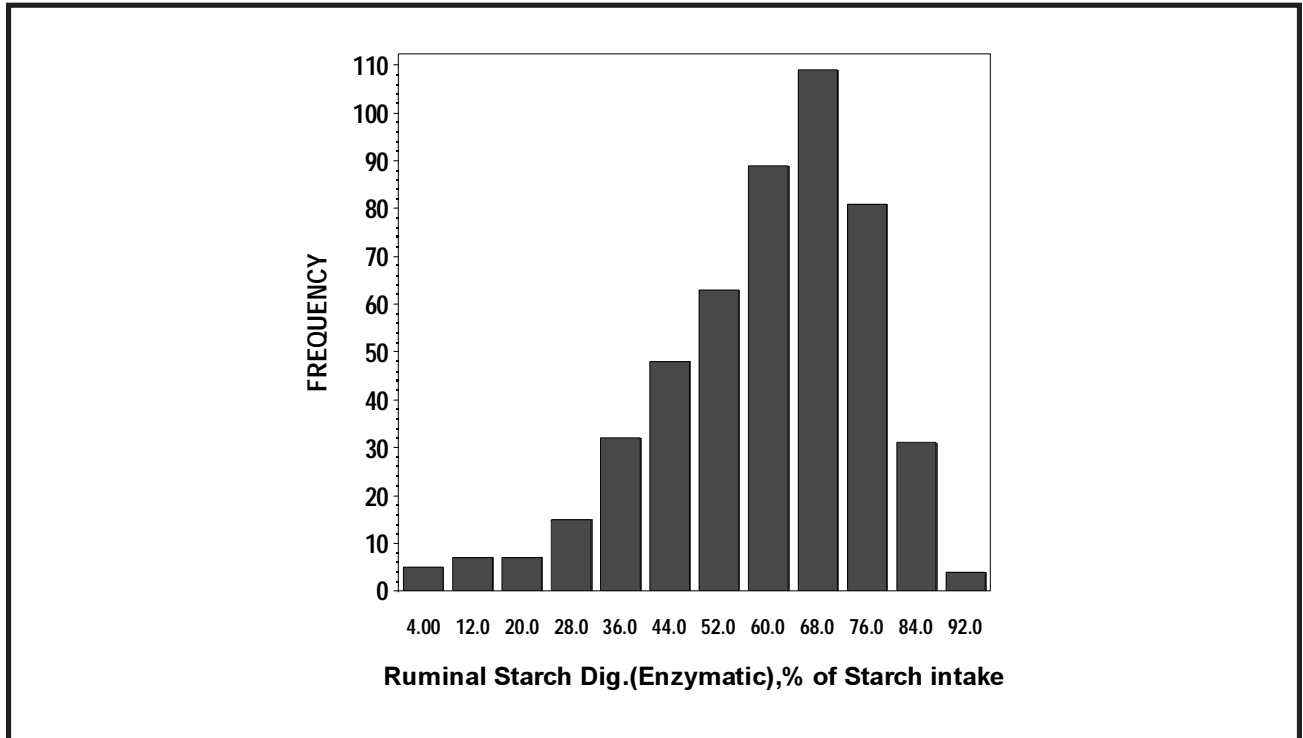
Figure 6. Based on the distribution of data, it becomes apparent there can be a 3 to 4 fold range in ruminal starch digestibility coefficients.

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Figure 7. While there was a positive relationship between the amount of ruminal feed protein digestion and ruminal starch digestibility ($P \leq 0.01$), no such relationship existed between ruminal ammonia concentrations and ruminal starch digestibility.

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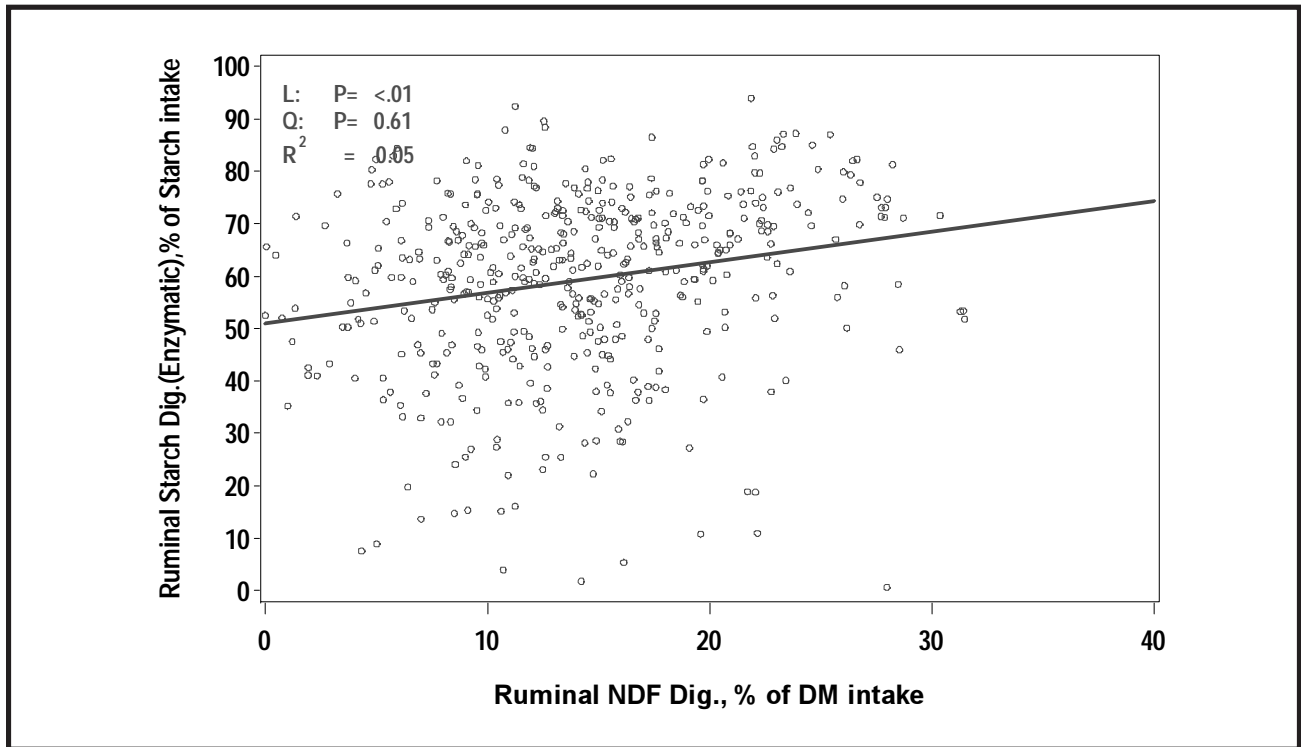
Figure 8. There was a positive relationship (P ≤ 0.01) between the amount of NDF digested ruminally and ruminal starch digestibility.

Data from 44 experiments with 671 Holstein steers (fitted with duodenal and ileal cannulas), conducted by the authors at the Purina Animal Nutrition Center (formerly, the Purina Research Center), at Gray Summit, MO, from 1984 until 2009, encompassing 172 different treatments. Where they existed, linear and quadratic relationships were identified, along with their significance (P values) and their coefficient of determination (R^2).
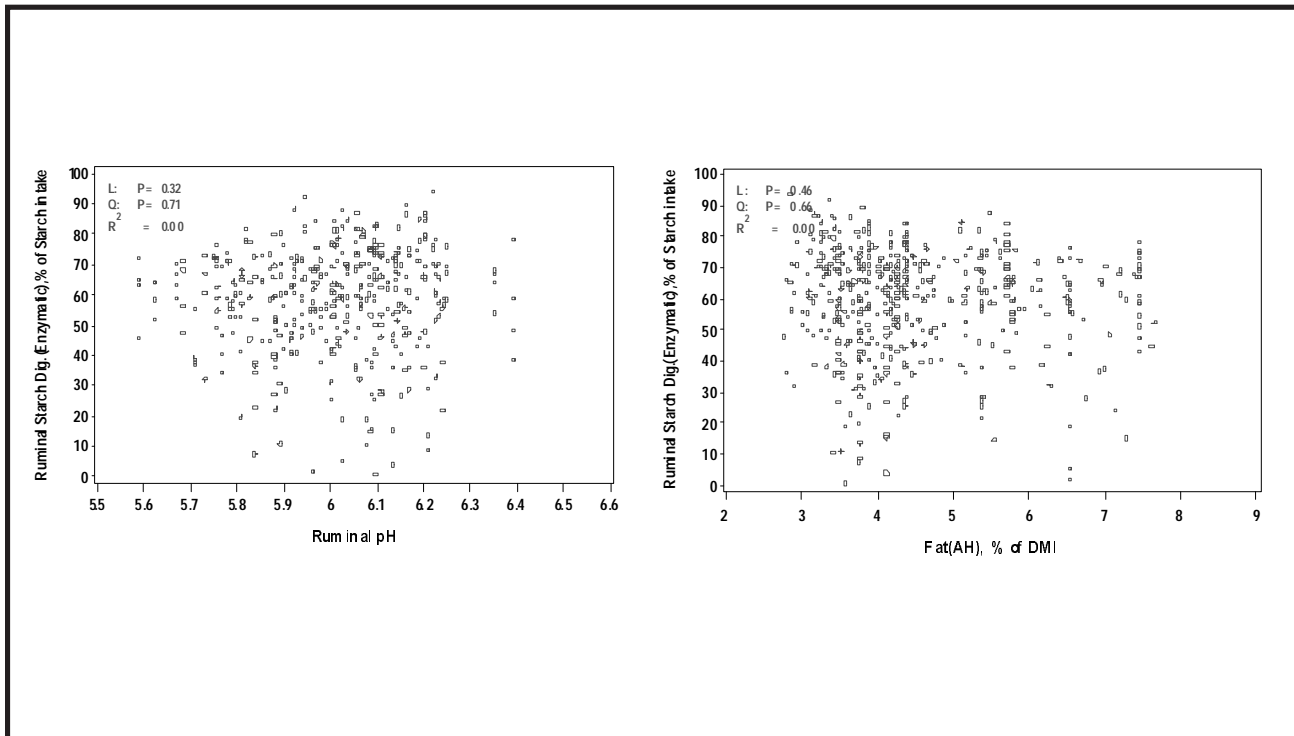
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Figure 9. Neither rumen pH nor fat (by acid dialysis; FatAH) level in the diet had any relationship with ruminal starch digestibility.

Data from 44 experiments with 671 Holstein steers (fitted with duodenal and ileal cannulas), conducted by the authors at the Purina Animal Nutrition Center (formerly, the Purina Research Center), at Gray Summit, MO, from 1984 until 2009, encompassing 172 different treatments. Where they existed, linear and quadratic relationships were identified, along with their significance (P values) and their coefficient of determination (R^2).
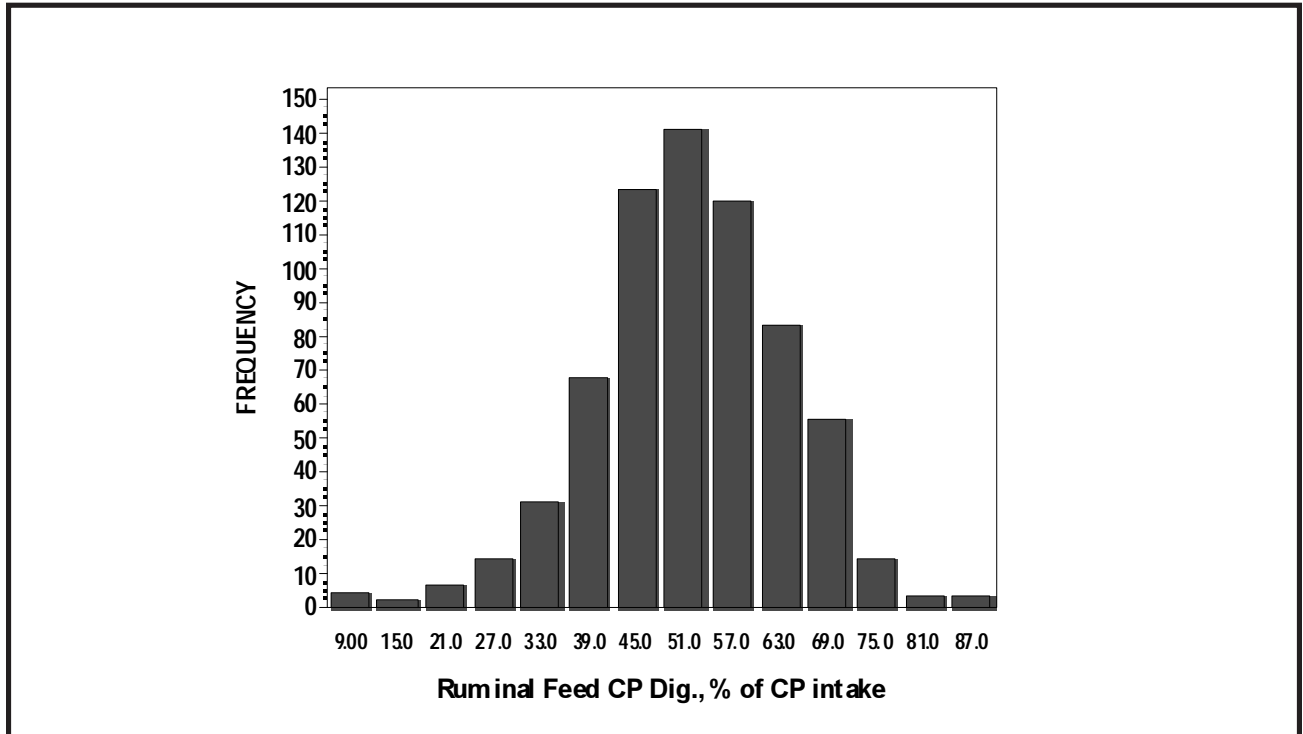
Figure 10. Based on the distribution of data, the 3 to 4 fold range in ruminal feed protein digestibility coefficients is surprising wide.

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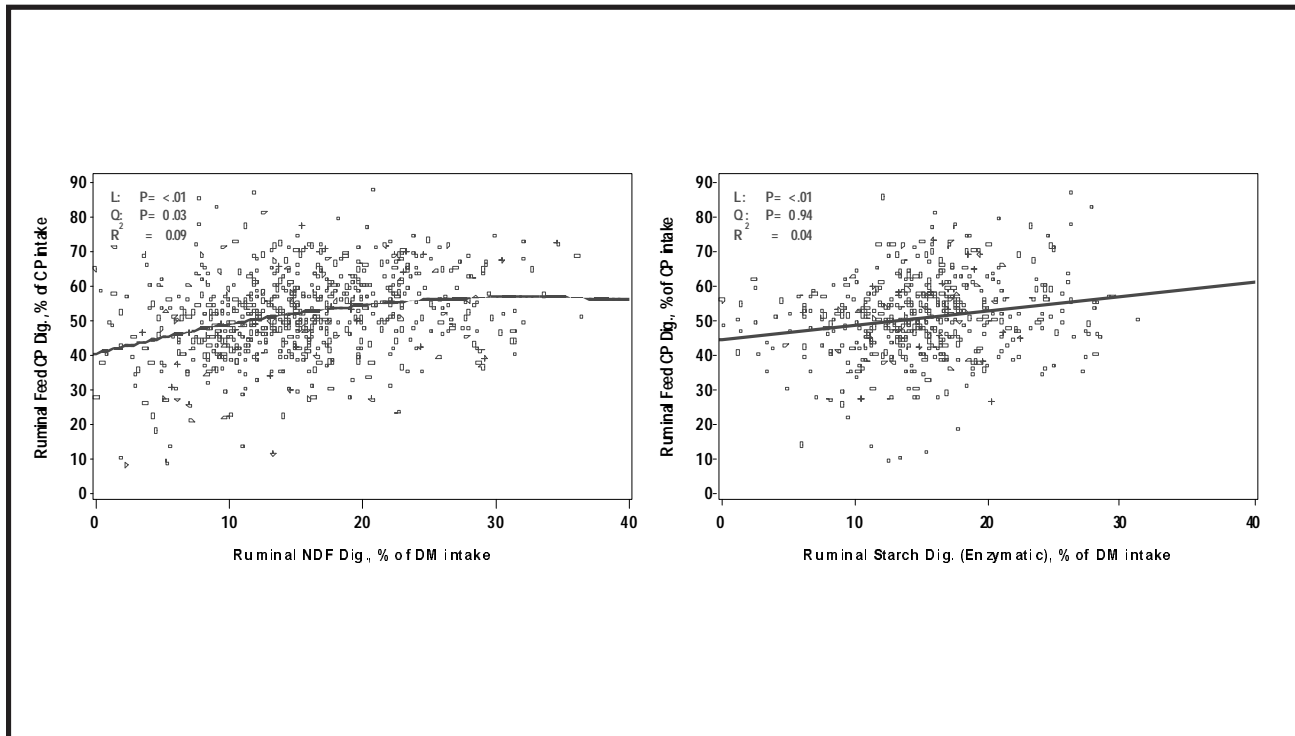
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Figure 11. There was a relatively stronger positive effect from the amount of NDF digested in the rumen ($P \leq 0.03$; $R^2 = 0.09$), than there was from the amount of starch digested in the rumen ($P \leq 0.01$; $R^2 = 0.04$) on ruminal feed protein digestibility.

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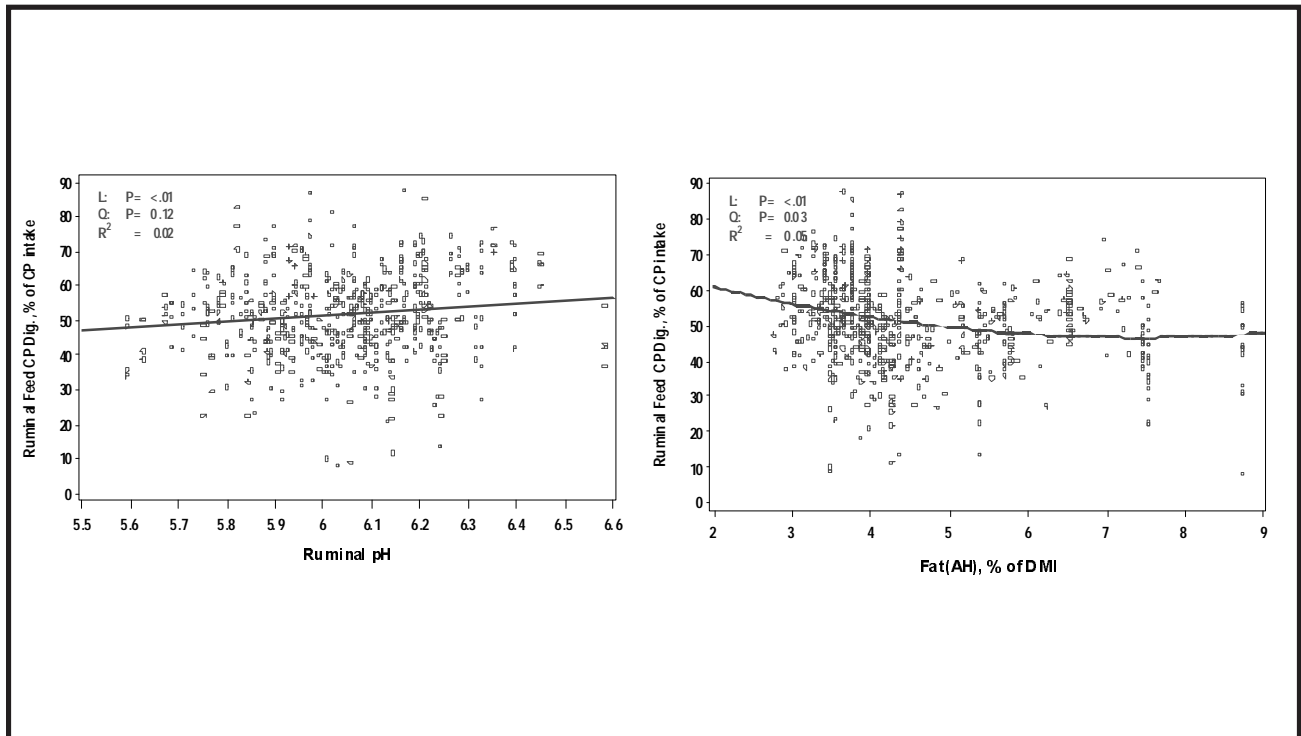
Figure 12. Feed protein digestibility in the rumen increased as pH increased in the rumen ($P \leq 0.01$). However, there was a negative impact of fat (by acid dialysis; FatAH) level in the diet on feed protein digestibility in the rumen
($P \leq 0.01$).

Data from 44 experiments with 671 Holstein steers (fitted with duodenal and ileal cannulas), conducted by the authors at the Purina Animal Nutrition Center (formerly, the Purina Research Center), at Gray Summit, MO, from 1984 until 2009, encompassing 172 different treatments. Where they existed, linear and quadratic relationships were identified, along with their significance (P values) and their coefficient of determination (R^2).