Nutrient Digestibility for High-Producing Dairy Cows: How Much Milk Can You Get from a Ration?

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Introduction

Dietary energy comes from four main feed compound classes: fiber, starch, protein, and fat. Although fiber and starch are both carbohydrates, we will separate them in this paper is if they are different "nutrients", and we will define fiber as neutral-detergent fiber (**NDF**). There are other feed compounds (such as sugars, soluble fiber, and organic acids) that do not fit into one of these four categories, but we will ignore them in this discussion. The typical Gross Energy (**GE**), Digestible Energy (**DE**), Metabolizable Energy (**ME**), and Net Energy for Lactation (**NE_L**) values for these nutrients are shown in Table 1. Because the content of protein and fat is relatively constant, the major determinant of the energy available from a diet is the amount of starch and fiber and the digestibility of each. Starch is generally about 90% digested, whereas the digestibility of fiber (as NDF) can vary widely among feeds but is usually 40 to 50%. Fiber could be subdivided into that from forage and that from nonforage sources. The fiber from some nonforage sources can be quite digestible.

In the 6th edition of the Nutrient Requirements for Dairy Cattle by the National Research Council (NRC, 1989), and previous versions, feeds were each given fixed NE_L values that could be used to balance the energy supply of feeds with the energy requirements of a cow. Because protein and starch had roughly the same NE_L value, and because fat is only a minor part of a dairy diet, balancing diets was largely a matter of altering the amount of individual feed ingredients of varying energy intake based on their starch and fiber contents. The NE_L value of starch is considerably greater than that of fiber, so to achieve high energy intake, high starch feeds were added in place of high fiber feeds to increase the NE_L density of the ration. If the forage had more digestible fiber, less starch from grain was needed. Based on these fixed NE_L values, nutritionists frequently talked about ration targets of 0.76 to 0.80 Mcal/lb NE_L of dry matter intake (**DMI**) when feeding high-producing cows.

The 7th edition of the Dairy NRC (NRC, 2001) introduced a new concept: feed energy values are not constants but instead depend on composition of the total diet and on the animal being fed. The fact that feed NE_L values were not constant was frustrating for many nutritionists, especially at first. Feed labs still predict the NE_L value of feeds, but the values are not used in a system where NE_L values are not constants.

In the 2001 NRC, the total possible DE (**DE1X**) content of a diet is first calculated based on feed ingredients, nutrients within feeds, and the expected digestion coefficients for each nutrient when a nonlactating animal is eating just enough feed to maintain life. This DE1X

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value is then adjusted based on the level of milk production and the diet composition to give a DE value at production level (**DEp**). The DEp of the total diet is then used to predict the ME and NE_L values of the ration at production levels.

As cows eat more, the DEp value of a diet decreases, and so its ME and NE_L values also decrease. Intake should be considered relative to an animal's body weight (**BW**), as a 2 lb increase in intake is biologically more important in a small cow than a large cow. One way to consider level of intake relative to a cow's BW is by calculating her "multiple of maintenance" (**MM**), with 1 MM being a level of intake that sustains life with no gain or loss of body mass and no milk production. Each MM above 1 is used for milk production, activity, or body tissue gain. The 2001 NRC used this MM concept to estimate the digestibility depression of diets, or the calculation of DEp from DE1x. For the typical high starch diet fed to a high-producing cow in the midwest, the digestibility depression in the 2001 NRC was 3 to 4% per MM.

In the 2001 NRC, the digestibility of individual feed components was not altered per se, but the total possible DE1X of a diet was adjusted based on the level of milk production (see Figure 1). This decrease in DEp was greater for diets that contained a greater content of non-fat DE, which would be highly correlated with the content of non-fiber carbohydrate (mostly starch). This interaction of non-fat DE content, level of intake, and digestibility was commonly called an "associative effect", because the digestibility depression for the diet was dependent on how much nonfiber carbohydrate was associated with it.

New Equations Based on Dietary Starch

Because starch was not commonly measured before 2001, the 2001 NRC committee had insufficient data to quantify the effect of starch on fiber digestion. Since 2001, several studies have reported new digestibility values along with animal and diet characteristics. Most of these newer studies reported dietary starch content. Using newer data from individual cows also enables us to get a better estimate for the effect of high feed intake. Finally, statistical tools have become more sophisticated, and we are better able to unravel the multitude of factors that influence nutrient digestion.

Using new data and new tools, we recently published a study (de Souza et al., 2018) with the goal of developing new equations for predicting nutrient digestibility in high producing cows, using data from individual cows to get a better estimate for how variation in intake alters digestibility. Coauthors were Mike Allen and Rob Tempelman (Michigan State), Bill Weiss (Ohio State), and John Bernard (University of Georgia). First, we compiled a database of 1900 observations from 660 cows in 54 studies from Michigan, Ohio, and Georgia to determine the effects of DMI, BW, and diet characteristics on total tract digestibilities of DM, NDF, and starch in high-producing dairy cows. On average, cows ate 51 lb/day of feed DM (3.5% of BW), weighed 1470 lb, and produced 84 lb/day of milk. Cows near the top ate 68 lb/day of feed DM (4.6% of BW) and produced 130 lb/day of milk. Diets averaged 31% NDF, 27% starch, 2.6% fatty acids, and 17% crude protein. The average digestibility values were 66% for DM, 42% for NDF, and 93% for starch. Data from individual cows were analyzed using mixed models including diet composition (chemical composition, forage source, and corn source), DMI as percentage of BW (**DMI%BW**); location; and 2-way interactions as fixed effects, and cow, block, period, treatment, and study as random effects. Best fitting candidate models were generated, as well as a simple model using only DMI and location as fixed effects and all random effects. Candidate models were cross-validated across studies. For each nutrient, the digestibility model that resulted in the highest predictive correlation coefficient and lowest root mean square error of prediction was determined to be the best fitting model. Coefficients for factors were averaged across locations. After averaging for location effects, the overall best fitting prediction equations were determined (Table 2).

Our results confirm that digestibility is reduced as DMI increases, albeit at a lower rate than that reported in NRC (2001), or more recently by Huhtanen et al. (2009). Our decrease in DMD of 0.83 percentage units per unit DMI%BW is a 1.0 percentage unit depression in DMD per MM. Using the diets in our database, the expected decreases in DMD would have been 2.4 and 1.9 percentage units per MM in NRC (2001) and Huhtanen et al. (2009). The studies used in our analysis had much higher average milk production than in NRC or Huhtanen. In addition, the diets in Huhtanen et al. (2009) were mostly high in grass and averaged only 14% starch. Thus, we believe the data from our study are more relevant for modern dairy cows fed diets typical of most US cows today.

Whereas DMD can be predicted based only on DMI, the best predictions for NDFD and StarchD required DMI and diet characteristics. Some feed characteristics used in the NDFD and StarchD equations are likely due directly to characteristics of the NDF or starch. For example, if the diet contains more starch that is highly fermentable (**HFERM**), StarchD will be greater, or if the diet contains more NDF from grass, NDFD will be greater. This effect of grass is not so much an effect of grass on the digestibility of NDF in general, but simply reflects the fact that the NDF of grass is more digestible than the NDF of alfalfa in the total tract at the range of intakes in the studies. However, NDFD was also altered by dietary starch, and this general effect of starch is presumably an effect on all the NDF in the diet.

The effects of starch and DMI on NDFD are shown in Figure 2. In this figure, we show the original prediction of Souza et al. (2018) along with estimates for linear relationships based on the original prediction. Souza's original data included a study with very low intakes and very low digestibilities, and the 95% confidence interval around the prediction at low intakes was broad. Thus, we developed another response that was linear. The linear relationship was set to match the Souza curves at DMI > 3.5% of BW and to be consistent with predictions based on the previous NRC. Note that even with this change, the effect of starch is still much greater than the effect of DMI within the range of normal intakes expected for high producing cows (>3% of BW). The resulting change in NDFD with changes in intake and starch is:

Change in NDFD as %NDF = -0.59 (change in % starch) - 1.1 (change in DMI%BW)

Our equation presents a middle ground on predicting NDFD between two other recent meta-analyses. Ferraretto et al. (2013) reported a similar drop in NDFD from starch but no change due to feed intake, whereas White et al. (2017) reported no change in NDFD due to starch but a greater effect of intake. One problem with analyzing the effects of DMI and starch on NDFD is that seldom does one change without a change in the other. Level of intake is strongly associated with starch content of a diet. The depression in NDFD as dietary starch increases is reflective of the "associative effect" described in the 2001 NRC. In NRC 2001, diets with a greater %TDN from nonfiber carbohydrate had greater depressions in digestibility at high intakes. This was complicated by the fact that diets with more starch (higher %TDN) are less filling, and thus enable greater intake; and conversely, that cows on low starch diet (low %TDN) cannot eat as much. Thus, the digestibility depression caused by high feed intake was overestimated in NRC 2001. Greater intake is associated with lower NDFD for two reasons: 1) greater intake might directly increase passage rate and so decrease NDFD, and 2) greater intake is often the result of a greater %starch, which also decreases NDFD. In the new equation, we account for these two factors (%starch and DMI) separately, although changes in one are almost always concurrent with changes in the other. NRC 2001 also accounted for these separately, with starch accounted for as basal TDN. However, NRC 2001 only predicted changes in digestibility for DE, not individual nutrients. If we assume that much of the change in DE digestibility in NRC was due to changes in NDFD and that the effect of basal non-fat TDN in NRC was due to starch, then NRC 2001 predicted an interaction on NDFD between DMI and starch content. We saw no evidence for this interaction. In addition, the effect of starch was much greater than the direct of intake. All cows were fed ad lib in de Souza et al. (2018), so we are not sure these equations are relevant for cows fed at restricted feed intake.

The effect of intake on starch digestion is less than that of Ferraretto et al. (2103). They found a drop in total tract starch digestibility of 0.24% units per kg of DMI, which would be 1.7% for a 1 unit of DMI per BW in a 700 kg cow (1540 lb).

In the Souza et al. (2017) study, the level of intake was described as DMI as a % of BW, rather than as MM. Multiples of Maintenance can be a problem to quantify intake because it presumes that we accurately know maintenance requirements and because it can cause circular arguments (level of MM alters digestibility, which alters the amount of feed needed for maintenance, which alters level of MM at any given intake). A more direct way to consider level of intake is to simply avoid estimating maintenance and instead divide daily intake by BW. Because maintenance is considered a function of BW to the 0.75 power, these two methods differ (Figure 3), but for a cow at 1500-1600 lb body weight (**BW**), 1 MM is about 1 lb/day of feed DM per 100 lb of BW. Most high-producing lactating cows eat between 3 and 5% of BW per day during lactation.

Implications

So how would these new equations affect the energy value of feeds? In Table 3, we show the implications of changing DMI and starch content on the predicted NE_L of the diet and expected milk production if energy is the limiting factor for milk.

Using the new equations, increasing intake depresses digestibility of fiber and starch a little and decreases the NE_L of the total diet. As expected, increasing DMI can greatly increase the energy available to make milk, regardless of this small depression in digestibility.

Starch is about twice as digestible as fiber, and feed laboratory reports typically give NE_L values for grains that are considerably greater than those of forages. Thus, one would expect that increasing starch would increase the energy available for milk, as shown in the second tier of rows in Table 3. If starch had no effect on NDFD, then the increase in milk would be 7.4 lb/day for every increase of 8% units of starch (not shown in table). Instead, because starch depresses fiber digestibility, the increase is only 5 lb, and financial advantage from replacing fiber with starch may be lost. The NE_L available would increase just as much by increasing the base NDFD of the diet by 8% units as by increasing starch content 8 % units.

As an example, if intake were held constant, the addition of soyhulls to a diet in place of forage with low NDFD would increase diet NE_L supply as much as would corn grain, because the soyhulls are high fiber with a high basal NDFD and contain no starch to depress NDFD as does the corn grain.

Finally, the table demonstrates that if greater dietary starch enables cows to eat more, then milk yield can increase dramatically with the higher starch diet. The values in the table are for purposes of illustration only and do not necessarily reflect the expected changes in DMI with different starch concentrations. In the end, the predicted changes in NE_L supply for milk using these new equations is similar to the predictions based on NRC 2001. However, the direct effect of starch (or % basal non-fat TDN in NRC) is greater and the direct effect of DMI is less in the new equations than in the NRC 2001.

The changes in expected NE_L values in Table 3 may still be unrealistic. When balancing or evaluating diets, we typically calculate the NE_L value of a diet based on its nutrients, digestibility and expected losses in urine and gas energy and heat, as was done for Table 3. We could also calculate the apparent NE_L value of the diet if we know how much NE_L she apparently consumed based on her response to a diet. Apparent NE_L supply can be calculated as the sum of NE_L for maintenance (0.08 x BW0.75) + NE_L for BW change (~6 Mcal/kg) + milk energy output. In recent studies at MSU, where we had accurate measures of BW and BCS change, cows have been fed diets with varying amounts of forage NDF, nonforage NDF, and starch. Replacing NDF with starch causes even less difference in the apparent NE_L value of a diet than expected based on diet calculations, such as those in Table 3 (Carrasquillo-Mangual et al., 2017; Potts et al., 2017). The major benefit of replacing forage fiber with starch was that it increased feed intake in high-producing cows.

Limitations

In this study of de Souza et al. (2018), we had insufficient data to account for the ruminal digestibility of starch, as was previously shown to be important in Ferraretto et al. (2013). We recognize that dietary starch content alone is inadequate to describe the mechanisms for the effect of starch on NDFD. Future studies should further examine the impact of ruminally-available starch. In addition, we expected to find that the NDF from grass would be more digestible than alfalfa NDF at low intakes but then become less digestible relative to alfalfa as intake increased. The studies included in Souza et al. had insufficient diets containing grass to accurately assess the interactions of DMI for NDFD of grass and alfalfa.

One reason to predict energy values of feeds is to choose feeds that will give the most profit; this requires having some knowledge of the available energy from a feed relative to its cost. Various systems have been developed to account for the additional value of protein or other nutrients within a feed. More sophisticated methods might even assign feeds a cost related to nutrient excesses (such as for phosphorus) and try to account for all of the other feeds that are actually available for use on a farm. Implicit in any least-cost or profit-maximization balancer is the assumption that we can accurately model how feeds alter energy availability from the feed, intake of the diet, and partitioning of available energy; none of these are true.

Our proposed system clearly shows that NE_L can only be predicted for a complete diet, not for individual feeds (NRC 2001 also showed this). The idea that a feed has one energy value (as feed labs indicate) is just not true. If adding more corn to a diet decreases the digestibility of the alfalfa, then single NE_L values for feeds are meaningless. Should we give alfalfa a lower NE_L

value because it might be fed with corn? Should we give corn a lower NE_L value because it can decrease the digestibility of alfalfa? There is no way to accurately compare the price of feeds that vary in starch without first determining what their effect will be in the total diet. The idea that individual feeds have their own NE_L values is clearly not the way that the real world works.

Not only can one feed alter the digestibility of another, but feeds can alter appetite and nutrient partitioning. Unless we can accurately predict nutrient digestibility, intake, and partitioning in cows fed ad libitum, we cannot use models to accurately formulate diets, as we cannot accurately predict many of the intermediates needed in ration formulation, such as microbial protein yield and mammary amino acid requirements (if a diet increases intake, both will likely increase). New equations have been developed that seem to do a reasonably good job of predicting feed intake based on feed factors (Sousa et al., 2017), but these have not yet been implemented in ration balancing models, and how they should be implemented is not a simple decision. Equations that work in peak lactation may not work in later lactation because cow nutrient demand, which is the cumulative effect of stage of lactation, milk production, milk composition, body condition score, and maturity, alters how a cow responds to dietary changes. Low producers with heavier body condition scores will not respond to dietary starch the same way as a high producing cow (Boerman et al., 2015).

Until we can accurately predict responses in the voluntary feed intake, digestion, and partitioning of nutrients in response to dietary changes, we cannot predict how diets will alter milk income and profitability. More than ever, we need to pay attention to cows, not just computers, when formulating diets for high production (Allen and VandeHaar, 2016).

Summary

NE_L values of individual feeds, whether from feed tables or from feed analyses, are largely irrelevant, and even worse, they can be misleading. Energy availability must be considered on a total diet basis because nutrients interact with each other. Both level of intake and dietary starch content alter fiber digestibility, and starch content seems more important than level of intake. Increasing dietary starch decreases fiber digestibility so that the predicted increase in NE_L density of a diet is less than expected and may not change very much. The real value of feeding grain to a high producing cow whose intake is limited by gut fill is that the grain enables greater feed intake per day. With greater intake, more energy is available to produce milk, and feed efficiency and profitability will generally increase. This can and should be monitored on farms so that starch is used most effectively.

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Table 1. Energy values of nutrient based on average conversions.

	Fiber	Starch	Protein	Fat
Gross Energy (GE), kcal/g	4.2	4.2	5.7	9.4
Conversion of GE to DE	50%	90%	90%	75%
Digestible Energy (DE), kcal/g	2.1	3.8	5.1	7.1
Conversion of DE to ME[1]	81%	86%	70%	100%
Metabolizable Energy (ME), kcal/g	1.7	3.3	3.6	7.1
Conversion of ME to NE_L[2]	66%	66%	66%	80%
Net Energy for Lactation (NE_L), kcal/g	1.1	2.1	2.3	5.6
Net Energy for Lactation, Mcal/lb	0.5	1.0	1.1	2.6

[1]Conversions of DE to ME are based on Appuhamy et al. (2016) and Ermias Kebreab (personal communication).

[2]Conversions of ME to NE_L are based on Moraes et al. (2015), except fat is based on NRC (2001).

Table 2. Total tract digestibility equations for DM, NDF, and Starch (de Souza et al., 2018).

DM Digestibility (DMD) = 69 – 0.83 x DMI%BW where DMI%BW is DMI as a % of BW.
NDF Digestibility (NDFD) = 53 + 0.26 x Grass%DM - 0.59 x Starch%DM + 3.06 x DMI%BW – 0.46 x DMI%BW2 where Grass%DM is the DM of grass in the diet as percentage of total diet DM, and Starch%DM is the starch DM in the diet as a % of total diet DM.
Starch Digestibility (StarchD) = 96 + 0.19 x HFERM%DM – 0.12 x Starch%DM – 1.13 x DMI%BW where HFERM%DM is highly-fermentable starch as percentage of DM.

Table 3. Predicted total tract digestibilities for starch and NDF, dietary NEL content, and energy-available milk at various intakes and dietary starch contents.

DMI % of BW	Dietary Starch	Dietary NDF	Predicted StarchD[1]	Predicted NDFD[1]	Predicted Diet NE_L Mcal/lb[2]	NE_L-available 3.5% Fat-Milk lb/day[3]
Effect of increasing intake with 26% starch diet						
2.0%	26%	36%	94%	48%	0.750	40
3.5%	26%	36%	92%	46%	0.739	94
5.0%	26%	36%	91%	44%	0.729	146
Effect of increasing starch at DMI of 3.5% of BW						
3.5%	18%	44%	92%	51%	0.718	90
3.5%	26%	36%	92%	46%	0.739	94
3.5%	34%	28%	92%	41%	0.768	99
Effect of increasing intake with diets that increase in starch						
2.0%	8%	54%	94%	58%	0.713	36
2.5%	14%	48%	93%	54%	0.718	54
3.0%	20%	42%	93%	50%	0.726	73
3.5%	26%	36%	92%	46%	0.739	94
4.0%	30%	32%	92%	43%	0.749	114
4.5%	34%	28%	91%	40%	0.761	135
5.0%	36%	26%	91%	38%	0.766	156

[1]In this example, base NDFD at 26% starch and DMI of 3.5% of BW is considered to be 46% and the NDF quality of the diet is not altered with different scenarios. Base starchD is 92%. In real life, higher NDF diets are frequently associated with greater inclusions of more digestible NDF sources.

[2]Predicted NE_L assumes the diet also contains 5% ash, 2% fatty acids, 17% CP, and 14% other organic material (such as sugars, soluble fiber, and silage acids). The DE to ME and ME to NE_L conversions were those used in Table 1.

[3]NE_L-available milk was calculated by subtracting 10.9 Mcal/day for maintenance from the NE_L supply and assuming no change in BW.

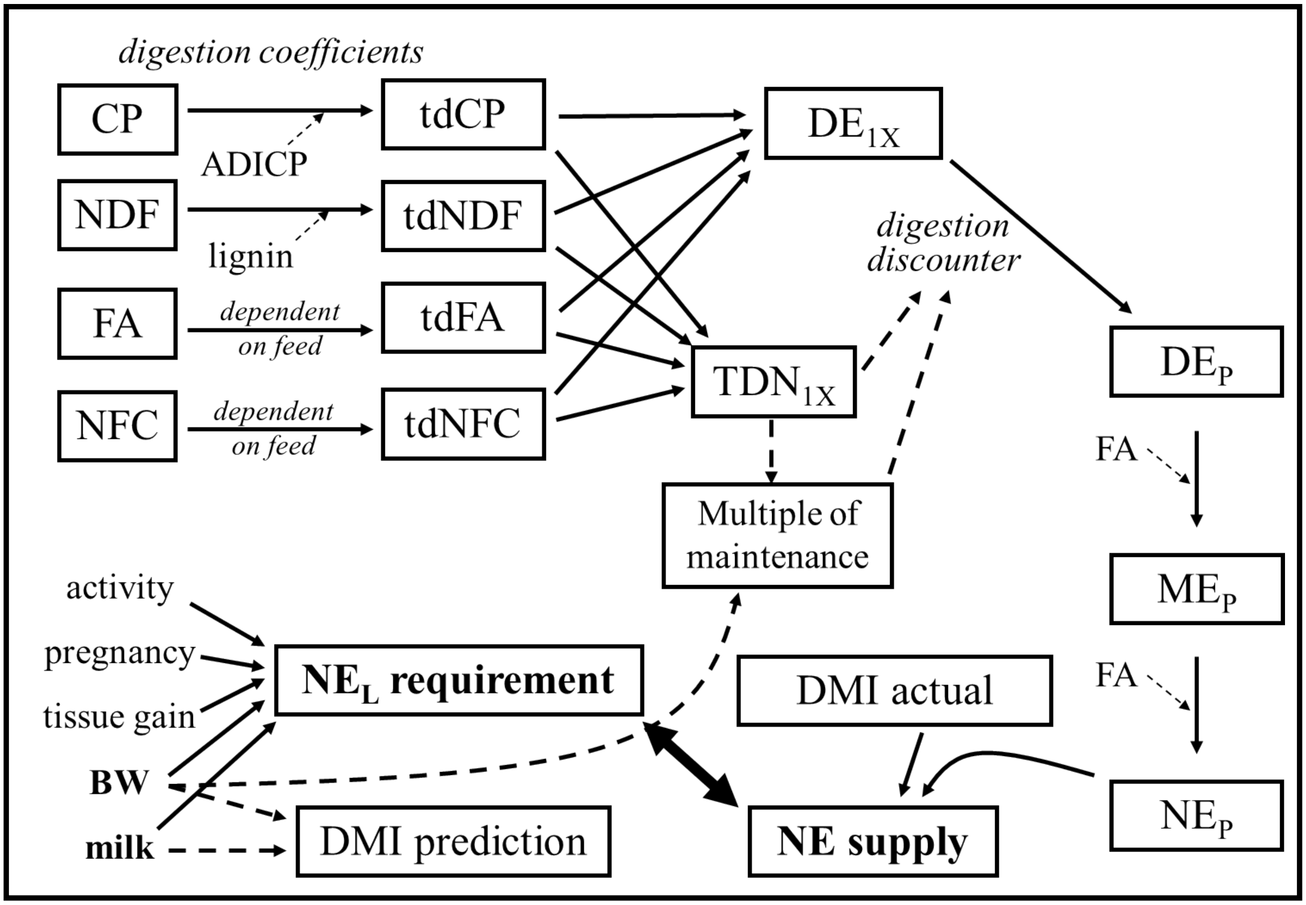

Figure 1. Energy calculations in the 2001 Dairy NRC. DE1X is calculated for each feed based on its nutrients and digestion coefficients, and then DE at production level is determined by the multiple of maintenance and base TDN value of the total diet. Finally, ME and NE_L values for each feed are predicted, and the total NE_L supply is a function of the amount of each feed and its NE_L content.

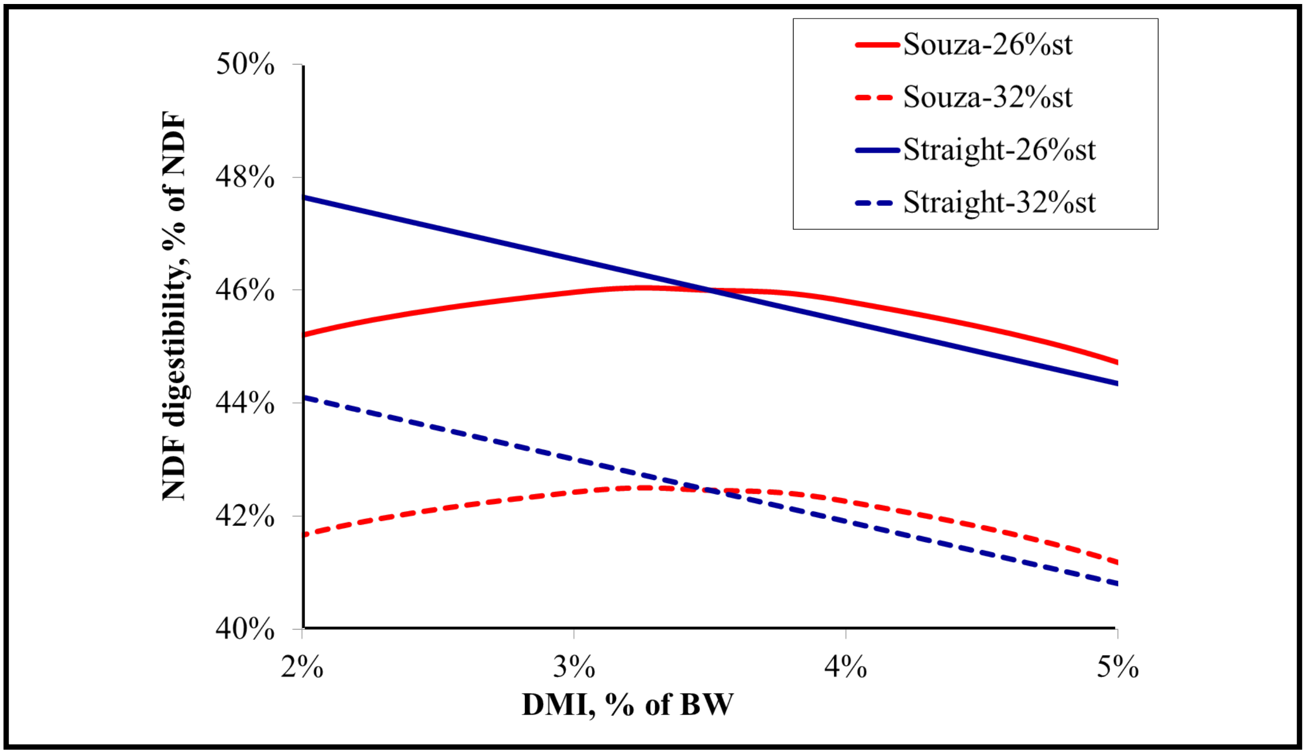

Figure 2. Effects of % starch in the diet and DMI as % of BW on the digestibility of NDF in a typical dairy diet. The response of NDFD to 26 (solid) and 32% (dashed) starch diets is shown using the original equation of Souza et al. (2018) or a derivation that includes only a linear relationship between intake and NDFD. Note that the effect of starch is greater than the effect of DMI.

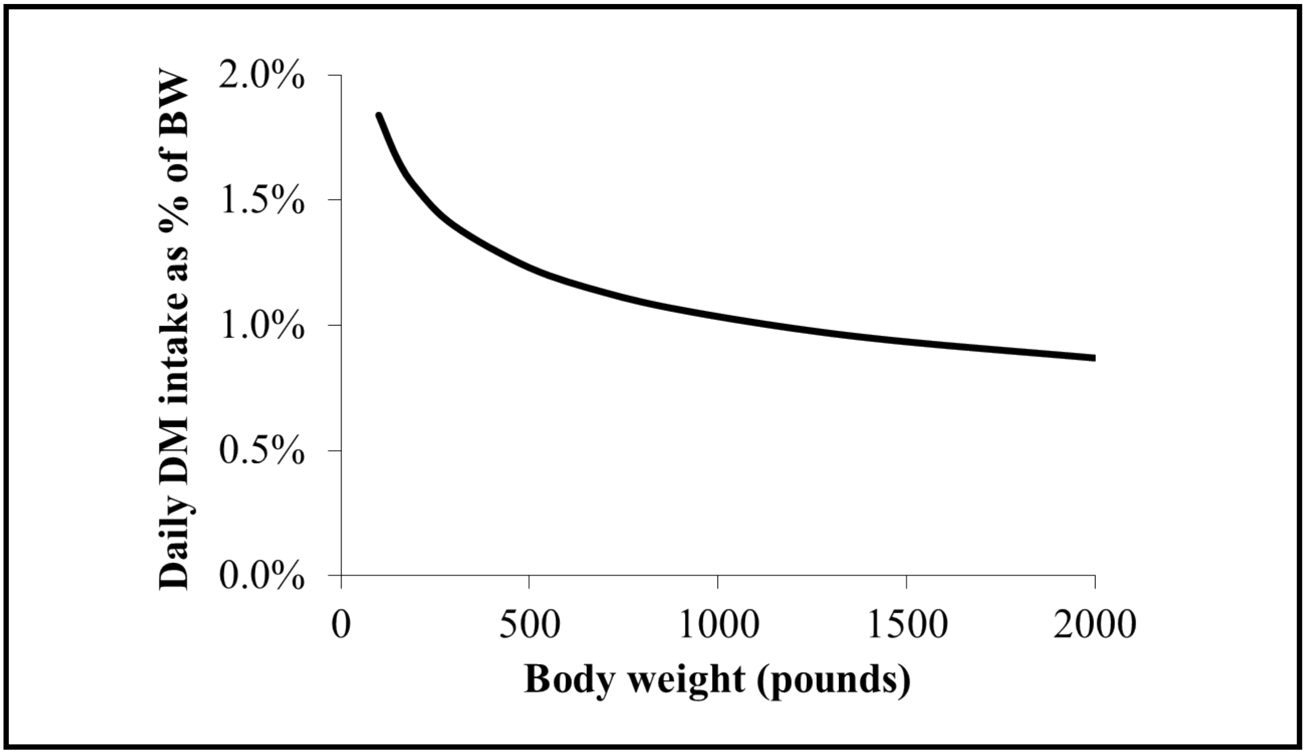

Figure 3. Amount of DM intake as a % of BW to meet the maintenance requirement of an animal if the diet contains 0.76 Mcal of NE for maintenance per pound. For a 1500-lb cow, an intake of 1 multiple of maintenance is equal to a DMI of 1% of BW.