# Carbohydrate Nutrition

## Managing Energy Intake and Partitioning Through Lactation

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**KEYWORDS**

- Energy intake • Energy partitioning • Energy balance • Feeding behavior
- Grouping cows • Maintenance group • Ruminal starch fermentability
- Fiber digestibility

**KEY POINTS**

- Energy intake and partitioning are affected by the interaction between diet and the physiological state.
- Control of feed intake is complex and involves the integration of multiple signals by brain feeding centers; dominant control mechanisms vary within a day and across diets and physiological states.
- Energy partitioning is affected by insulin concentration, insulin sensitivity, and the type and temporal supply of fuels provided by the diet.
- Concentration and digestion characteristics of forage fiber affect the filling effect of diets and feed intake, especially when ruminal distention dominates control of feed intake around peak lactation.
- Concentration and ruminal fermentability of starch are primary factors related to metabolic control of feed intake, which likely dominates in the transition period and midlactation to late lactation.
- The optimal diet will vary with the physiological state; therefore, different rations must be offered through the lactation cycle to maximize milk yield, efficiency of production, and cow health.

## INTRODUCTION

Carbohydrates normally compose more than 60% of the diets of lactating cows and can have large effects on energy intake and partitioning. These effects depend on the type and digestion characteristics of carbohydrates, which interact with the

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physiological state of cows. Forage fiber is more filling than other diet fractions because of its initial bulk and because it is digested more slowly over time. Therefore, concentration of forage fiber in diets can limit feed intake during periods when control of feed intake is dominated by ruminal distention. Feed intake can also be limited by ruminal fermentability of starch, through fuels that stimulate hepatic oxidation and increase hepatic energy status, especially during the transition and midlactation to late-lactation periods. Starch supplies glucose and glucose precursors for synthesis of milk lactose, the production of which is the primary determinant of milk yield. However, some starch sources are rapidly fermented; excessive ruminal fermentability can decrease ruminal pH and alter ruminal biohydrogenation pathways, reducing milk fat concentration and yield. Milk fat depression (MFD) spares glucose, potentially increasing plasma insulin concentration and energy partitioned to body reserves. The objective of this article is to discuss carbohydrate type and digestion characteristics and how they interact with the physiological state of cows to affect energy intake and partitioning and ultimately milk yield and cow health.

## CONTROL OF FEED INTAKE

Energy-intake control mechanisms are complex and involve multiple signals, redundancies, and levels of integration. Signals related to hunger and satiety are integrated in brain feeding centers to control feeding behavior and, consequently, energy intake.[1] It is important to understand that there is rarely, if ever, a single signal controlling feeding behavior but rather multiple signals that are integrated to determine feeding. At times, certain signals dominate control of feeding; these signals vary temporally, within days, as well as across physiological states and diets. Feeding behavior is determined by meal size and frequency and is not only affected by physical, metabolic, and endocrine signals but also by management and environment (Fig. 1).

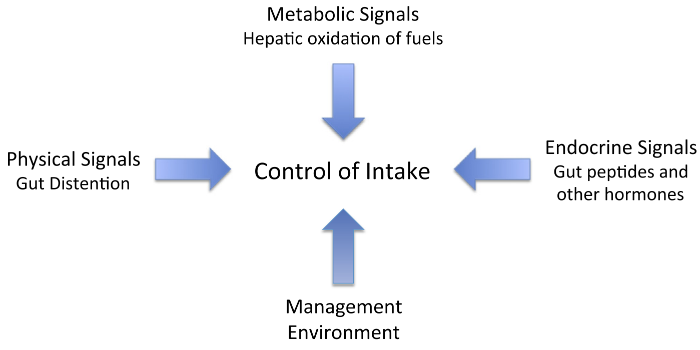


**Fig. 1.** Intake is controlled by signals from physical, metabolic, and endocrine origin as well as by the environment and management. Metabolic signals likely predominate during the transition period and midlactation to late lactation: increased hepatic oxidation of fuels can increase energy status of the liver, inducing satiety and the end of a meal. Signals from gut distension start to predominate as lactation progresses after the fresh period and during peak lactation, when milk production is greatest, and are affected by concentration and digestion characteristics of forage neutral detergent fiber (NDF). Endocrine signals contribute to the control of feed intake throughout lactation and are affected by nutrients in the chyme (eg, cholecystokinin, glucagon-like peptide 1) and energy balance of the cow (eg, leptin). Management (eg, competition, access to feed, availability of feed) and the environment (eg, heat index) can also affect feed intake, especially during periods of stress (ie, transition period). All signals can occur simultaneously and are integrated in brain feeding centers to affect control of feed intake within a meal, within a day, and in the long-term.

### *Physical Control*

Physical constraints to feed intake in ruminants have been previously reviewed.[2] Ruminal distension stimulates tension receptors located in the reticulum and cranial sac of the rumen,[3] and the resulting signal is conveyed to brain feeding centers via vagal afferents. Rumen distension is affected by both the volume and weight of digesta,[4] which is primarily determined by forage neutral detergent fiber (NDF) concentration and NDF digestion characteristics[5] (eg, fragility, rates of digestion and passage). Signals from ruminal distention likely dominate control of feeding when milk yield is greatest (peak lactation, high-producing cows) and when high forage rations are fed and have relatively less effect during the fresh and late-lactation periods (**Fig. 2**A, B).

### *Metabolic Control*

Research in laboratory animals suggests that meals can be terminated by signals carried to the brain via hepatic vagal afferents.[6] A decrease in the firing rate of the vagus nerve, associated with increased oxidation of various metabolites, induces satiety, whereas an increase in the firing rate causes hunger. The signal likely originates in the liver because vagotomy of the hepatic branch of the vagus nerve decreased hypophagic effects of propionate in sheep.[7] Moreover, the signal is likely related to hepatic energy charge (phosphorylation potential), which is determined by the balance between the rate of production of high-energy phosphate bonds from oxidation of fuels and the rate of utilization by energy-consuming reactions, and not only by oxidation of fuels.[8] We call this the Hepatic Oxidation Theory (HOT) of the control of feed intake.[9] Briefly, meal size and frequency, which determine feeding behavior, are altered by temporal patterns of fuel absorption, mobilization of body reserves, and hepatic oxidation.[9] Fuels that can be oxidized in the ruminant liver include those mobilized from body reserves and provided by the diet, such as nonesterified fatty acids (NEFA), glycerol, amino acids, and lactate as well as fuels exclusively derived from the diet, such as propionate and butyrate. Fatty acids (FA) are the primary fuel oxidized in the liver, and their supply varies both within the day (negatively related with plasma insulin concentration) as well as throughout lactation, as the physiological state of cows changes. Of fuels derived from the diet, propionate is most likely the one to stimulate satiety because it can be rapidly produced in the rumen, absorbed, extracted by the liver, and oxidized.[5] Readers interested in a more detailed discussion of HOT are referred to reviews for ruminants,[9] a comparison across species,[10] and its relationship with metabolic disease in the postpartum period in dairy cows.[11]

### *Endocrine Control*

Besides insulin, other hormones can potentially contribute to both short- and long-term control of feed intake. Gut peptides, such as cholecystokinin (CCK) and glucagon-like peptide 1, have been implicated in the short-term control of feed intake,[12,13] whereas leptin has been implicated in the long-term control of feed intake.[14] Gut peptides are usually secreted in the small intestine in response to different nutrients in the chyme and have been related to decreased gastric emptying (potentially increasing gut distention) and increased digestive enzyme release, which might improve nutrient digestibility. Leptin is secreted by adipocytes, and its secretion is correlated to the size of the body fat depots.[14] Leptin induces satiety and might help maintain body weight over the long-term. Signals related

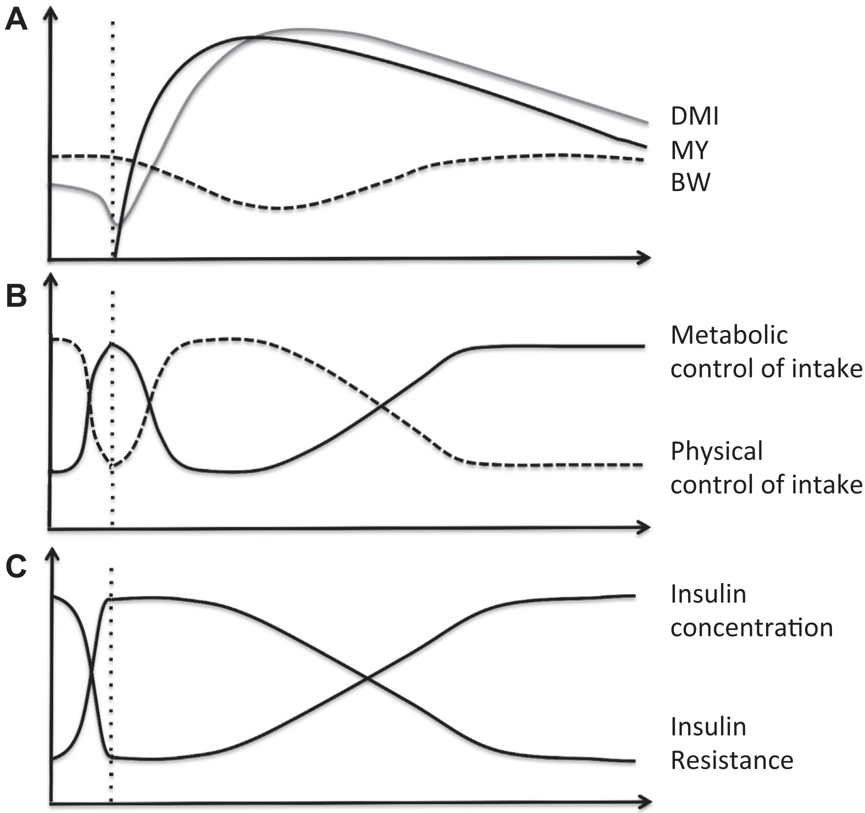


**Fig. 2.** Suggested schemes for primary mechanisms of control of energy intake and partitioning through lactation. The vertical doted line in each panel indicates parturition. (*A*) Dry matter intake (DMI) is generally depressed in the peripartum period and increases postpartum, driven by milk production. Milk yield (MY) increases postpartum until it reaches peak and then declines. The difference between milk energy output and feed energy input determines energy balance and body weight (BW) loss, which increases as lactation progresses and decreases after peak production. (*B*) Metabolic control of intake is likely dominant during the dry, early postpartum, and midlactation to late-lactation periods; physical control of intake is likely dominant during peak lactation. Note that as one control mechanism increases in dominance, the other one decreases; but both may occur at all times. (*C*) As insulin concentration decreases during the dry period, insulin resistance increases. During early postpartum, the cow goes through a phase of insulin resistance and low insulin concentration, mobilizing body energy reserves. As lactation progresses, insulin concentration increases and insulin resistance decreases, which allow the cow to replenish body energy reserves while producing milk.

to gut peptides are integrated in brain feeding centers with other signals originated in the gastrointestinal tract and the environment to determine feeding behavior.

### *Other Factors*

Other factors that affect feed intake include the environment (eg, heat index) and management (eg, competition, access to feed).

## CONTROL OF ENERGY PARTITIONING

### *Insulin Concentration and Insulin Sensitivity*

The effects of insulin on the metabolism of carbohydrates, proteins, and lipids play an essential role in energy partitioning in the dairy cow.[15] Energy partitioning between milk and body condition is affected by both insulin concentration and the sensitivity of tissues to insulin (**Fig. 3**). Low plasma insulin concentration results in greater lipolysis in adipose tissue, increasing plasma NEFA concentration, and potentially energy in milk. Muscle, adipose tissue, and liver are insulin-sensitive tissues, whereas the mammary gland is not. Insulin resistance of insulin-sensitive tissues varies through the lactation cycle and has been associated with increased plasma concentrations of adipokines and NEFA and overconditioning.[16] Somatotropin also decreases insulin sensitivity of adipose tissue.[17] Insulin resistance might be associated with excessive accumulation of visceral fat, which is related to increased secretion of adipokines, such as resistin, interleukin 6 (IL-6), and tumor necrosis factor (TNF)-alpha.[18,19] These molecules are thought to increase insulin resistance by altering insulin signaling in the cell, but their mechanisms have not been fully elucidated. Overconditioning induces a state of systemic chronic inflammation, evidenced by increased plasma concentrations of TNF-alpha, IL-6, and NEFA, and increased oxidative stress,[20] all of which have been related to the alteration of the insulin signaling pathway.[19] Around parturition, the excessive lipid mobilization usually observed in overconditioned cows

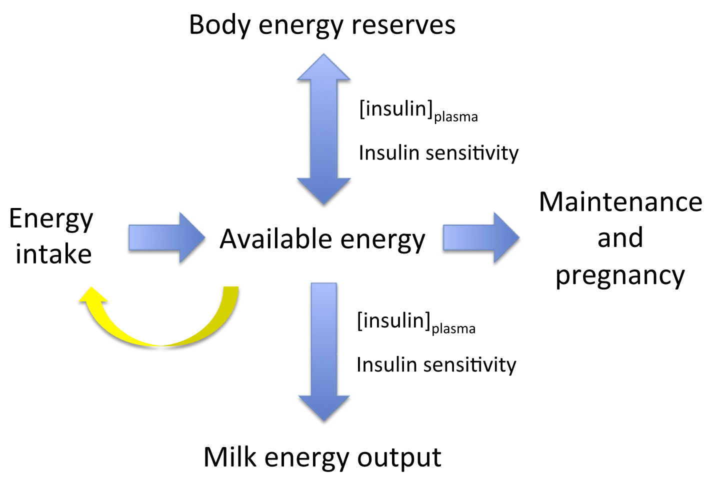


**Fig. 3.** Available energy in excess of that required for maintenance and pregnancy will be partitioned to milk and body reserves depending on plasma insulin concentration and adipose tissue sensitivity to insulin. During the postpartum and early lactation periods, low plasma insulin concentration and low sensitivity of adipose tissue to insulin result in a lipolytic state. Body energy reserves are mobilized, and this increases energy available for milk production but can also decrease energy intake by metabolic signals (eg, hepatic oxidation). As lactation progresses, the lipolytic state ceases and energy intake gradually increases; at peak lactation, energy partitioning to milk is greatest. As lactation proceeds past peak lactation and milk yield declines, available energy increases and body energy reserves begin to be restored as plasma insulin concentration and insulin sensitivity of adipose tissue increase. The increase in plasma glucose and insulin concentrations and downregulation of gluconeogenesis increase the availability of fuels for oxidation in the liver, decreasing energy intake. A reduction in milk energy output (eg, milk fat depression) can increase energy partitioning to body reserves and reduce energy intake by metabolic mechanisms (eg, hepatic oxidation) by increasing available energy and insulin concentration.

increases the risk of metabolic disorders; accumulation of NEFA in plasma can contribute to oxidative stress and increased expression of TNF-alpha and, therefore, elicit inflammatory responses[20] and insulin resistance.[21]

### *Recombinant Bovine Somatotropin*

Recombinant bovine somatotropin (rbST) favors partitioning of energy to milk by increasing nutrient uptake for milk synthesis, decreasing the loss of secretory cells in the mammary gland, increasing gluconeogenesis in the liver, decreasing uptake of glucose in muscle, and decreasing lipogenesis in positive-energy balance and increasing lipolysis in negative energy balance in adipose tissue.[17] With proper management, supplementation of rbST increases milk production, persistency of lactation, dry matter intake (DMI), and production efficiency, with no effect on milk composition.[22] Besides diluting maintenance requirements by increasing milk yield and efficiency of production, rbST is useful for managing energy reserves through lactation in individual cows.

### *Milk Fat Depression*

MFD is characterized by a decrease in milk fat concentration and yield, with no change in other components, milk yield, or DMI (see Chapter 6 on Lipids and Milk Fat Depression).[23] Fuels spared by the reduction in milk fat synthesis are partitioned to body reserves[24] or might increase energy balance and reduce feed intake[25] by hepatic oxidation of fuels. MFD is caused by altered microbial biohydrogenation of unsaturated long-chain fatty acids (LCFA) to specific conjugated linoleic acid (CLA) isomers in the rumen. Several LCFA isomers that cause MFD have been identified, including trans-10, cis-12 C18:2.[23] This CLA isomer inhibits milk fat synthesis in the mammary gland by downregulating the expression of several genes involved in lipogenesis, decreasing de novo FA synthesis in milk.[26] Furthermore, this CLA isomer has the opposite effect in adipose tissue, increasing the expression of genes involved in lipogenesis, likely because MFD increases energy balance by sparing energy for lipid synthesis, suggesting a role of trans-10, cis-12 CLA in energy partitioning. Feeding highly fermentable starch sources can cause MFD, likely by reducing ruminal pH. Concentration of fat in milk is positively related to ruminal pH,[27] and a reduction in ruminal pH could favor ruminal microorganisms with alternative biohydrogenation pathways, increasing the synthesis of trans-10 intermediates and, therefore, MFD.[28] However, low ruminal pH is not a prerequisite for the shift in biohydrogenation.[29] Factors that can potentially increase the amount of trans-10, cis-12 CLA reaching the duodenum for absorption and, therefore, MFD are related to diet formulation (eg, concentration of unsaturated LCFA,[30] low fiber/high concentrate, the use of ionophores) and management (eg, slug feeding, mixing errors).

## CHANGES IN PHYSIOLOGICAL STATE THROUGH LACTATION

Several weeks prepartum, insulin concentration decreases[31] and insulin resistance of adipose tissue increases (see **Fig. 2**C)[32] resulting in lipolysis and increased plasma NEFA concentration. The decrease in plasma insulin concentration and the increase in insulin resistance are associated with a decrease in glucose uptake by maternal muscle and adipose tissue and an increase in NEFA supply to the liver and extrahepatic tissues. Using NEFA as a fuel spares glucose for the fetus when conceptus growth and metabolic activity are maximal. Export of acetyl coenzyme A (CoA) (derived from β-oxidation of NEFA) from the liver as ketone bodies spares glucose for the fetus in late gestation and for production of milk lactose in early lactation.

Insulin resistance and low concentration of plasma insulin persist during early lactation causing sustained elevation of plasma NEFA concentration. High plasma NEFA concentration will increase milk fat concentration to allow for the survival of the neonate. The plasma concentration of bovine somatotropin increases around parturition and decreases as lactation progresses, and insulin sensitivity of tissues gradually increases. As milk production begins to decline and energy intake increases, euglycemia is restored and plasma insulin concentration increases. As energy balance improves, the lipolytic state ceases and restoration of body energy reserves begins. Great variation exists among cows for the duration of the lipolytic state depending on the extent to which energy intake is limited by metabolic mechanisms.

## EFFECTS OF DIET ON FEED INTAKE

Dietary characteristics that determine the filling effect and type and temporal absorption of fuels vary greatly across dietary ingredients and can affect voluntary feed intake. The filling effect of diets is largely affected by the concentration and digestion characteristics of forage NDF, and absorbed fuels vary mainly with concentration and ruminal fermentability of starch as well as with concentration and type of supplemental fat.[5]

### *Filling Effects of Diets*

The filling effect of a diet is determined primarily by the initial bulk density of feeds as well as their filling effect over time in the rumen. The overall filling effect is determined by forage NDF concentration, forage particle size, fragility of forage NDF (determined by forage type: legumes, perennial grasses, annual grasses), and NDF digestibility within a forage family.[5] Forage NDF is less dense initially, digests more slowly, and is retained in the rumen longer than other diet components. Increasing the diet forage NDF concentration can dramatically reduce feed intake of high-producing cows that are limited by fill to the greatest extent. Several studies in the literature reported a decrease in DMI of up to 4 kg/d when the diet NDF concentration was increased from 25% to 35% by substituting forages for concentrates.[5] Although most studies reported a significant decrease in DMI as forage NDF increased, the DMI response was variable, depending on the degree to which intake was limited by ruminal fill.

Experiments that have evaluated the effects of forage particle size have generally shown small effects on DMI.[5] In one experiment, alfalfa silage particle size showed little effect on DMI when fed in high-grain diets; but when fed in a high-forage diet, alfalfa silage with a longer chop length reduced DMI.[33] Feed intake might have only been limited by ruminal fill in the high-forage diet, which could explain the interaction observed. Increasing the diet NDF concentration by substituting nonforage fiber sources (NFFS) for concentrated feeds has shown little effect on DMI in studies reported in the literature.[5] NFFS include byproduct feeds with high NDF concentrations, such as soyhulls, beet pulp, cottonseeds, corn gluten feed, almond hulls, and distillers grains. Fiber in NFFS is likely less filling than forage fiber both initially (smaller particle size) and over time in the rumen (faster fermentation and passage rates).

Forage NDF has a much longer ruminal retention time than other major dietary components. The retention time in the rumen is longer because of the longer initial particle size and a slow rate of comminution, which differs greatly across forages. As forages mature, the NDF fraction generally becomes more lignified. Lignin is a component of plant cell walls that helps stiffen the plant and prevents breakage of the stalk. It is also essentially indigestible by ruminal microbes and limits fermentation of cellulose and hemicellulose. Within a forage type, the degree to which NDF is lignified is related to the filling effects of the NDF. Fiber that is less lignified clears from the rumen faster, allowing more space for the next meal. However, the ruminal retention time of NDF from perennial grasses is generally longer than for legume NDF despite being less lignified.[34–37] Because of this, perennial grasses are more filling and should be limited in diets when feed intake is controlled by distension, unless it is of exceptionally high quality. Corn is an annual grass, and corn silage NDF digests and passes from the rumen quickly compared with perennial grasses and can be an excellent source of forage NDF for high-producing cows.

***Importance of maintaining rumen fill***

Although ruminal distention becomes a primary limitation to feed intake as milk yield increases, it normally has little effect on feed intake during the transition period, when feed intake is likely controlled by hepatic oxidation.[9] Glucose demand of fresh cows is high when glucose utilization for milk production outpaces gluconeogenesis. Although cows require diets with adequate glucose precursors (ie, starch from grains), it is important to also maintain rumen fill. Formulating diets to maintain rumen fill with ingredients that are retained in the rumen longer, and have moderate rates of fermentation and high ruminal digestibility, will likely benefit cows through the transition period. Increased ruminal digesta mass can provide more energy over time when feed intake decreases at parturition or from metabolic disorders and infectious diseases. This increase will help maintain euglycemia and prevent even more rapid mobilization of body reserves. In addition, ruminal digesta is very important to buffer fermentation acids, and the buffering capacity is directly related to the amount of digesta in the rumen.[2] Therefore, diets formulated with ingredients that increase the amount of digesta in the rumen will have greater buffering capacity and will maintain buffer capacity longer if feed intake decreases. Inadequate buffering can result in low ruminal pH, decreasing fiber digestibility and acetate production, and increasing propionate production, possibly stimulating propionate oxidation in the liver and decreasing feed intake. Low ruminal pH can increase the risk of health problems, such as ruminal ulcers, liver abscesses, and laminitis, likely increasing stress and mobilization of body reserves even further during the postpartum period. Moreover, diets formulated with ingredients that maintain digesta in the rumen longer when feed intake decreases will likely decrease the risk of abomasal displacement.

***Physically effective fiber***

Diets must contain adequate effective fiber for proper rumen function at all stages of lactation, and this can be achieved with the inclusion of low-energy roughages in diets. However, when the drive to eat is high, signals from ruminal distension dominate control of feed intake over metabolic mechanisms (eg, cows at peak lactation); therefore, high concentrations of low-energy forages can limit feed intake. Optimum particle length of individual forages depends on several factors, including forage type, silo type (if ensiled), other forages in the diet, diet fermentability, the physiological state of the cow consuming the forage, and stocking density/competition for feed. An adequate concentration of long particles is required to form a rumen mat to retain small particles that would otherwise escape the rumen, increasing diet digestibility, efficiency of feed utilization, rumen fill, and buffering capacity. Some forages that are particularly fragile (eg, brown midrib corn silage) benefit from a longer chop length; but forages that are resilient to packing might have to be chopped shorter, particularly when packing is difficult (eg, upright silos). Forages lacking physically effective fiber must be limited in diets and combined with forages with adequate particle length. When overcrowding causes competition at the feed bunk and slug feeding, diets with more physically effective fiber can limit the rate of feeding, decreasing the risk of low ruminal pH, especially for highly fermentable diets.

### *Starch Concentration and Ruminal Fermentability*

Starch is a highly digestible and energy dense feed component that typically ranges from less than 20% to more than 28% of dietary DM in rations fed to lactating dairy cows. Starch is composed of polymers of glucose (amylose and amylopectin) with bonds that are readily cleaved by mammalian enzymes. However, starch is packaged in the seed endosperm in granules that are embedded in a protein matrix, which varies in solubility and resistance to digestion.[38] The endosperm type affects the ruminal fermentability of starch, which ranges from less than 30% to more than 90% across starch sources.[39,40] Altering the concentration and ruminal fermentability of starch in rations affects the digestibility of starch,[41] ruminal pH and fiber digestibility, and the type, amount, and temporal absorption of fuels (eg, acetate, propionate, lactate, glucose) available to the cow,[5] and therefore, has great effects on the lactational performance by affecting energy intake and partitioning as well as absorbed protein.[9] Diets with greater ruminal starch fermentability can depress feed and energy intakes. Increasing ruminal starch fermentation by substituting a more fermentable starch source for a less fermentable starch source decreased feed intake of cows by more than 3 kg/d in several studies reported in the literature.[5] Oba and Allen[42] showed that a more rapidly fermentable starch source (high-moisture corn) reduced feed intake of cows in midlactation 8% compared with a less fermentable starch source (dry ground corn) by decreasing meal size. The more fermentable starch source nearly doubled the rate of starch digestion in the rumen, increasing propionate production, compared with the less fermentable starch source. The reduction in meal size and DMI by the more fermentable starch source is likely because of a more rapid flux of propionate to the liver stimulating oxidation and satiety.[9]

#### *Factors affecting ruminal starch fermentability*

Ruminal fermentability of starch is affected by grain type (eg, corn, wheat, barley, sorghum), processing (eg, rolling, grinding, steam flaking), conservation method (eg, dry, ensiled), ration composition, and animal characteristics (eg, rumen microbial population, rate of passage). Starch in wheat, barley, and oats is generally more readily fermented than starch in corn; starch in sorghum is most resistant to fermentation in the rumen and digestion by the animal.[43] These differences are primarily because of differences in the endosperm type rather than differences in starch composition (amylose vs amylopectin) per se. Floury endosperm contains proteins that are readily solubilized, allowing greater access of enzymes to starch granules, whereas vitreous endosperm contains prolamin proteins that are insoluble and resistant to digestion, decreasing access of the enzymes to starch granules.[44] Starch sources vary in amount and proportion of the two types of endosperm, and there is large variation in vitreousness of the endosperm (percent of the total endosperm that is vitreous) among varieties within certain grain types. Endosperm vitreousness in corn harvested at physiological maturity ranges from 0% to more than 75%, and corn with a more vitreous endosperm is more resistant to both particle size reduction (by grinding) and digestion[45] than corn with a more floury endosperm. Vitreousness increases with increasing maturity at harvest,[46] so differences among corn hybrids are greatest when field dried. Because corn silage is harvested earlier than high-moisture corn, the grain will have less vitreous endosperm and more moisture if harvested as a whole plant for silage than as high-moisture corn from the same field. However, there can be large differences in vitreousness within corn silage harvested between 30% and 40%

DM and within high-moisture corn harvested between 60% and 75% DM (40% and 25% moisture) from the same field.

When grains are ensiled, ruminal fermentability of starch can be greatly affected by both the grain moisture concentration and storage time because ensiling solubilizes endosperm proteins over time, increasing starch fermentability. The increase in protein solubility and starch fermentability over time is greatest for grains with higher moisture concentration.[47] Therefore, the change is greatest for wetter corn silage and least for drier, high-moisture corn. The greatest change occurs over the first few months of ensiling and must be anticipated and accounted for when formulating rations. Because of this, it is recommended to wait several months after ensiling before feeding corn silage. However, proteolysis continues for months at a slower rate, and corn silage and high-moisture corn stored for long periods (1 or 2 years or even more) can be difficult to feed in high concentrations because they are so readily fermented.

Processing increases the rate of starch digestion; the effects are greater for grains with more vitreous endosperm, such as sorghum and corn.[43] Steam flaking causes swelling and disruption of the kernel structure, increasing access of the enzymes to starch granules. Rolling or grinding whole grains, or processing silage to crush kernels, reduces the particle size, increasing the surface area. Dry grains can be finely ground, greatly reducing the effects of endosperm vitreousness on ruminal fermentability. Processing (rolling) corn silage is not as effective at increasing the surface area as fine grinding; however, it can reduce differences in digestibility of sources varying in vitreousness.

### *Measurement of starch concentration and fermentability*

Starch concentration is relatively consistent within cereal grain types but varies greatly within forages containing starch, such as corn silage and small grain silages. Therefore, book values for starch concentration may be acceptable for cereal grains; but starch concentration must be measured for forages from grain crops. For instance, the starch concentration of corn silage varies from less than 20% to more than 50% of DM depending on grain concentration, which, in turn is dependent on genetics, environment, and maturity at harvest.[48] The starch concentration of corn silage is inversely related to NDF concentration; the fibrous stover fraction of the plant is enriched if kernels are not filled.

The nonfiber carbohydrate (NFC) concentration of diets is not an accurate measure of starch concentration. The NFC fraction is calculated by subtracting measured components (NDF, crude protein (CP), ether extract, ash) from total DM. It contains other carbohydrates, such as sugars and pectin, and can be underestimated to the extent that nonprotein nitrogen is present. Although starch, sugars, and pectin are generally highly digestible, their effects on rumen microbial populations and fuels available to the animal differ greatly. Starch that is ruminally fermented increases propionate production in the rumen,[49] and starch that escapes ruminal fermentation provides glucose that is absorbed or metabolized to lactate in the small intestine.[50] Sugars are nearly completely fermented in the rumen and generally increase butyrate production.[51] Most strains of pectin-degrading rumen bacteria produce acetic and formic acids and relatively little propionic acid.[52] Propionic and lactic acids are glucose precursors, whereas formic, acetic, and butyric acids are not. In addition, propionate can decrease feed intake under some conditions[5]; starch, sugars, and pectin can affect fiber digestion and ruminal biohydrogenation of FA through different effects on ruminal microbial populations. Therefore, NFC is not a useful proxy for starch when formulating rations for lactating cows.

Relative differences in rate of starch digestion can be determined by in vitro starch digestion (IVSD) with ruminal microbes. This process can be done by incubating samples over time in rumen fluid with buffered media and evaluating the rate of starch disappearance or, less costly and equally informative, by evaluating starch disappearance over a period of time (eg, 7 hours). A 7-hour incubation time seems to be a reasonable mean residence time of starch in rumens of lactating cows; therefore, it is used to predict in vivo ruminal digestibility of starch. However, it is naïve to think this technique (or any other) can provide an absolute number for starch digestibility because ruminal digestibility of starch in vivo is highly affected by the enzyme activity of the rumen fluid and particle size of the starch source and because residence time of starch in the rumen is extremely variable, not only across cows but also across sources of starch.[53] Nevertheless, 7-hour retention time IVSD provides useful information about the relative rates of fermentation among starch sources. Samples must be ground before analysis, which removes important variation for many comparisons (eg, processed vs unprocessed corn silage). Because IVSD of the same sources are highly variable across runs, comparisons must be done in the same in vitro run (at the same time). This requirement is because enzyme activities (amylases and proteases) of rumen fluid are highly variable from cow to cow, time relative to feeding, and diet consumed. For example, in our laboratory, the coefficient of variation for 7-hour IVSD across runs can be as high as 25% even after attempting to minimize variation by taking rumen fluid from several cows fed a specific diet at the same time of day relative to feeding. This is much higher than our coefficient of variation for 30-hour in vitro NDF digestibility of less than 3%.

Insoluble endosperm proteins inhibit starch digestion, and the solubility of protein has been measured as an indicator of relative differences in starch digestibility. Like IVSD, the determination of protein solubility requires grinding samples, which remove variation among sources. Because it is a chemical rather than a biological measure, it is less variable across runs than IVSD. The accuracy of ruminal starch digestibility prediction from protein solubility is limited by the relationship between protein solubility and rate of starch digestion as well as our limited knowledge of the passage rate of starch from the rumen. Therefore, like IVSD, measures of protein solubility provide some information related to ruminal starch digestion but cannot be used to measure in vivo ruminal starch digestibility accurately.

### *Fat Type and Concentration*

Fat sources are often added to dairy cattle diets with the goal of increasing energy intake to increase milk energy output or energy balance. However, fat supplements have had inconsistent effects on energy intake in dairy cows, partly because of the differences in type and amount of fat included in the diet. Feed intake is often decreased and rarely increased with the addition of fat to diets.[5] In several experiments, the depression in feed intake by dietary fat more than offset the increased energy density of the diet resulting in decreased energy intake. The extent of intake depression by dietary fat is related to unsaturated FA reaching the duodenum.[5,24] The mechanism by which dietary fat affects feed intake is complex and likely involves the effects of FA on gut peptides and pancreatic hormones and direct and indirect effects on the hepatic oxidation of fuels. Unsaturated FA are more likely to be oxidized, whereas saturated FA are more likely to be stored,[54] consistent with greater hypophagic effects of unsaturated compared with saturated fats. Gut peptide responses likely affect hepatic oxidation through their effects on pancreatic hormones, and CCK may directly affect the firing rate of the vagal afferents causing satiety.[55]

## EFFECTS OF DIET ON ENERGY INTAKE AND PARTITIONING THROUGH LACTATION

Diet composition interacts with the physiological state of cows to affect energy intake and partitioning because differences in the supply and fate of fuels depend on the lipolytic state and glucogenic capacity. In the periparturient period, feed intake is limited primarily by metabolic mechanisms; but as lactation progresses, feed intake increases and distention increasingly dominates control of feed intake. As lactation proceeds and the milk yield decreases, signals from distention diminish and feed intake is increasingly dominated by signals derived from the metabolism of fuels.

### *Effect of Diet and Physiologic State on Energy Intake*

The extent to which ruminal distention limits feed intake is positively related to milk yield. This relationship was shown in two studies in which groups of cows with a wide range of milk yield were offered diets differing in their filling effects. The first study compared brown midrib corn silage to a control corn silage.[56] Both silages had similar DM and NDF concentrations, but in vitro NDF digestibility (30 hours) was nearly 10% higher for the low-lignin brown midrib corn silage than for the control silage. When both forages were offered to a group of cows with a wide range of milk yield, DMI and fat-corrected milk (FCM) responses to the brown midrib corn silage compared with the control corn silage increased linearly with initial milk yield of cows. Silage hybrid did not affect DMI or FCM for the lower-producing cows (∼32 kg/d), but brown midrib corn silage increased FCM by approximately 8 kg/d for the highest-producing cows (∼55 kg/d) compared with the control corn silage. The second study compared diets differing in forage to concentrate ratio.[57] Diets contained either 44% forage (24.3% NDF and 33.8% starch) or 67% forage (30.7% NDF and 23.1% starch). The low-forage diet increased DMI linearly with milk yield of cows (up to ∼4.5 kg/d for the highest producing cows) compared with the high-forage diet, and FCM yield increased approximately 2.2 kg for each kg increase in DMI for cows producing more than approximately 40 kg FCM/d. Although the low-forage diet increased DMI across production level of cows, the forage level of the diets did not affect FCM in cows producing less than approximately 40 kg/d.

The effects of starch fermentability on DMI[58] and production[59] responses are affected by the physiological state of cows. Increased ruminal starch fermentability of rations had opposite effects on milk production depending on the initial milk yield of cows: high-moisture corn increased concentration of milk fat and FCM yield of cows producing more than approximately 40 kg of milk per day but decreased both for cows with lower milk yield.[59] Propionate flux to the liver increases when more fermentable starch is fed, which likely stimulates oxidation more quickly within the time frame of meals, increasing hepatic energy status and satiety, and decreasing meal size and DMI. However, the rate of increase in hepatic energy status depends on glucogenic flux, which varies among cows and for individual cows across lactation. Propionate carbon will increasingly oxidize acetyl CoA as propionate uptake by the liver exceeds glucogenic capacity, increasing energy charge and ultimately stimulating satiety.[9] A more rapidly fermentable starch source (high-moisture corn) depressed feed intake compared with a less-fermentable starch source (dry ground corn) for cows with greater plasma insulin concentration[58] likely because glucogenic flux is downregulated by chronically elevated plasma insulin concentration and propionate stimulates oxidation of acetyl CoA sooner during meals, stimulating satiety.

### Effect of Diet and Physiological State on Energy Partitioning

Early postpartum cows are in a lipolytic state and differ greatly from cows in positive energy balance. Propionate is more hypophagic for fresh cows than cows in midlactation despite the greater glucose demand and the lower plasma insulin concentration,[60] likely because of a consistent supply of acetyl CoA derived from β-oxidation of NEFA.[9] Although high glucose demand and low plasma insulin concentration result in greater glucogenic flux, making it unlikely for propionate to be oxidized per se, uptake of propionate by the liver and entry into the tricarboxylic acid cycle increases oxidation of the pool of acetyl CoA within meals, increasing energy charge and causing satiety.[61,62] Feed intake of high-producing cows is less likely affected by propionate from highly fermentable diets because plasma glucose and insulin concentrations are low, hepatic gluconeogenesis is upregulated, and hepatic acetyl CoA concentration is low. Therefore, stimulation of oxidation within meals by propionate is likely delayed compared with fresh cows and cows in late lactation. Consequently, feed intake increases until signals from ruminal distention trigger the end of the meal. As lactation proceeds past peak and milk yield declines, feed intake is increasingly dominated by metabolic signals once again. In midlactation to late-lactation cows, highly fermentable diets often decrease feed intake and FCM yield, whereas reducing ruminal starch fermentability often increases energy intake and partitioning to milk.

Fuels derived from starch digestion include glucose precursors that are needed in greater supply as milk yield increases, whereas fermentation of fibrous feeds yields fuels that can spare glucose (eg, acetate) but provide little glucose precursors. Glucose precursors are more limiting as milk yield increases, and rations that provide more glucose precursors result in a more positive response in milk yield for higher-producing cows. Milk yield response to dry ground corn substituted for soyhulls at 30% of the diet DM increased linearly with initial milk yield of cows ranging from 28 to 62 kg/d.[63] However, there was no benefit for additional starch from corn for cows at the lower end of the range in milk yield. In an experiment mentioned previously in which the starch concentration of the ration offered to lactating cows was increased from approximately 23% to approximately 34% by decreasing the forage NDF concentration of the diet (from 24% to 16% forage NDF, respectively), DMI response to the high-starch, low-forage NDF ration increased linearly with increasing milk yield of cows, but FCM response increased only for cows producing more than approximately 40 kg/d of FCM.[57]

Energy partitioning between milk production and body condition varies depending on the fuels available and as the physiological state changes throughout lactation (see Fig. 3). Substitution of fiber for starch greatly alters the fuels available for intermediary processes and often results in greater partitioning of energy to milk rather than body reserves in midlactation to late-lactation cows with a low to moderate milk yield. Ipharraguerre and colleagues[64] showed that substitution of up to 40% of diet DM of soyhulls for dry ground corn increased milk fat percent (linearly from 3.60% to 3.91%) and decreased body weight gain (linearly from 1.02 to −0.14 kg/d) with no effect on milk yield (∼29 kg/d) and a slight decrease in DMI (tendency, linearly from 23.8 to 22.7 kg/d). In addition, Voelker and Allen[65] demonstrated that beet pulp decreased body condition score (BCS) without decreasing yields of milk or milk fat when substituted for high-moisture corn up to 12% of the diet DM. Furthermore, a 69% forage diet (0% corn grain) containing brown midrib corn silage increased energy partitioned to milk, decreasing body weight gain while numerically increasing FCM yield compared with a 40% forage diet (29% corn grain) containing a control corn silage.[66]

In contrast, DMI and milk yield were reduced when the control corn silage, which had approximately 20% lower in vitro NDF digestibility than the brown midrib corn silage (46.5% vs 55.9%), was fed in the higher-forage diet.

As lactation proceeds, insulin concentration and sensitivity of tissues increase and energy is increasingly partitioned to body reserves. Increasing the supply of glucose precursors beyond that required for milk production increases energy partitioning to body reserves. Intravenous glucose infusion of up to 30% of the net energy requirement linearly increased plasma insulin concentration, energy balance, body weight, and back fat thickness, without affecting DMI or milk yield of midlactation cows.[67] An experiment conducted with cows in the last 2 months of lactation showed that the substitution of beet pulp for barley grain linearly decreased BCS and back fat thickness, maintained milk yield, and linearly increased milk fat yield and milk energy output.[68] The decrease in BCS and the increase in milk fat yield were associated with a linear decrease in plasma insulin concentration as well as with a linear increase in plasma NEFA concentration. High-starch diets might result in greater insulin concentration, increasing the partitioning of energy to adipose at the expense of milk; but they can also result in lower ruminal pH, decreasing fiber digestibility, and inducing MFD and, therefore, reducing milk energy output. The energy spared from the reduction in milk fat synthesis during MFD will likely be partitioned to body energy reserves, possibly by altering gene expression in adipose tissue.[25] Decreasing fermentability of diets by increasing fiber from forages or NFFS can maintain the milk yield while decreasing gain in body condition.

## RECOMMENDATIONS

All forages should be tested for concentrations of DM, NDF, CP, as well as lignin or in vitro NDF digestibility. Most laboratories report lignin as a percentage of DM, which is not directly useful because lignin only limits digestion of fiber. Therefore, lignin (percentage of DM) should be divided by NDF (percentage of DM) to determine the extent to which the NDF is lignified. There are several measures of lignin used although the predominant measure is acid detergent sulfuric acid lignin (ADL). Acid detergent lignin as a percent of NDF ranges from approximately 3% to 9% for corn silage and from approximately 11% to 20% for alfalfa (hay and silage). Within a forage type, forage NDF with the lowest ADL/NDF is the least filling. Additionally, mixed grass-legume forages should be tested for acid detergent fiber (ADF) to help determine the fraction of grass and legume in the forage; ADF/NDF is approximately 0.8 for legumes and approximately 0.6 for grasses. Mixed forages with more grass should be limited for high-producing cows with intake limited by rumen fill. The following recommendations focus on meeting the energy needs through lactation by considering the concentration and digestibility of fiber and starch and their interaction with stage of lactation.

### *Far-off Dry Cows (8 Weeks–3 Weeks Prepartum)*

The goal is to meet, but not exceed, energy requirements and maintain BCS.

#### *Allocation of forages*

Use forages with high NDF and low crude protein concentrations, such as mature grass hay or silage and straw, to limit the energy intake to requirements. Forages with low NDF digestibility and long ruminal retention times can be used. Limit corn silage with high grain concentrations.

#### *Supplementation*

Add grain only to meet the energy requirements, limiting body condition gain.

### *Close-up Dry Cows (3 Weeks Prepartum to Parturition)*

The goal is to meet, but not exceed, energy requirements and maintain rumen fill through the transition period. The pool of ruminal digesta will provide energy, buffering capacity, and distention to reduce the risk of ketosis, acidosis, and displaced abomasum, respectively, following parturition.

#### *Allocation of forages*

Wheat straw digests and likely passes from the rumen slowly and it can be used to dilute energy density of corn silage in total mixed rations (TMRs) for dry cows. Grass silage or hay might be more beneficial because the fiber is more digestible and it provides energy for a longer time when feed intake decreases around calving. However, the use of grasses with high potassium concentrations should be limited to reduce milk fever in the postpartum period. Avoid finely chopped silages (to ensure adequate rumen retention time) and forages with high protein concentrations (to decrease nitrogen excretion).

#### *Supplementation*

Include a limited amount of moderately fermentable starch to stimulate insulin secretion and limit fat mobilization while maintaining rumen fill. NFFS do not provide glucose precursors or rumen fill and should be limited. Measure and record BCS at dry-off and at parturition to adjust the energy concentration of dry cow diets.

### *Fresh Cows (Parturition to ∼2 Weeks Postpartum)*

These cows require glucose precursors, and rations should contain higher starch concentrations to the extent possible. However, they also have lower rumen digesta mass, which increases the risk of low ruminal pH as well as displaced abomasum. Therefore, the goal with this diet is to maintain rumen fill and to provide glucose precursors in a form that will maximize energy intake. Cows should be switched to the high-group ration when they are cleared of health problems, have increasing milk production, and are aggressive at the feed bunk following feeding. Most cows will be in this group for less than 2 weeks, but cows with excessive body condition at parturition might be in this group for longer.

#### *Allocation of forages*

Use forages with a moderate to high NDF concentration and high NDF digestibility but long ruminal retention times, such as grass hay or silage. The use of forages with high NDF concentrations will allow adequate dietary space for grain while maintaining rumen fill. Avoid finely chopped silages. Consider that long fiber particles are necessary to form a mat and increase digesta retention in the rumen; but excessive length of cut can increase sorting, particularly in dry diets. Corn silage can be used; but limit highly fermentable corn silage (eg, aged corn silage ensiled for more than 1 year, corn silage less than 30% DM, overprocessed corn silage) because it might be too fermentable and, therefore, limit feed intake during this period.

#### *Supplementation*

Avoid feeding very highly fermentable starch sources (eg, wheat, barley, low-density steam-flaked corn, and aged [>1 year old] high-moisture corn and corn silage) to fresh cows because rapid production and absorption of propionate can stimulate hepatic oxidation and suppress feed intake, particularly for cows in a lipolytic state.[9,61] Starch sources with moderate ruminal fermentability and high digestibility in the small intestine, such as dry ground corn, can be fed at higher concentrations in the diet to provide more glucose precursors without suppressing feed intake or decreasing ruminal pH. Reduction in ruminal pH can reduce fiber digestibility and energy intake. Dry ground corn (finely ground) is the preferred starch source because of its moderate rumen fermentability (~60%) but high whole-tract digestibility (>90%). Supplementing corn silage–based diets with dry ground corn works well for this ration, with a total starch concentration of 22%–25% (DM basis). Starch concentration must be decreased when feeding highly fermentable starch sources. Because feed intake is less limited by ruminal distention and greater rumen digesta mass is desirable during this period, the forage NDF concentration should be relatively high (~22% of diet DM) and NFFS should be limited to diluting starch concentration when necessary. NFFS can be used to dilute starch when high NDF forages are used but should otherwise be limited because they provide few glucose precursors and little rumen fill.

## *High-Producing Cows (~2 Weeks Postpartum to ~3 Body Condition Score)*

Cows in early to midlactation have a high glucose requirement for milk production and partition relatively little energy to body reserves. They respond well to rations with low forage NDF concentration (low fill) and highly fermentable starch. Therefore, the goal is to feed a low-fill, highly fermentable diet as gut fill begins to dominate control of feed intake. Gut-fill might begin to dominate control of feed intake beginning 2 weeks after calving for some cows in the herd or after 3 weeks for others, and is likely indicated by low plasma NEFA and ketone concentrations, increasing milk production, and aggressive intake. Cows should be switched to the maintenance ration when BCS exceeds 3.0 on a 1-to-5 scale.

### *Allocation of forages*

Use forages with high fiber fragility, such as brown-midrib corn silage and legume hay or silage; these forage sources will clear from the rumen at a faster rate and will allow greater feed and energy intakes compared with forages that have longer retention times in the rumen (eg, mature grasses). Adequate long particles are needed to retain potentially fermentable particles, increasing the overall diet digestibility. Forages with low NDF concentrations (except for corn silage) might limit the diet space for starch, which is needed to provide glucose precursors; therefore, it should be used sparingly. For instance, it is difficult to meet the requirements for physically effective fiber and include an adequate starch concentration in the ration using alfalfa silage with 35% NDF.

### *Supplementation*

High-producing cows respond favorably to highly fermentable diets. Starch sources, such as low-density steam-flaked corn, high-moisture corn, or rolled barley, work well in these diets. However, starch sources that are very rapidly fermented, such as ground wheat, should be limited. Starch concentration of rations should be in the range of 25% to 30% (DM basis), although the optimum concentration depends on competition for bunk space, forage/effective NDF concentration, and starch fermentability. Higher-starch, lower-fill rations generally increase peak milk yield and decrease the loss of body condition in early lactation. Once the body condition that was lost in early lactation is replenished, cows should be switched to a maintenance diet with a lower starch concentration and ruminal fermentability. NFFS can be used to dilute starch, if needed, but should otherwise be limited because they provide few glucose precursors. Restoration of body condition will occur sooner in lactation for diets with lower forage NDF and greater starch concentrations because the extent and duration of the negative energy balance will be lessened. Therefore, the number of cows receiving both this and the maintenance diet is affected by the composition of this ration; this diet must be adjusted according to the number of stalls and bunk space available for cows in each diet group.

### *Maintenance Group (>150 Days Postpartum and ~3 Body Condition Score)*

The maintenance ration is the key component of a ration formulation/grouping system to increase the health and production of cows. The goal is to maintain the BCS (preventing further body weight gain) while also maintaining or increasing milk yield. Cows should be offered the maintenance ration when they have replenished body reserves, reaching a BCS of 3. Cows gain body condition when offered rations with greater starch concentrations than required for milk production, which increases plasma glucose and insulin concentrations and partitions energy to body reserves. If they continue receiving a high-starch diet, BCS will continue to increase and they will be at increased risk of metabolic disease following parturition. Moreover, as lactation progresses past midlactation, the highly fermentable diet that is optimal for high-producing cows can depress feed intake as milk yield and glucose demand decreases, increasing the risk of abomasal displacement and MFD. It is, therefore, suggested to feed a more filling, less fermentable diet as milk yield declines. This practice will increase feed intake and provide a more consistent supply of fuels, partitioning more energy to milk rather than body reserves.

#### *Allocation of forages*

Forages with a wide range of NDF concentration can be used in these diets, but the NDF should be potentially digestible. More grass can be included in these diets; although grass fiber may have longer retention time in the rumen and be more filling, it is generally more digestible than fiber from legumes. High-protein forages should be limited to avoid feeding excess protein.

#### *Supplementation*

Lowering ration starch concentration should limit the body condition gain while maintaining and possibly improving feed intake and yields of milk and milk fat. The optimal concentration of starch depends on the milk yield of the herd and possible physical groups but will likely be in the range of 18% to 22% (DM basis). The BCS should be determined and recorded when cows are moved to the maintenance group and again at dry-off. Monitoring BCS is essential to adjust the starch concentration of the maintenance diet over time. Highly fermentable starch sources (eg, aged corn silage, high-moisture corn, bakery waste, ground barley, wheat) should be limited, if not avoided, by substituting less fermentable feeds, such as dry ground corn or NFFS. Nonforage fiber sources (beet pulp, corn gluten feed, soyhulls, and so forth) can be used to dilute starch to the target concentration. These flex-fuel cows have lower requirements for glucose precursors and can better use nonstarch feeds to provide energy in a form to spare glucose. Unsaturated fats likely decrease feed intake and increase the risk of MFD and subsequent partitioning of energy to body reserves and should, therefore, be limited.

## SUMMARY

The management of energy balance through lactation is necessary to maximize milk yield, efficiency of milk production, and animal health. Carbohydrates compose the largest fraction of diet DM of lactating cows and vary greatly in physical form and products of digestion.

The type and temporal supply of fuels interact with the physiological state of cows to affect the energy intake and partitioning. Consideration of the physical and digestion characteristics of diets beyond their nutrient composition and how they interact with physiological stages as they change through lactation to affect energy intake and partitioning is of crucial importance to optimize forage allocation and supplementation for lactating cows as well as to formulate and adjust diets to maximize milk production and promote animal health.

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