MAKING NUTRITIONAL SENSE OF NONSTRUCTURAL CARBOHYDRATES

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Introduction

The nonstructural carbohydrates (NSC) have been an important but vexing part of ration formulation. Feeding NSC has been related to both high production and health problems. These carbohydrates can constitute up to 45% of ration dry matter, yet the number used to describe them has been a calculated value. The carbohydrates found in NSC are sufficiently diverse in their nutritional characteristics and presence in feedstuffs that their partitioning and individual examination is in order.

Current NSC Estimation

The NSC include all carbohydrates not found in neutral detergent fiber (NDF). Their content in feeds has been a calculated rather than directly analyzed value because of the many types of carbohydrates included in this fraction. The lack of methods or problems with the assays has prevented individually measuring NSC and summing the components. Currently, the NSC content of feedstuff dry matter (DM) is a calculated value based upon nutrient percentages subtracted from 100% of feed DM:

$$NSC\% = 100\% - (CP\% + NDF\% + EE\% + Ash\%)$$

or

$$NSC\% = 100\% - [CP\% + (NDF\% - NDFCP\%) + EE\% + Ash\%]$$

where,
CP = crude protein,
NDF = neutral detergent fiber,
NDFCP = neutral detergent-insoluble crude protein, and
EE = ether extract (crude fat).

Although the first equation is most commonly used, the second equation is preferable because it corrects for CP in NDF (NDFCP) and so avoids subtracting NDFCP twice (as part of CP and as NDFCP).

Errors that are associated with each component in the equations, either with how the assay was carried out or inherent within the assay itself, shift the estimated NSC from its true value. Because it is calculated by difference, the errors from each of the

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component analyses accumulate in NSC. In specific cases where NSC is underestimated because the mass of CP from non-protein nitrogen sources is overestimated, computing a more accurate NSC value may be possible (21). However, correcting for known errors in these equations still does not accurately describe NSC's nutritional value.

Carbohydrates in NSC

A great variety of carbohydrates are soluble in neutral detergent. Based upon their locations in the plant cell and THEIR nutritional characteristics, they should be called neutral detergent-soluble carbohydrates (NDSC), rather than NSC or NFC (non-fiber carbohydrates). The NDSC include both structural and non-structural, and fiber and non-fiber carbohydrates (Figures 1 & 2). Overall, NDSC are considered to be more rapidly and readily digested or fermented than NDF, but their nutritional characteristics and compositions are far from uniform.

The carbohydrates, or carbohydrate derivatives included in NDSC are organic acids, sugars, oligosaccharides, starch, fructans, pectic substances, (1→3)(1→4)-β-glucans, and other carbohydrates of the appropriate solubility. One way they can be partitioned is based on their digestion by the cow vs. ruminal microbes. The only carbohydrate linkages that mammalian enzymes can hydrolyze are those in sucrose and starch, leaving all other polymerized carbohydrates indigestible, except by microbes. "Fiber" is the nutritional term applied to carbohydrates not digestible by mammalian enzymes. Accordingly, NDSC can be allocated into non-fiber, and fiber components. The non-fiber carbohydrates include organic acids, sugars, and starches. The fiber fraction includes fructans, pectic substances, and (1→3)(1→4)-β-glucans. Classification of oligosaccharides depends upon their composition and linkages.

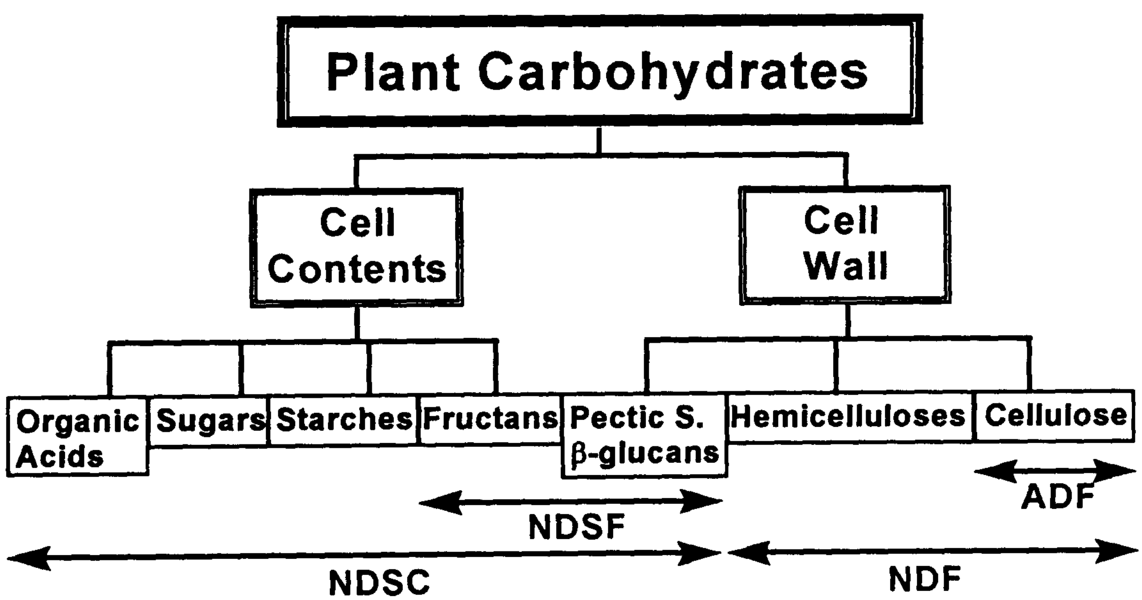

Figure 1. Plant carbohydrate fractions.

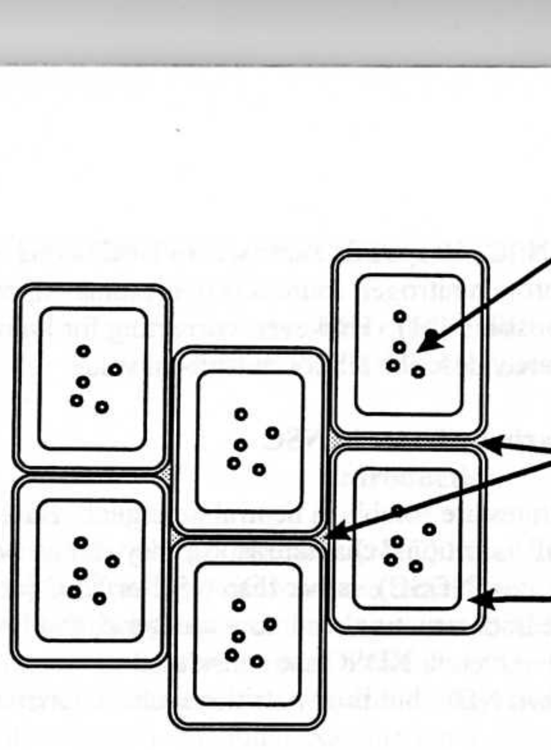

Figure 2. Locations of carbohydrates and lignin in plant cells.

Neutral Detergent-Soluble Carbohydrates: Non-Fiber

Organic Acids

Organic acids are not carbohydrates per se, but derivatives or precursors of carbohydrate. They generally come from two main sources: those within growing plants, and fermentation acids. In unfermented plant material, the organic acids are generally intermediates of the citric acid cycle, or plant defensive compounds. They include citrate, malate, quinate, succinate, fumarate, oxalate, shikimate, *trans*-aconitate, and malonate among others. The range of organic acids present in forage has made complete analysis for them difficult, a reason that there are relatively few values available for them. The concentrations of organic acids tend to decrease as plants age (7,34). Total levels in plant dry matter reported in cool season grasses are 1.3 to 4.5% (34), 5.8 to 9.8% for alfalfa, 2.8 to 3.8% in red clover, and 3.0 to 3.5% in white clover (10). Bermudagrass, contains little water-soluble carbohydrate (3 to 4% of DM) (65), but has been reported to contain low levels of oxalic acid (0.02 to 0.16% of DM)(10), and higher levels of malate (1.9 to 4.5% of DM) (7). Alfalfa varieties may contain 2.9 to 7.5% malate, depending upon variety and age (7). Citrus peel contains 3 to 4% of DM as organic acids (67).

Fermented feeds contain a different complement of organic acids than does fresh plant material. In the ensiling process, bacteria ferment sugars, starch, organic acids (42), and fructans (44) to a number of compounds including lactate, acetate, and other organic acids. Lactate (12.1%) and acetate (3.6%) can represent more than 15% of the dry matter in direct cut silage, however, the levels are typically lower in wilted material (42). Silage made from bermudagrass tends to have lower concentrations of organic acids than temperate forages, largely due to the low levels of carbohydrates available to be fermented (2 to 4% of DM). In a comparison of wilted and direct-cut bermudagrass silages, wilted silages contained more lactic acid and less acetic acid than direct-cut materials (65)

Table 1. Lactic and acetic acid contents of direct cut or wilted bermudagrass silage with or without lactic acid bacteria inoculation 114 days after ensiling (% of DM) (65).

	Control		Inoculated	
Harvest method	Lactic acid	Acetic Acid	Lactic acid	Acetic Acid
Direct cut	2.95	4.54	1.56	4.69
Wilted	2.97	0.67	3.62	0.93

(Table1). It should be noted that volatile fatty acids (VFA) such as acetate, propionate, and butyrate are not represented in feed analyses because they volatilize and are lost during the estimation of dry matter. Lactic acid is included in the NDSC.

The nutritional value of organic acids to the cow and microbes depends upon the particular organic acid. The cow can digest and absorb organic acids directly. Volatile fatty acids such as acetate, propionate, and butyrate have already been digested to their endpoint by microbes, and are not fermented to any great extent in the rumen. These VFA are available to the cow but not to rumen microbes.

The non-VFA organic acids are likely fermented in the rumen. Acetate is the primary fermentation product for the organic acids common in forage (citrate, *trans*-aconitate, malate, malonate, quinate, shikimate)(53). Among these acids, malate has been reported to enhance the uptake of lactate by certain rumen microbes, and may have a role in reducing the incidence of lactic acidosis (41). Lactic acid is fermented largely to propionate or to acetate (3,12,18,29,31). One study indicated that the ratio of acetate to propionate produced from the fermentation of lactate was related to the ration an animal was consuming. Fermentations performed with rumen inoculum from a cow fed a high grain ration produced a lower acetate to propionate ratio from lactate than did those from rations higher in forage (3). Although it is fermentable, lactate supports little microbial yield from the rumen (29).

In terms of the energy that lactate offers to the animal, a study with sheep (18) indicated that 90% of the lactate fed was fermented in the rumen, with little being absorbed directly by the animal. The molar ratios of VFA derived from fermentation of lactate were 1.0:0.57:0.08 for acetate:propionate:butyrate, respectively. Although lactate itself provided no direct contribution to gluconeogenesis, 10% of total lactate was converted to glucose through propionate which was derived from fermented lactate (18). In all probability, factors such as rumen pH, rate of passage, ration composition, and rumen microbial population affect the amount and type of organic acids digested by the ruminal microbes or cow.

Sugars and Oligosaccharides

Simple sugars are comprised of single sugar molecules with glucose and fructose being the most common in plants. Oligosaccharides are short chains of sugars, from 2 to 20 sugar residues in length, with sucrose, a disaccharide, the most prevalent. Together, glucose, fructose, and sucrose are the predominant low molecular weight carbohydrates in forages, and will be referred to in this paper as "sugar(s)". These water-soluble cell contents are reported to account for 1 to 3% of forage DM for the simple sugars, and 2 to 8% for sucrose in "field grown herbage" (temperate forages) (57). Citrus pulp may contain 20% or more of DM as sugar (R. DeStefano, personal communication), but the sugar content will vary with the amount of citrus molasses applied and the citrus variety used to produce the pulp (61). Cane molasses may contain approximately 60% of DM as sugars (expressed as invert sugars; U.S. Sugar, Clewiston, FL), however, there is variation among molasses sources. Almond hulls contain 19 to 34% soluble sugars (1), varying by variety. An interesting note on almond hulls is that the sugars can be "washed out" when the hulls are rained upon, decreasing their content in the feed (1). This same scenario conceivably applies to sugars in other feedstuffs.

Glucose, fructose and sucrose are readily digested directly by the cow, if they reach the small intestine. By virtue of their chemical composition and high solubility, simple sugars and oligosaccharides are also among the most rapidly fermented carbohydrates. The fermentation of sugars is similar to that of starch in that both can ferment to lactic acid. Fermentation of sucrose by rumen microbes resulted in similar concentrations of microbial protein, acetate, and propionate as compared to starch, but more butyrate and lactate at pH 6.7 (59). Although we usually think of depressions in fiber digestion at low pH, changes also occur in the digestion characteristics of the NDSC. At a more acidic pH (5.5), fermentation of sucrose produced more lactate than did that of starch, and microbial protein yield from sucrose was reduced by 34% (59). More lactate, less acetate and butyrate, and the same amount of propionate were produced from sucrose fermented at pH 5.5 vs. 6.7 (59).

The rapid fermentation of sugars yields acid, which can rapidly decrease rumen pH. In cattle fed diets containing grass silage, sugar beet pulp or barley, minerals, and no or 17.4% of DM as molasses (26), rumen pH decreased more rapidly and went lower (rumen pH $\leq$ 6.0) than with diets without molasses. With molasses feeding, molar proportions of propionate and butyrate in the rumen tended to increase, which agrees with in vitro results (59). As for effects on production, inclusion of molasses (0, 4 or 8% of DM) in lactating cow rations varied in having positive or negative effects on milk yield, milk components, and DM intake. The effect appeared to depend upon the level of molasses offered and the type and amount of roughage in the diet (43). If they are added to the point that they depress pH, sugars can depress fiber digestion in the rumen, however, it appears that they may also be capable of enhancing it. Addition of molasses can decrease the lag time of silage and hay DM fermentation (26), possibly due to increasing the total microbial numbers available to ferment feeds (25).

Starch

Starch is the main storage polysaccharide in forage legumes, tropical grasses, and grass and legume seeds (58). Consisting entirely of glucose, it is arranged in two types of polymers: amylose, a linear molecule with α-(1→4) linkages, and amylopectin, an α-(1→4)-linked glucose polymer with α-(1→6)-linked branches. Because of its α-linkages, starch is digestible by mammalian enzymes, whereas cellulose, which consists entirely of β-(1→4)-linked glucose, is not. The simple change in the type of bond entirely changes a glucose polymer's susceptibility to enzymes. The difference in bonding is the reason we cannot simply analyze for glucose in a feedstuff and expect it to have nutritional relevance.

Fermentation of starch by rumen microbes has a variety of similarities to that of sugars. Starch may ferment to lactate (59), and tends to produce a lower acetate to propionate ratio than cell wall carbohydrates (40,59). Although starch fermenting bacteria are more tolerant of acidic conditions than are fiber digesters, growth of starch digesting microbes declines as pH declines (52,60). At acidic vs. neutral pH (5.8 vs. 6.7), yield of microbial protein decreased by 35% when starch was fermented by mixed rumen microbes (59). Consequently, microbial protein available to the cow likely decreases with decreasing ruminal pH.

The rate and extent of starch digestion is affected by a variety of factors. Particle size, grain type, steam flaking, preservation method (dry or ensiled) all affect the availability of starch. In feeds such as corn, the smooth covering of the seed offers the first barrier to digestion, and the protein matrix that surrounds the starch granules the second (37). For whole grain, approximately 30% may pass undigested into the manure in cattle (48). But as particle size in whole corn decreases, ruminal starch disappearance generally increases (16,17). Processing methods which disrupt the protein matrix around the starch granules have been shown to increase grain digestibility (28,63). Subjecting starch to heat and moisture gelatinizes it, destroying the crystalline structure of starch granules, and increasing digestibility (19,22,28,33,63) in the rumen and total tract (49). It has been suggested that overall metabolizable energy yield to the cow is best when starch is fermented in the rumen, due to possible limitations on its digestion in the small intestine (27). However, if digestion of starch in the small intestine were enhanced, there are possibilities for improving the animal's capture of glucose from starch (27).

Neutral Detergent-Soluble Carbohydrates: Fiber

Fructans (Fructosans)

Fructans are water-soluble chains of fructose found in the cell contents of plants. These carbohydrates may have β-(2→1) linkages as in inulin found in Jerusalem artichokes, or β-(2→6) linkages with some β-(2→1) branches as in levan found in temperate grass species (57). They are the principal storage carbohydrates of temperate cool season grasses (58). Depending upon the species and environmental conditions, temperate grass forage has been reported to contain less than 1% and up to 30% fructan (57).

Although mammals can utilize fructose, they do not have the enzymes to digest fructans (46,47). In the rumen, both bacteria and protozoa ferment fructan (68). Fructans can be fermented to lactic acid during ensiling (44,45) and in the rumen (68). Additionally, rumen microbes can degrade fructan and store it as "microbial starch" (glucose polymers with the same bonding as starch) and utilize it at a later time when other nutrients are no longer available (68).

(1→3)(1→4)-β-Glucans

The (1→3)(1→4)-β-glucans are found in the endosperm and cell walls of grasses (66). They have the same β- (1→4) linkage between glucose molecules that cellulose does, but the β- (1→3) linkages create bends in the chain. These bends prevent the molecules from achieving the linearity and crystallinity of cellulose. Barley and oats are major sources of β-glucans, containing from 4 to 12% by weight (32).

Just as mammals cannot digest cellulose, neither can they digest (1→3)(1→4)-β-glucans. However, this carbohydrate appears to be very rapidly fermented. In steers fed barley, ruminal in sacco disappearance of β-glucans varied by lot of barley, but was between 61.4 and 70.4% of DM at time 0, and 93.8 to 96.2% of DM by 8 hours. Disappearance of β-glucan was greater from dry rolled than from steam rolled barley (13). The fermentation of β-glucans does not appear to give rise to lactic acid (66).

Pectic Substances

'Diverse' describes both the concentrations and compositions of pectic substances in plants. Pectic substances are found chiefly in the middle lamella of the plant cell wall. They have been operationally defined as non-starch polysaccharides soluble in water, in chemicals which remove divalent cations (eg., Ca^{++}, Mg^{++}), and in dilute acids or bases that break covalent bonds (11,14,50). In terms of sugar composition, they contain a galacturonic acid backbone with rhamnose inserts that is the portion we think of as pectin, plus neutral sugar side chains made up largely of arabinose and galactose (30). There are differences among plants and plant parts in the content and composition of pectic substances (2,20,50,54,56). Because they are very complex carbohydrates, analysis for pectic substances has been difficult, and there are few values available. By-products such as citrus pulp, sugar beet pulp, and soybean hulls are reported to contain 29, 33.7, and 20% pectin, respectively (36,51,55). Among forages, grasses are low in pectic substances (2 to 5%) (15), while legumes contain higher quantities (7 to 14%) (8,15). Pectic substances decline with increasing plant maturity in alfalfa stems (23).

Due to their carbohydrate composition and bonding, pectic substances are not digestible by mammalian enzymes. However, they are rapidly and extensively degraded by rumen microbes. In vitro fermentation rates of 30 to 40% per hour for pectin have been reported (24). The extent to which they are fermented does not appear to be affected by lignification (35) or, in alfalfa, by plant part (62). Pectin fermentation tends to produce high acetate to propionate ratios and relatively little or no lactate (9,24,40,59). Still, the organic acid contribution from the fermentation of pectic substances depends upon its sugar composition (24). The yield of microbes from pectin or pectic substances is not different from starch (38,39,59). However, the fermentation of pectin at low pH (5.8) is reduced, resulting in a lower extent of degradation, and up to70% less microbial protein produced (59). A more acidic ruminal pH translates into decreased amounts of pectin

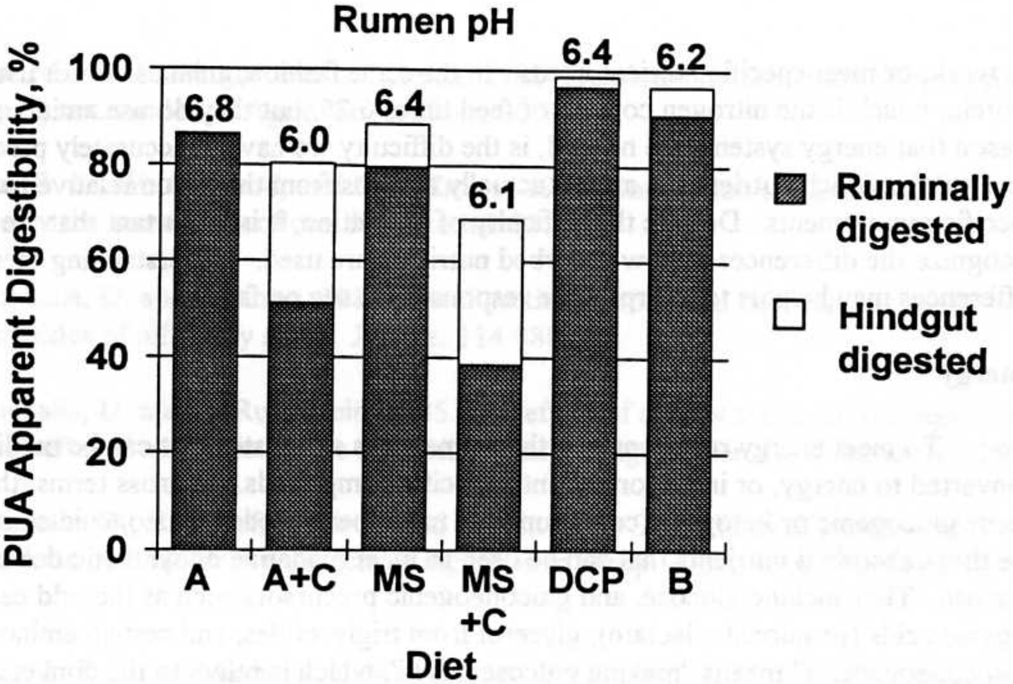

Figure 3. Changes in pectic uronic acid (pectin) digestibility in the rumen and hindgut, and changes in rumen pH when starchy concentrate is fed. Note how digestion of pectin is shifted out of the rumen and to the hindgut as rumen pH decreases. Experiment 1: A = alfalfa diet, A+C = alfalfa + concentrate; Experiment 2: MS = maize (corn) silage, MS+C = maize (corn) silage + concentrate; Experiment 3: DCP = dried citrus pulp, B = barley concentrate source (4, 5, 6).

fermented in the rumen (6) (Figure 3), and a decrease in the amounts of microbial protein and VFA available to the animal. Unlike starch, the cow cannot digest pectic substances that escape the rumen.

Uses of Metabolizable Nutrients From Carbohydrates

The digestion or fermentation of carbohydrates provides the animal with amino acids from rumen microbes, various VFA, lactate, and glucose. Since different carbohydrate sources offer different profiles of nutrients to the animal, it is worthwhile to consider the nutritional implications of their feeding.

The energy systems that we use are proxies to match animal requirements and nutrient efficiencies to estimated supplies of nutrients. For instance, animals do not use net energy or metabolizable energy, per se. They metabolize absorbed nutrients such as amino acids, acetate, propionate, butyrate, glucose, and fatty acids to generate energy to do work, or meet specific nutrient needs. In the same fashion, animals do not use crude protein, which is the nitrogen content of feed times 6.25, but they do use amino acids. A reason that energy systems are needed, is the difficulty we have in accurately predicting how much of each nutrient the animal actually absorbs from the ration relative to their specific requirements. Despite the difficulty of prediction, it is important that we recognize the differences in how absorbed nutrients are used. Understanding these differences may help us to interpret the responses we see on farms.

Energy

To meet energy requirements, the animal uses substrates that can be oxidized and converted to energy, or incorporated into specific compounds. In gross terms, the cow needs glucogenic or ketogenic compounds to meet these needs. Glucogenic compounds are those absorbed nutrients that can be used to meet oxidative or synthetic demands for glucose. They include glucose, and gluconeogenic precursors such as the odd carbon organic acids (propionate, lactate), glycerol from triglycerides, and certain amino acids. "Gluconeogenesis" means "making glucose anew", which is refers to the conversion of the gluconeogenic precursors into glucose in the liver. Since the glucose absorbed directly by the cow is not sufficient to met her requirements, gluconeogenesis provides much of the glucose that the cow requires. Ketogenic compounds cannot be converted to glucose, but can give rise to ketone bodies (acetoacetate, β-hydroxy-butyrate, etc.), may be oxidized to provide energy, or incorporated into lipids in the animal. Ketogenic compounds include the even carbon organic acids (acetate, butyrate), some amino acids, and fatty acids. Although non-ruminants can convert glucose to fat, glucose is typically at a premium in ruminants, and they lack the enzyme for this conversion. Protein or fats incorporated into body tissues contribute to total energy accretion by the animal. Glucose may be stored as glycogen in the liver, and sugars may become associated with proteins.

Protein

Animals use absorbed amino acids from rumen microbes and rumen escape feed sources. The non-protein nitrogen fed to the cow is only made useful to her when the microbes convert it to protein, which occurs given enough fermentable carbohydrate and appropriate minerals. All of the proteins that animals produce, such as milk protein, lean tissue, and enzymes, each have a specific amino acid composition. Accordingly, animals have requirements for specific amino acids. Provision of amino acids that are most limiting can improve animal performance and feed efficiency.

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