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Review
Factors Affecting Digestibility of Feeds in Ruminants

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ABSTRACT

Increased digestion of legume forages alone or in combination with grasses in ruminants is attributed to shorter lag time and lower cell wall contents of the diets. Fibre digestion decreased significantly when excessive amounts of concentrates were added to the diet. The depression in fibre digestion was caused by factors other than low ruminal pH and was termed as carbohydrate effect. The proportion of non-structural carbohydrate (NSC) necessary to depress ruminal pH and fibre degradation was dependent on the rate of solubility of readily fermentable carbohydrates to the rumen organisms and was, therefore, influenced by the degree of processing. The depression in cellulolysis associated with the addition of a readily degradable supplement may be due to increased competition among the rumen microbes for essential nutrients. Cellulolytic microbes may be unable to reproduce at a rate fast enough to compete for these nutrients and maintain themselves in the rumen when high concentrations of NSC were fed and this reduced cellulolytic numbers might have decreased cellulolysis. In addition to this, mono- and di-saccharides might have inhibited some enzymes in the cellulase system, indicating that neutral detergent fibre (NDF) digestibility decreased significantly, when excessive amounts of concentrates were added to the diet. Ruminal NDF rate of passage increased linearly when cows were fed forage diets at increasing levels of intake. Increased feed intake and addition of legumes to grass diets resulted in faster rate of passage from the rumen. Feeding of mixtures of legumes and grasses at high intake increased ruminal passage rate of large particles which resulted in reduced digestibility. Both fluid and particle dilution rates were affected by forage: concentrate ratio and the effect was more pronounced at low rather than high intakes. Fluid dilution rate was depressed when concentrates were increased at the expense of forage in diets. At low intake, particle dilution rate in the rumen was decreased as per cent concentrate in the diet was increased. Passage of poor quality forage was decreased more than a good quality forage due to increasing concentrate in the diet.

Key Words: Lag time; Digestion; Forage; Ruminal pH; Passage rate

INTRODUCTION

The proportion of consumed nutrients that becomes available to ruminants is the result of competition between digestion and rate of passage (Mertens, 1993). Thus, the nutrient value of forage eaten by ruminants is influenced both by the rate at which it is degraded in the rumen and the rate of its physical removal from the rumen. These processes largely determine not only the release of nutrients for the rumen microbes and the host but also the amount of forage that can be eaten; rates of digestion and passage seem imperative to understand the performance of ruminants (Faichney, 1986).

With advancement in genetic make up of dairy cows, milk production from them has gone up tremendously. Therefore, formulating rations to meet the nutritional requirements of genetically superior cows has become a challenge for dairy nutritionists. Maximum dry matter (DM) intake by these cows may not be achieved until approximately twelve weeks postpartum, despite the peak milk yield occurring about seven weeks earlier. Thus most cows are in negative energy balance for much of the first trimester of lactation (Tice *et al.*, 1994). This problem results in weight loss and subsequently lower milk yield. Beef cattle, on the other hand, may have lower energy requirements than dairy cattle but typically consume bulky diets that are high in fibre (except in feedlots). High fibrous, less digestible diets stay longer in the rumen and may limit intake due to gut fill and thus reduce the productivity of these animals (Shaver *et al.*, 1988). Therefore, understanding the factors that influence digestibility of feeds by the animals is of considerable economic importance.

Kinetics of digestion and passage help us understand the mechanism of nutrient availability from the feed consumed by the animal. The knowledge of digestion kinetics and passage not only provide an opportunity to understand the factors limiting digestive process but also help develop feeding strategies for optimizing system output. Thus, understanding the relationship among changes in rate of passage, lag time, extent and site of digestion of fibre sources may help nutritionists formulate rations that maximize nutrient availability to the animals by manipulating rate of passage from the rumen. The objective of this paper is to review the factors influencing the digestibility of the feeds in ruminants.

Effect of forage type on digestion. Sari (1991) reported higher DM, organic matter (OM) and crude fibre (CF) digestibilities of legumes than those of grasses. Shoroma *et al.* (1990) reported decreased DM digestibility by goats fed grasses when compared to goats fed grasses in combination with lucern hay cubes. Similar results were reported by other workers in sheep (Cruickshank *et al.*, 1992), steers (Kung *et al.*, 1992) and buffaloes (Sarwar & Nisa, 1999). Kung *et al.* (1992) also reported higher ruminal pH and lower ruminal ammonia in steers fed lucern based diets than those fed maize silage based diets. The increased CF digestibility may be due to higher ruminal acetate: propionate ratio in steers fed lucern based diets. This high ruminal acetate: propionate ratio might have enhanced the number of cellulytic microbes, resulting in increased CF digestibility. Forages of lowest cell wall contents gave highest ruminal degradability for OM and NDF (Kamatali *et al.*, 1992; Sarwar *et al.*, 1995). Brown *et al.* (1991) also reported higher digestibility of legume and grass mixture and likely mode of action was reduced lag time for the initiation of fibre digestion. In conclusion, feeding legume forages or in combination with grasses, shorter lag time and reduction in the cell wall contents of the diets resulted in the increased digestion in ruminants (Sarwar *et al.*, 1996; Nisa & Sarwar, 1998; Sarwar & Nisa, 1999).

Effect of NSC on digestion. It has been demonstrated that supplementation of roughage with rapidly fermentable source of energy, such as barley, ground corn or molasses, depressed rumen cellulolysis and DM digestion (Burroughs *et al.*, 1949; Chimwano *et al.*, 1976; Kartchner, 1980). Woodford *et al.* (1986) conducted a trial using lactating cows. They formulated diets containing alfalfa hay at 28, 36, 45 and 53% of total DM. Apparent digestibility of dietary constituents was not different except that NDF and acid detergent fibre (ADF) digestibilities increased ($P<0.05$) as per cent forage in the diet increased (for NDF 45.6 to 50.8%; for ADF 46.9 to 50.7%). Decrease in digestibility is associated with increasing concentrate in the diet. Mould *et al.* (1983) observed no difference in 24 h degradation of washed hay in situ with up to 50% supplementation with barley, but it decreased 36% when 75% barley was supplemented. Poore *et al.* (1990) reported no change in total tract NDF digestibility, but ruminal digestibility of potentially digestible NDF decreased ($P<0.05$) from 92 to 70 to 48% as concentrate increased from 30 to 60 to 90% of diet DM fed to steers. Digestibilities of NDF decreased ($P<0.05$) by 72, 57 and 34% for straw, hay and grain, respectively, when concentrate was increased from 30 to 90%. This indicated that fibre digestibility was more depressed for forage NDF than for grain NDF. Thus the influence was greatest upon the slower digesting fraction of the plant cell wall and was inversely related to the degree of lignification (Van Soest, 1994). Digestibility of cellulose and hemicellulose decreased at a rate about three times greater than that of starch (Tyrrell & Moe, 1975). Starch increased the digestibility depression, probably by decreasing digestion of fibre. Chappell and Fontenot, (1968) reported that fibre digestion was reduced when purified starch was added to forage diets of sheep.

If the lower ruminal pH is the only cause for the depressed fibre digestibility, then depression can be removed by maintaining ruminal pH above 6.2. Mould and Orskov, (1983) conducted a research trial in which sheep were fed diets comprising only hay or hay plus higher amounts of barley. The ruminal pH was manipulated by adding mixtures of mineral acids and $NaHCO_3$ They stated that microflora associated with the all hay diet were readily inhibited when ruminal fluid pH levels were maintained below 6.1 and both fibre digestion and intake were depressed. When the ruminal pH of sheep fed barley was increased above 6.2 by adding $NaHCO_3$, DM intake, starch degradation, or cellulolysis did not increase to values for sheep fed high forage diets, indicating that high amounts of barley starch in the rumen can have detrimental effects on ruminal cellulolytic activity aside from their effects on pH. In another trial (Mould & Orskov, 1983), the ruminal pH of sheep was maintained at 6.7 ± 0.15, but the reduction in fibre degradation was not removed completely. Therefore, the residual depression in fibre digestion as caused by factors other than low pH that was termed as carbohydrate effect. They also reported that proportion of barley necessary to depress ruminal pH and fibre degradation was dependent on the rate of ruminal solubility of readily fermentable carbohydrates and was, therefore, influenced by the degree of processing.

The depression in cellulolysis associated with the addition of NSC may be due to increased competition among the rumen microbes for essential nutrients such as ammonia (Burroughs *et al.*, 1949; El-Shazly *et al.*, 1961). Cellulolytic microbes may be unable to reproduce at a rate fast enough to compete for these nutrients and maintain themselves in the rumen when high concentrations of NSC are fed and thus, reduced cellulolytic numbers may decrease cellulolysis. Furthermore, mono- and di-saccharides may inhibit some enzymes in the cellulase system (Mackie & White, 1990). This indicated that NDF digestibility decreased when excessive amounts of concentrates were added to the diet.

Effect of pH on fibre digestion. One of the critical factors responsible for reduced fibre digestion is ruminal pH. Ruminal microbes are very sensitive to changes in pH and most of these microbes perform effectively when ruminal pH ranges from 6.2 to 6.8 (Terry *et al.*, 1969; Hiltner & Dehority, 1983; Shriver *et al.*, 1986) and *in vivo* (Mould & Orskov, 1983; Mould *et al.*, 1983). Mould & Orskov (1983) reported severe reduction in cellulolysis when pH dropped below 6.1. Erdman (1988) reported that ruminal ADF digestion decreased by 3.6% for every 0.1 pH unit decrease below 6.3. McCullough (1969) noted that pH of rumen digesta decreased with increasing amounts of rapidly fermentable carbohydrates in the diets of cattle. When rumen contents from these animals were incubated *in vitro*, the fluid with lower pH reduced cellulolysis. Terry *et al.* (1969) also reported that the extent of cellulose digestion by mixed rumen microbes was dependent on the pH of incubation media. One of the most detailed studies of interrelationship between rumen pH and fibre digestion was conducted by Orskov and Fraser (1975). They fed a common barley and dried grass diet to all sheep but varied the methods of barley processing. The ruminal pH remained above 6.0 when both daily intakes of dried grass and whole barley were 42.8 and 50 g kg^{-1} metabolic body weight, respectively. However, when barley was pelleted and fed at the same rate, the ruminal pH declined to less than 5.5, and both fibre digestibility and intake of grass were reduced.

The effect of low ruminal pH on fibre digestion could be partially due to changing kinetics of digestion. Mertens and Loften (1980) reported a linear increase in the lag time for fibre digestion *in vitro* as the proportion of starch increased. Similar effects have been found *in vivo* (Aitchison *et al.*, 1986). Hiltner and Dehority (1983) suggested decreased lag time for cellulose digestion by Fibrobacter succinogenes when soluble carbohydrates were added to the medium. They related this effect to an increase in bacterial numbers. They also reported reduction in pH and rate of cellulose digestion after the depletion of soluble carbohydrates in the medium.

Miller and Muntifering (1985) conducted an experiment with five rumen-fistulated Holstein steers and determined the effect of dietary concentrate (0, 20, 40, 60 or 80% cracked corn) on kinetic characteristics influencing forage fibre digestion *in vivo*. They reported that rates of forage fibre digestion ranged from 3 to 6%/h for diets containing 20 and 80% grain, respectively but did not differ (P>0.05) among treatments. They suggested that concentrate addition to forage did not reduce fibre digestibility by slowing rate of digestion. They also stated that the potential extent of forage NDF digestion was lower (P<0.5) for 80% grain (28.7%) compared with all other treatments (average 51.2%).

Low ruminal pH could affect attachment of microbes to fibre particles, which seems to be needed by many species of bacteria before most efficient digestion occurs (Hoover, 1986). Shriver *et al.* (1986), using continuous cultures, reported a marked reduction in attached microbes at pH 5.8 compared to pH 6.2, which corresponded to a significant decrease in NDF digestion. It was reported that bacterial proliferation was evident during low pH conditions, but none were tightly adherent to fibre particles as viewed from electron micrographs (Cheng *et al.*, 1983). Increased concentration of H^+ may displace divalent calcium or magnesium which may be needed by some bacteria to attach to feed (Allen & Mertens, 1988).

Low ruminal pH can reduce the bacterial growth rates (Russell *et al.*, 1979). Russell and Dombrowski (1980) reported reduced yields of cellulolytic bacteria in continuous culture when pH decreased below 6.0. Reduction in the number of cellulolytic bacteria from 10^6 to 10^4/ml was also noted *in vivo* due to reduced ruminal pH (Mould & Orskov, 1983; Mould *et al.*, 1983). This could be due to the destruction of membrane potential of cellulolytic bacteria, causing lower viability at low pH (Russel *et al.*, 1990).

The diurnal fluctuation in ruminal pH can have detrimental effects on the rumen microbes. Goetsch and Owens (1984) conducted a trial in which four intestinally cannulated dairy cows were fed diets containing 65, 50 or 35% concentrate twice daily, or a fourth, alternate (ALT) diet in which the diets containing 65 and 35% concentrate were fed in the morning and evening, respectively. They reported that ruminal digestibility of OM tended to decrease with increasing roughage level, but cows fed the ALT diet had the lowest OM digestion. Ruminal starch digestion was slightly more, but total tract starch digestion was lower, when the ALT diet than the 50C diet was fed. This difference may be due to fluctuation in ruminal pH because cows fed the 50C diet maintained a more stable ruminal pH. It was also reported by other workers (Mould *et al.*, 1983) that diets supplemented with molasses produced the greatest diurnal variation in the ruminal pH, but the overall pH was higher than that found with sheep fed diets supplemented with barley. Those fed the diet supplemented with molasses had lower fibre digestion. This can be due to the reduced ability of the cellulolytic microbes to adjust to changing ruminal pH.

Effect of intake level on digestion. Digestibility decreases as feed intake increases (Van Soest, 1994). The digestibility depression is a consequence of competition between digestive processes and passage rates. Increased feed intake (Poppi *et al.,* 1981a; 1981b; Okine & Mathison, 1991; Faichney, 1993; Baurquin *et al.,* 1994) and addition of legumes in grass diets (Moseley & Jones, 1979; Bowman *et al.,* 1991) resulted in faster rate of passage from the rumen. Ruminal NDF passage rate increased linearly (Okine & Mathison, 1991) when cows fed forage-based diets (mixture of Bromegrass, Timothy and alfalfa) at various levels of intakes (1.0, 1.3, 1.5 and 1.7 times maintenance). Supplementation of legumes (25% of diet DM) for Orchardgrass in heifers increased ruminal passage rate of large particles by 21% (Bowman *et al.,* 1991).

Maturity of forage also influences the digestive parameters. Rate and extent of Orchardgrass NDF disappearance in situ increased by 20 and 60% in heifers fed early versus late maturity grass, respectively (Bowman *et al.,* 1991). Rate and extent of fibre digestion of various perennial grasses evaluated at different stages of maturity decreased with increased maturity (Cherney *et al.,* 1993). Similarly, rate and extent of NDF digestion in situ was increased by 24 and 35%, in prebloom versus full bloom alfalfa, respectively, (Shaver *et al.,* 1988). The decreased rate and extent of digestion *in situ* in late versus early maturity of forages probably was due to the increased fibre content in late maturity (Bowman *et al.,* 1991). In the same study (Bowman *et al.,* 1991), mean retention time (MRT) of large and small particles increased by 29 and 37%, respectively, when heifers were fed early versus late maturity grass. Rate of passage is influenced by morphological characteristics of grasses (Poppi *et al.,* 1981b; Luginbuhl *et al.,* 1994) and forage type (Prigge *et al.,* 1990). In sheep offered oat or barley hay at 115 or 100% of *ad libitum* or 1.8% of body weight, MRT of total tract of leaves was lower than for stem (Cherney *et al.,* 1991). In steers fed Bermudagrass at four levels of intake (55,77,88 and 99% of *ad libitum*), whole-tract passage rate was 38% greater for masticated leaves than for masticated stems (Luginbuhl *et al.,* 1994). Higher passage rate of leaves than stems could be due to smaller mean particle diameter of the former than later (Cherney *et al.,* 1990), resulting in low relative resistance to passage (Poppi *et al.,* 1985), or due to effects on fractional specific gravity resulting from varying hydration rates (Cheney *et al.,* 1991). Mixing of concentrate in grass-based diets increased ruminal passage rate (Galloway *et al.,* 1993a; 1993b). Addition of ground corn, whole corn or ground sorghum at 46% of diet DM increased ruminal passage rate of digesta by 15 ($P<0.05$), 7 and 6% ($P>0.05$), respectively, for steers fed Bermudagrass at 1.5% of body weight (Galloway *et al.,* 1993a). However, supplementation of wheat in the same study had no effect on passage rate. The lower passage rate of wheat could be its higher ($P<0.05$) true ruminal OM digestion (57.3%) than those of ground corn (50.7%), whole corn (51.0%) or sorghum grain (42.0 %).

Nutrient interactions. Negative associative effects occur when digestibility of a feed mixture is less than that of the sum of the individual components of the diet. Byers *et al.* (1975) fed steers diets containing 100,75, 25, or 0 % corn silage plus whole shelled corn. Digestibilities of energy and DM of the mixed diets were lower ($P<0.01$) than values predicted from all silage or all grain diets, indicating negative associative effects. Similarly, Bines and Davey (1970) conducted an experiment in which four diets containing 0, 20, 40 or 60% chopped straw and the remainder concentrates were fed to non-lactating dairy cows. The diets containing 0, 20, 40 or 60% straw had 8.05, 16.22, 25.24 or 32.47% cellulose, respectively. They reported that digestibilities of DM of the four diets were 81, 69, 59 and 55%, respectively. Cellulose degradation in the rumen was depressed (42.9%) when cows were fed the diet containing 20% roughage (20R) compared with those (47.1 and 49.9%) for cows fed 40R and 60R diets. Rate of breakdown of cotton threads in situ increased as the roughage content of the diet increased. Liebenberg (1979) carried out an experiment involving 36 lactating cows to determine the effect of concentrate: forage ratio on digestibility. He reported that crude fibre digestibility decreased from 54.1 to 44.6% when concentrate increased from 35 to 65%.

The level of feed intake by animals can interact with the magnitude of the associative effect. Williams *et al.* (1986) conducted an experiment with steers fed high and low starch diets at maintenance. They did not observe any major effect on the digestibility of straw in diets containing rapidly fermentable carbohydrates. Negative associative effects on digestibility were small at low level of intake (<1.5 times maintenance) but became significant when energy intake increased to 2.5-3 times maintenance. Negative associative effects may be a major problem in lactating dairy cows, which normally consume above 3 times maintenance (Tyrrel & Moe, 1975).

In an earlier study (Mould *et al.,* 1983), overall average DM digestibility was reduced by 12.2% units when barley was fed to sheep at a rate of 60 g/kg. Digestibility of the hay fraction was reduced to 32.8% compared to the expected value of 52.2%. This was equivalent to a 37.2% decrease in hay digestibility. Because sheep consumed about 40% more hay, this 12.2% unit decrease in digestibility increase the amount of digestible DM voided in the feces by 17% units [12.2 plus (40% x 12.2%)].

Forage to concentrate ratio. The extent of degradation of a diet is related to its ruminal retention time (RRT). When RRT was reduced by an increase in feed intake (Weston & Hogan, 1971) or by increasing forage: concentrate ratio (Bines & Davey, 1970), a concurrent decrease in DM digestion was noted. Colucci *et al.* (1982) reported that ruminal passage rate of both concentrate and forage particles were reduced (28 and 44%, respectively) when concentrate levels for non-lactating dairy cows were increased from 17 to 68% of the diets at low intake. However, at high intakes, similar particle passage rates were noticed for both forage and concentrates in cows fed diets with low (32%) and high (83%) forage. Colucci *et al.* (1990) reported that dilution rate in the rumen decreased ($P<0.05$) linearly as the proportion of concentrates in dairy diets increased at low intakes, but no difference was detected at high intakes. Cecava *et al.* (1990) reported no difference in ruminal dilution rates in steers fed high (40%) or low (24%) NDF diets at 2% body weight. The average dilution rates were 7.35 and 4.15% h^{-1} for fluid and particulate matter, respectively.

Poore *et al.* (1990) conducted an experiment in which six ruminally cannulated steers were used to examine the influence of various dietary forage: concentrate ratios on ruminal rate of passage. Diets had 30, 60 or 90% flaked sorghum grain plus a 50: 50 mixture of wheat straw and alfalfa hay. Ruminal passage rate for straw (3.4 and 3.0%/h) and hay (4.6 and 4.7%/h) remained unaltered when concentrate increased from 30 to 60%, respectively, but passage rates for straw and hay decreased by 38 (2.2%/h) and 13% (4.1%/h), respectively, when concentrate increased to 90%. However, passage rates for grain (5.3, 5.1 and 4.4%/h) and fluid (9.3,10.0 and 8.2%/h) were not affected by concentrate percentage. They attributed these differential effects of dietary concentrates to differences in ruminal stratifications. As compared to sorghum grain, ruminal passage rate of alfalfa hay was relatively unaffected by dietary concentrate levels, indicating that increased concentrate levels may have a greater impact on passage of low quality forage than on passage of either grain or high quality forage.

Hartnell and Satter (1979) reported no change in particulate rate of passage with variation in forage contents of diets. However, liquid rate of passage was lower in cows fed diets containing 45% forage (4.7%/h) than when dietary forage concentration was raised to 67% (9.3%/h). The increased fluid dilution rate at high forage content was due to greater rumination resulted in more salivation (Luginbuhl *et al.*, 1988).

Briefly, both fluid and particle dilution rates were affected by forage: concentrate ratio and the effect was more pronounced at low (below 2% BW) rather than high intakes. Fluid dilution rate is generally depressed as concentrates increased at the expense of forage in diets. Moreover, the particle dilution rate in the rumen is often decreased at low intakes as per cent concentrate in the diet increased. Passage rate of a poor quality forage decreased more than that of a good quality forage due to increased concentrate in the diet.

Processing. Processing of feeds has variable effects on the rate of passage (Faichney, 1986; Ali *et al.*, 1993). Alwash and Thomas (1971) studied the effect of physical form of grass hay at different levels (1.0, 2.0, 2.6, and 3.1 x maintenance) of intake by sheep. The RRT of chopped hay was higher by 29 and 28% than ground and pelleted hay in sheep fed at 1.0 and 3.1 x maintenance, respectively. For each form of grass, the retention time decreased by 39% as intake increased from the lowest to the highest level. Alwash and Thomas (1974) also reported that MRT of digesta in the gastrointestinal tract decreased as the mean particle size of the hay decreased from 0.64 to 0.20 mm at two levels of intake (1 and 2.1 x maintenance). Increasing feed intake decreased the MRT of all the particle sizes tested. On the other hand, Firkins *et al.* (1986) reported no difference in the ruminal particulate passage rate of steers fed chopped or ground hay at two levels of intake. In this study, however, the intake levels were always less than *ad libitum* (60 and 90% of ad libitum). In sheep fed diets containing 75 or 25% alfalfa at two levels of intake (fed at 1.6 and 2.6% of body weight), particulate passage rate was not affected by intake but increased ($P<0.05$) when wethers were fed 75% alfalfa versus 25% alfalfa in the diet (Merchen *et al.*, 1986). Hay was chopped through a .95 cm screen before feeding. In another study (Slabbert *et al.*, 1992) in which feedlot steers were fed diets with forage: concentrate ratios of 20: 80, 45: 55 or 70: 30 at three levels of intake (80, 90 or 100% of ad libitum), both increases in feeding level and forage: concentrate ratio decreased the ruminal OM retention time linearly ($P<0.01$).

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