FACTORS AFFECTING DIGESTION KINETICS OF FORAGES IN RUMINANTS (A: REVIEW)

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ABSTRACT

Ruminal NDF and DM digestion and digestibility of OM decreased with increasing level of feed intake. Legumes had higher rates and lower extents of NDF digestion compared with grasses. Extent of digestion of legume NDF was lower than for grass because of lower cell wall content and higher lignification of the former. Rate of cell wall digestion was related to the anatomical structure of plant tissues, or greater microbial colonization of legumes than grasses. Increased intake and performance by ruminants can be obtained with the addition of alfalfa to grass based diet and this may be attributed to the positive associative affects of legumes, which had a higher digestion than grasses. Alfalfa supplementation increased the voluntary DM intake from 615 to 815 g/d for sheep fed ammoniated wheat straw and from 520 to 715 g/d for those fed untreated straw. Digestibility of treated straw increased from 39 to 43% and of untreated straw from 26-31% as a result of alfalfa inclusion in the diet. The digestibility of both treated and untreated straw was also increased. Legumes fed together with maize stover increased digestibility of cell-wall constituents compared with maize stover alone. The increased digestibility by legume supplementation could result from an improvement in the ruminal environment by supplying deficient nutrients or readily digestible cell wall substrate for cellulolytic bacteria. Fractional rate of NDF digestion was higher and extent was lower, respectively, in full bloom alfalfa (0.075 h^{-1}, 43.3%) compared with mature bromegrass (0.043 h^{-1}, 61.7%). Rate and extent oforchard grass NDF disappearance *in situ* was increased by 20 and 61%in heifers fed early versus matured grass, respectively. Rate and extent of fiber digestion *in vitro* decreased with increased maturity and cell wall digestibility was 77% higher in immature grass than in immature legume stems. Rate and extent of NDF digestion *in situ* was increased by 24 and 35%, respectively, in prebloom versus bloom alfalfa hays. The decreased rate and extent of digestion *in situ* in late versus early matured forages was probably due to the increased fiber contents. Wethers fed forage with more stem had lower digestibilities of NDF and OM than those fed forages with less stem. Decreasing forage:concentrate ratio of diets led to greater reductions in the fractional digestion rate of cell wall components. Species of animal also had their influences on digestibility of forage consumed.

INTRODUCTION

Kinetics of digestion helps understand the mechanism of nutrient availability from the feed consumed by the animal. The knowledge of digestion kinetics not only provides us an opportunity to understand the factors limiting digestive process but also helps develop feeding strategies for optimizing system output. Thus, understanding the relationship among changes in rate of passage, lag time and extent of digestion of fiber sources may help nutritionists to formulate rations that maximize nutrient availability to the animals by manipulating degradation rates in the rumen.

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 12 weeks postpartum, despite the peak milk yield occurring about 7 weeks earlier. Thus most cows remain in negative energy balance for much of the first trimester of lactation (Tice *et al.*, 1994). This 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 fiber (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)

In this modern age of science, ration formulation is touching new heights of sophistication. The latest approach to fetch greater productivity from ruminant animals is to feed diet which not only promotes better ruminal fermentation to get the maximum out of ruminal microorganisms (Nikolic *et al.*, 1981) but must also supply the required nutrients to meet the needs of the host animal. This can avoid uncoupling of essential nutrients at the ruminal level which consequently results into an effective and profitable livestock keeping.

Therefore, understanding the factors influencing digestion kinetics is of considerable economic importance. The objective of this paper is to enhance the knowledge of both changes in rate of degradation and digestion and role of their relationship to help maximize nutrient availability to the animals.

Dry matter intake, type of forage, associative effects of C_3 and C_4 plants, physiological stage, plant morphology and forage:concentrate ratio are some of the most important factors affecting the rate and extent of digestion of feed and ultimately nutrient availability to the animals.

Dry matter intake

In a study with dairy cows fed at different levels of intake (1.0, 1.3, 1.5 and 1.7 x maintenance), rate and extent ($P<0.04$) of ruminal neutral detergent fiber (NDF), digestion decreased with increasing level of feed intake (Okine and Mathison, 1991). In sheep, digestibility of organic matter (OM) decreased when intake was increased form 1.0, 2.0, 2.6, and to 3.1 x maintenance (Alwash and Thomas, 1971). The magnitude of this decrease was, however, higher in sheep consuming ground and pelleted hay compared with chopped hay. In a similar study (Alwash and Thomas, 1974), OM digestibility was greater at 1.1 x maintenance than at 2.4 x maintenance when sheep consumed ground hay of different particle sizes. Decreasing the particle size from 0.64 to 0.020 cm, in this study, also reduced OM digestibility. In another study (Firkins *et al.*, 1986) with steers fed chopped or ground hay, apparent ruminal NDF digestion decreased as intake increased from 60 to 90 per cent of *ad libitum*. Total tract digestibility of nutrients usually remained unaltered when the intake levels were below *ad libitum* feeding (Firkins *et al.*, 1986; Slabbert *et al.*, 1992). Feedlot steers when fed at three levels of intake (80, 90 and 100% of *ad libitum*), total tract DM digestibility did not change (Slabbert *et al.*, 1992), and this was probably because of compensation in the hindgut.

Forage type

Weiss and Shockey (1991) evaluated the feeding values of high quality orchardgrass and alfalfa silages for lactating cows, and reported that total tract DM and NDF digestibilities of orchardgrass (67 and 72%) were higher ($P<0.01$) than alfalfa (63 and 48%). Glenn et al. (1989) also reported a higher ($P<0.01$) total tract NDF digestibility of orchardgrass than alfalfa in holstein steers. However, total tract DM digestibility showed the opposite trend, and was higher ($P<0.05$) for alfalfa than orchardgrass. Schafield and Pell (1995) reported higher ruminal DM digestibility in legumes than grasses and higher digestibility in legumes may be due to greater concentration of neutral detergent soluble (NDS) carbohydrates in legumes compared to the grasses. They further reported that NDS carbohydrates had higher ($0.52h^{-1}$) rate of disappearance in legumes so legumes had greater amount of faster digesting material compared to the grasses. Cellulolytic activity as measured by carboxymethylcellulase (CMCase) was a good indicator of DM degradation (Silva *et al.*, 1987). Its activity had been used as an indicator for the population of fiber digesting bacteria closely associated with feed particles in the rumen (Silva *et al.*, 1987). This enzyme can be used to rapidly assess variations in the ruminal environment that affect the rate of fiber breakdown (Silva et al., 1987). Peaks of CMCase activity were indicators of higher colonization of cellulolytic microbes which were related to the kinetics of digestion in each forage. Sarwar *et al.* (1996) reported higher *in situ* DM digestibility of leguminous forages ($P<0.05$) than grasses in male buffalo Calves. However, the NDF degradability of grasses and legumes did not differ, but the legumes had higher ($P<0.05$) rates and lower extents of NDF digestion compared to grasses. In an other study in Sahiwal cattle, similar findings were reported (Sarwar *et al.*, 1995). Firkins *et al.* (1991) evaluated CMCase as a marker of cellulolytic bacteria colonization and concluded that CMCase activity gave a qualitative assessment of mass of cellulolytic bacteria colonizing plant fiber. Similar conclusions were drawn in a latter study (Bowman and Firkins, 1993). Using CMCase as an indicator of cellulolytic bacteria, it has been shown that cellulolytic bacteria were in higher concentration adherent to legumes than grass species during early (3 to 18 h) incubation (Bowman and Firkins, 1993). This difference in colonization rate of forage particle by cellulolytic bacteria was implicated as a reason for more rapid rate of fiber degradation for legumes than for grasses. Earlier, a study was conducted to evaluate the fiber disappearance *in situ* and relate it with CMCase activity of various grass-legume combination (Bowman and Bhatti, 1991). The activity of CMCase was higher for alfalfa than for big bluestem grass between 3 and 18 h of incubation. The substrates with 50 and 25 per cent alfalfa had greater CMCase activity than bermudagrass at 3 and 9 h. Freudenberger *et al.* (1994) reported higher NDF digestiblity of legume forage than the grass by ruminally fistulated deer and this increased digestibility was due to a faster fractional degradation rate and larger ruminal particulate mean retention time of legume forage, compared to grasses. Grant and Mertens (1992) also reported a higher ($P<0.05$) rate of NDF digestion *in vitro* for alfalfa (0.094 h^{-1}) as compared with bromegrass (0.58 h^{-1}). A similar trend in digestion rate of alfalfa (0.078 h^{-1}) and clover (0.062 h^{-1}) versus timothy (0.062 h^{-1}) and orchardgrass (0.056 h^{-1}) was reported by Varga and Hoover (1983). Fisher *et al.* (1989) summarized the data on NDF digestive kinetics *in vitro* for various legume and grass species. The average NDF digestion rate constant for legumes was 0.12 h^{-1} compared with 0.09 h^{-1} for grasses. Potentially digestible NDF was 1.8 times more in grasses than in legumes.

Rate and extent of cell-wall disappearance are two independent processes (Fisher *et al.*, 1989). Extent of digestion of legume NDF was lower than for grass because of lower cell wall content and higher lignification of the former (Van Soest, 1994; Jung, 1989). Rate of cell wall digestion was related to the anatomical structure of plant tissues (Akin, 1979; 1989) or greater microbial colonization of legumes versus grasses (Bowman and Firkins, 1993). In general, legumes had higher rates and lower extents of NDF digestion compared with grasses (Varga and Hoover, 1983).

Legume-grass mixture

There are several factors other than intake that can influence digestibility at the same level of intake (Bowman and Asplund, 1988; Shaver *et al.*, 1988; Cherney *et al.*, 1990; Bowman *et al.*, 1991). In a study with sheep consuming grass hay at restricted intake level (90% of *ad libitum*), alfalfa was supplemented at 0, 25, 75 or 100% of the dietary DM. Rates of DM and NDF disappearance and extent of DM disappearance decreased linearly as the percentage of alfalfa increased. In the digestion trial, DM, NDF and cellulose digestibility decreased linearly as dietary alfalfa was increased (Bowman and Asplund, 1988). In an other trial, in which feeding was *ad libitum*, animal performance was improved as a result of increased intake despite the reduced digestion. In heifers consuming grass hay *ad libitum*, substitution of red clover (25% of dietary DM) did not improve NDF digestion in the rumen (Bowman et al., 1991). However, the extent of orchardgrass NDF disappearance *in situ* was increased by 6% ($P<0.05$). Bird *et al.* (1994) studied the effects of supplementation of alfalfa in sheep fed straw based diets. Alfalfa supplementation increased the voluntary DM intake from 615 to 815 g/d for sheep fed ammoniated wheat straw and from 520 to 715 g/d for those fed untreated straw. Digestibility of treated straw increased from 39 to 43 per cent and of untreated straw from 26 to 31 per cent as a result of alfalfa inclusion in the diet. Bhat *et al.* (1988) studied the relation between straw quality and its colonization by rumen microbes *in situ*, using CMCase as an indicator of cellulolytic microbial population. CMCase reached a peak between 24 and 36 h of incubation, and the activity was highly correlated ($P<0.01$) with DM digestibility between 24 and 96 h. The *in situ* digestibility of both treated and untreated straw was also increased significantly. In another study with sheep, legumes fed together with cottonseed cakes as a supplement to maize stover increased digestibility of most dietary solubles and cell wall constituents compared with legume supplements alone (Gatachew *et al.*, 1994). The increased digestibility by legume supplementation could result from an improvement in the ruminal environment by supplying deficient nutrients or readily digestible cell wall substrate for cellulolytic bacteria.

Physiological stage

Maturity of the forages influenced digestive parameters. Shaver *et al.* (1988) evaluated bromegrass and alfalfa at various maturity stages and reported that fractional rate of NDF digestion *in situ* was higher and extent was lower, respectively,in full bloom alfalfa (0.075 h^{-1}, 43.3%) compared with mature bromegrass (0.043 h^{-1}, 61.7%). Rate and extent of orchardgrass NDF disappearance *in situ* was increased by 20 and 61 per cent in heifers fed early versus maturity grass, respectively, (Bowman *et al.*, 1991). In another study (Cherney *et al.*, 1993), in which various perennial grasses were evaluated at different stages of maturity, rate and extent of fiber digestion *in vitro* decreased with increased maturity. Buxton, (1989) reported that *in vitro* cell wall digestibility was 77 per cent higher in immature grass than in immature legume stems. When data were averaged for mature and immature stems, the digestion rate of NDF was 50 per cent faster in legume than in grass stems. Little difference was noted among the different species. Similarly,rate and extent of NDF digestion *in situ* was increased by 24 and 35 per cent, respectively, in prebloom versus bloom alfalfa (Shaver *et al.*, 1988). The decreased rate and extent of digestion probably were due to the increased fiber contents in late maturity (Bowman *et al.*, 1991).

Morphology

Cherney *et al.* (1990) studied the effects of forage morphology on ash-free NDF and OM digestibilities at three levels of intake (100 and 115% of *ad libitum*, and 1.8% of BW) in wethers. The forages offered were hays of sorghum-sudan, barley, oat and pearl millet. Hays were similar in NDF concentration but differed in morphological composition (leaf, blade sheath and stem). Wethers fed forage with more stem had lower DM intake and digestibilities of NDF and OM than those fed forages with less stem. Increased digestibilities were not always associated with decreased intake in this study. In cattle and sheep fed leaf or stem fractions of grasses, potential digestibility of NDF *in situ* was higher for the leaf than the stem fraction; however, no difference was found in their digestion rates (Poppi *et al.*, 1981). Stems are proportionately higher in lignin than are other morphological components; therefore, an increased stem intake would increase lignin, resulting in lower digestibility of stems (Cherney *et al.*, 1990).In another study (Flores *et al.*, 1993; Beauchemin, 1992) in cattle, *in situ* rate of NDF digestion was faster ($P<0.01$) for alfalfa than orchardgrass, and potential digestibility of alfalfa and orchardgrass decreased with increased maturity.

Forage:concentrate ratio

Bourquin *et al.* (1994) studied the effects of forage level and particle size on cell wall digestion of orchardgrass in steers. Decreasing forage:concentrate ratio of diets led to greater reductions in the fractional digestion rate of cell wall components when steers consumed orchardgrass in the ground versus long form. The authors further concluded that dietary forage:concentrate ratio and forage processessing did not consistently influence the potential extent of digestion of orchardgrass cell wall components. Huhtanen and Khalili (1992) studied the effect of sucrose supplements on the particle associated CMCase activity in cattle given silage based diets. Supplementation of the sucrose diet with sodium bicarbonate resulted in higher CMCase activity than did supplementation of the sucrose or basal diet. Inclusion of bicarbonate supplement was probably due to increased pH of the diets.They also noted that the CMCase activity was highly correlated with disappearance of NDF *in situ*. Slabbert *et al.* (1992) reported that in vivo extent of DM digestion decreased by increasing forage to concentrate ratio and, however, this increased forage to concentrate ratio did not affect DM digestibility when high quality orchard grass or alfalfa silages were used as forage source (Weiss and Shockey, 1991).

Animal species

Species of animal also had their influences on digestibility of forage consumed. The DM digestibility of low quality tropical grass was higher in cattle (49.61%) than in sheep (34.6%). This was attributed to better digestibility of NDF by cattle when compared to sheep (Playne, 1978). Similary the DM and NDF digestibilities of grasses were higher in buffalo calves than that of cow calves. However, no difference was noted in DM and NDF digestibilities of legume forages which indicated that buffaloes were more efficient in utilizing the poorly digestible roughages when compared to cattle (Sarwar, 1996).

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