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Pasture digestion in response to change in ruminal pH

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ABSTRACT

Four continuous culture fermenters were used to determine the ruminal pH required for the optimal digestion of pasture. Spring pasture was fermented at four controlled levels of ruminal pH (5.4, 5.8, 6.2 and 6.6) according to a 4x4 Latin square design. Decreasing pH from 6.6 to 5.4 reduced dry matter digestion by 14%, neutral detergent fibre digestion by 11%, total non-structural carbohydrate digestion by 5% and microbial nitrogen flow by 18%. A quadratic relationship was observed between ruminal pH and the true ruminal digestibility of dry matter ($R^2=0.94$, SE=2.06) and microbial nitrogen flow ($R^2=0.66$, SE=0.05).

The ruminal digestibility of pasture dry matter was optimised at pH 6.35, and synthesis of microbial protein was optimised at pH 6.13. This experiment indicated that digestion was largely insensitive to pH across a broad range of pH (5.8 to 6.6), but that a large reduction in digestion occurred when mean pH was less than 5.8.

Keywords: Pasture; rumen; pH; microbial protein synthesis; continuous culture.

INTRODUCTION

Fibre in high quality pasture is digested rapidly (10-16%/h; Kolver, 1997) and accounts for more than 50% of metabolisable energy (Van Soest, 1994). The volatile fatty acids (VFA) produced during digestion, in conjunction with the effectiveness of fibre at stimulating saliva production, determines the pH of the rumen (Pitt *et al.*, 1996). The mean ruminal pH of dairy cows fed spring pasture ranges from 5.8 to 6.2 (Kolver *et al.*, 1998). The extensive digestion of pasture fibre (79% NDF digestibility; Kolver *et al.*, 1998; Van Vuuren *et al.*, 1992) at a pH less than 6.2 contrasts with studies of forage-concentrate diets which exhibited impaired growth of fibre digesting microbes and reduced digestion of fibre when ruminal pH was less than 6.2 (Pitt *et al.*, 1996). At low pH the ability of rumen microbes to generate ATP is compromised by changes in ion concentrations and the permeability of cell membranes (Owens and Goetsch, 1988).

The pH at which optimal digestion of high quality pasture occurs is not well documented. It is also unclear to what extent results from continuous culture studies with forage-concentrate diets (Hoover *et al.*, 1984; Shriner *et al.*, 1986) can be applied to high quality pasture. The prospect that fibre digestion of high quality pasture may be limited by low ruminal pH was demonstrated in a modelling study of pasture and concentrate (Kolver *et al.*, 1998). The inclusion of a source of effective fibre was predicted to raise the ruminal pH above 6.0, which would increase fibre digestion, microbial growth and milk production.

The objective of this study was to establish the ruminal pH required for optimal digestion of pasture and synthesis of microbial protein, and to determine if pasture digestion is depressed at pH levels observed *in vivo* during spring. This study used a dual flow continuous culture system (Hannah *et al.*, 1986), which was designed to simulate ruminal digestion and solid and liquid outflow to the small intestine. This *in vitro* system allowed four pH levels to be maintained.

MATERIALS AND METHODS

Operation of the dual flow continuous culture system was similar to that described by Hannah *et al.* (1986) except that the mineral buffer solution had 0.4 g/l urea added. The liquid dilution rate was maintained at 12 %/h, and the solid dilution rate at 5 %/h (20 h retention time). The dilution rates were similar to those used in previous continuous culture studies (Hannah *et al.*, 1986; Hoover *et al.*, 1989; Mansfield *et al.*, 1995) where liquid dilution rates were 10-12 %/h and solid dilution rates were 4.5-5.5 %/h. These rates have also been found to optimise digestion (Shriner *et al.*, 1986), and are similar to those passage rates obtained from *in vivo* studies with pasture diets (Van Vuuren *et al.*, 1992). Four fermenter units were maintained at either pH 5.4, 5.8, 6.2, or 6.6. The experiment was conducted during four 9-day periods, with 6 days allowed for adaptation followed by 3 days for sample collection.

The pH levels (± 0.1) were maintained using alkali and acid infusion pumps, administering appropriate volumes of 5 N NaOH and 5 N HCl. The diet was high quality ryegrass-dominant pasture (Table 1) which had been freeze dried, ground to 1.6 mm and pelleted into loose pellets (25 x 15 mm). Freeze-drying, grinding and loose pelleting may have reduced the rate of protein digestion. While this may have made small changes to absolute digestibility of the diet, relative differences between treatments would be ex-

TABLE 1: Chemical composition of the pasture diet (%DM) and estimated metabolisable energy content (MJ/kg DM).

Composition	
Organic matter	89.0
Metabolisable energy	12.1
Crude protein	18.6
Soluble crude protein	5.1
Acid detergent fibre	27.8
Neutral detergent fibre	37.9
Total nonstructural carbohydrate ¹	15.8
Crude fat	5.0

¹ Water soluble carbohydrate and starch

pected to remain unchanged. Intake of dry matter (DM) was held constant across diets at 60g DM/fermenter/d and was added in equal portions at 0730, 1330, and 1930 h.

Rumen inoculum was obtained from a lactating, ruminally fistulated Holstein-Friesian cow grazing a ryegrass-dominant pasture. Solid and liquid effluent (simulating ruminal outflow to the small intestine) was sampled at 1300 h and homogenised. A 600-ml sample was collected on the last three days of each period. A 50-ml subsample was squeezed through two layers of cheesecloth and was preserved with 0.6-ml of 50% H_2SO_4 before analysis for ammonia-N and VFA content. The 600-ml sample was bulked across the three sampling days for each fermenter and DM content determined. The remaining effluent was freeze-dried and ground through a 1-mm screen. On the last day of each period, microbes were isolated from the fermenter contents, freeze-dried, and ground through a 1-mm screen.

Microbial samples were analysed for ash and nitrogen (AOAC, 1990), and purine content (Zinn and Owens, 1986) of microbial and effluent samples was determined. Pasture and effluent were analysed for ash, nitrogen, neutral detergent fibre (NDF) and acid detergent fibre (ADF) (Van Soest *et al.*, 1991), and total nonstructural carbohydrate (TNC) (Dubios *et al.*, 1956). The soluble nitrogen, crude fat and mineral content (AOAC, 1990) of the diet was also determined. A sample of the mineral buffer solu-

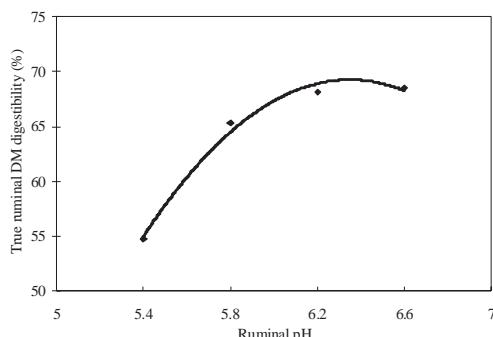
TABLE 2: Effect of ruminal pH on nutrient digestibility of pasture and microbial nitrogen metabolism in continuous culture

	pH 5.4	pH 5.8	pH 6.2	pH 6.6	SED	P ¹	P ²
True digestibility (%)							
Dry matter	54.8	65.3	68.1	68.5	1.41	0.001	0.002
Organic matter	57.6	66.7	69.9	70.3	1.40	0.001	0.004
Apparent digestibility (%)							
Total nonstructural carbohydrate	78.5	80.5	83.4	83.4	1.73	0.019	0.458
Neutral detergent fibre	59.8	67.7	71.4	71.1	5.69	0.081	0.346
Acid detergent fibre	60.5	70.3	74.1	74.8	5.41	0.034	0.275
Microbial nitrogen flow (g N/d)	0.54	0.71	0.69	0.66	0.03	0.020	0.005
Efficiency of microbial protein synthesis (g N/kg OM digested)	17.7	20.1	18.6	17.5	1.01	0.544	0.054

¹Linear relationship between pH treatments

²Quadratic relationship between pH treatments

FIGURE 1: True ruminal digestibility of dry matter (%) in response to change in ruminal pH ($y = -15.834x^2 + 201.03x - 568.8$, $R^2 = 0.94$, SE = 2.06).



tion was taken daily for DM and ash determination.

Data were analysed using the general analysis of variance procedure of Genstat (Version 3.2) according to a 4x4 Latin square design. Linear and quadratic models were evaluated. The linear model used for each dependent variable was: $Y_{ijk} = \mu + A_i + B_j + C_k + e_{ijk}$, where Y_{ijk} is the observations for dependent variables; μ is the population mean; A_i is the average effect of period i ; B_j is the average effect of the fermenter j ; C_k is the average effect of mean pH k ; and e_{ijk} is the residual error (0, s^2).

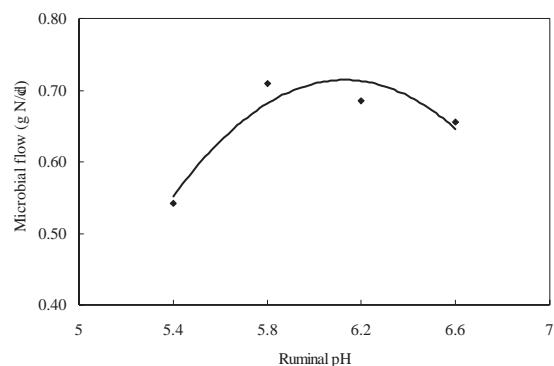
RESULTS

The true ruminal digestibility of DM (corrected for microbial DM) was significantly increased from 54.8% at pH 5.4 to 68.5% at pH 6.6 (Table 2). True ruminal digestibility of organic matter (OM) (corrected for microbial OM) was similarly significantly increased from 57.6% at pH 5.4 to 70.3% at pH 6.6. A significant quadratic relationship was observed between ruminal pH and the true ruminal digestibility of DM (Figure 1) and OM ($y = -13.707x^2 + 174.83x - 486.7$; $R^2=0.93$, SE=1.90). Both DM and OM digestibility were significantly impaired at pH 5.4, but no significant differences were observed from pH 5.8 to 6.6.

Apparent ruminal digestibility of NDF revealed a linear trend as it increased from 59.8% at pH 5.4 to 71.1% at pH 6.6. This trend became significant for ADF increasing from 60.5% at pH 5.4 to 74.8% at pH 6.6. Apparent ruminal digestibility of TNC also exhibited a significant linear increase from 78.5% at pH 5.4 to 83.4% at pH 6.6.

The quantity of microbial nitrogen flowing from continuous culture significantly increased from 0.54 g N/d at pH 5.4 to 0.66 g N/d at pH 6.6 and exhibited a quadratic relationship with microbial nitrogen greatest at pH 5.8 and 6.2 (Figure 2). The efficiency of microbial protein synthesis (g N/kg OM digested) also exhibited a significant quadratic relationship to increased pH ($R^2=0.71$, SE=1.50).

FIGURE 2: Flow of microbial nitrogen (g N/d) in response to change in ruminal pH ($y = -.305x^2 + 3.736x - 10.832$, $R^2 = 0.66$, SE = 0.05).



DISCUSSION

Based on the quadratic relationship obtained in this experiment, a ruminal pH of 6.35 was required to optimise digestion of pasture DM. This is in broad agreement with the pH range of 6.0 to 6.3 recommended to optimise digestion of forage-concentrate diets (Hutjens *et al.*, 1996; Pitt

et al., 1996). In contrast to other continuous culture studies that reported a reduction in OM digestibility (>19%) below ruminal pH 6.2 (Hoover *et al.*, 1984; Shriver *et al.*, 1986), our experiment found that the largest reduction in digestibility occurred when pH was less than 5.8. This suggests that elevated levels of digestion of high quality pasture can be maintained within the range pH of 5.8 to 6.6. The DM digestibilities measured in this experiment confirm observations based on forage-concentrate mixed diets (Hoover *et al.*, 1984; Pitt *et al.*, 1996) that a ruminal pH less than 6.2 will depress feed digestion.

Although less TNC was digested at low pH, the reduced digestibility of DM and OM at pH 5.4 primarily resulted from an 11% reduction in NDF digestibility. The proportionately larger decrease in digestibility of fibre in comparison to TNC is in agreement with other continuous culture studies (Hoover *et al.*, 1984; Shriver *et al.*, 1986). This occurs because cellulolytic microorganisms are less tolerant of low pH than are the amylolytic and saccharolytic microorganisms (Russell and Dombrowski, 1980).

The lower ruminal pH "threshold" for pasture digestion obtained in this study may be a consequence of the high content of digestible fibre. Grant and Wiedner (1992) concluded that the effect of low pH on fibre digestion appears to be a function of the forage fibre source. Within the pH range of 5.5 to 6.8, the *in vitro* digestion rate of NDF of bromegrass hay was not significantly influenced by pH, but the rate of NDF digestion of alfalfa hay was affected at low pH. Further, Mould *et al.* (1983) demonstrated that the reduction in digestibility associated with low ruminal pH was less for forages of high quality.

Our quadratic relationship obtained for microbial nitrogen shows that the synthesis of microbial nitrogen was optimised at a pH of 6.13, and was a function of increased OM digestion and increased efficiency of microbial protein synthesis at a pH of 5.8 and 6.2 (Table 2). The lower pH required for optimal microbial growth in comparison to DM digestion has also been reported by Shriver *et al.* (1986), indicating that the microbes were growing faster and required less energy for maintenance (Russell *et al.*, 1992).

The values for optimal digestion of pasture obtained in this experiment indicate that the empirical relationships between pH, digestion and microbial growth used by models of ruminant digestion, such as the Cornell Net Carbohydrate and Protein System (CNCPS) (Russell *et al.*, 1992; Pitt *et al.*, 1996), are relevant to pasture diets in New Zealand. However, the CNCPS prediction of the effect of ruminal pH on digestion is conservative at the lower end of the pH range assessed in this experiment. For example the CNCPS model, based on the inputs described by Kolver *et al.* (1998), predicted about the same NDF digestibility to that obtained in this experiment for pH 6.2 (78.9% predicted vs. 71.4% actual) and pH 6.6 (74.3% predicted vs. 71.1% actual), but under-predicted for pH 5.4 (19.6% predicted vs. 59.8% actual) and pH 5.8 (50.0% predicted vs. 67.7% actual).

The implication of a depressed digestibility of DM

at low ruminal pH can be evaluated in terms of the effect on the metabolisable energy available for milk production. Using the equation in Figure 1 to calculate DM digestibility, a 4.8% decrease in DM digestibility when pH is decreased from the optimal 6.35 to 5.8, represents an approximate difference of 0.7 MJME/kg of pasture DM. In contrast, the 9.5% reduction in DM digestibility when pH is reduced from 5.8 to 5.4 represents a decrease in energy content of approximately 1.5 MJME/kg of pasture DM. For a cow consuming 16 kg DM/d, and assuming the marginal difference in energy content is used for milk production, a reduction in ruminal pH from 5.8 to 5.4 may represent as much as 5 kg milk/d, or a difference in DM intake of 2 kg DM/d.

CONCLUSION

This experiment established that DM digestibility of pasture is optimised at pH 6.35, although a significant decrease in digestibility only occurred below a ruminal pH of 5.8. Future research will assess the influence of diurnal variation in ruminal pH on the digestion of pasture.

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