A GENERALIZED MODEL FOR DESCRIBING FIBER DYNAMICS IN THE RUMINANT GASTROINTESTINAL TRACT. 1. THE HETEROGENEITY OF THE POOL OF FIBER PARTICLES IN THE RUMINORETICULUM

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Summary

Data from 15 studies with sheep and cattle consuming at least 25% of forage in the diet were gathered to evaluate the current concept of a uniform fiber pool in the ruminoreticulum (RR). Variables analyzed were dry matter intake, fiber intake (NDFI), body weight (W), fresh rumen contents (Q_{FC}), dry matter of Q_{FC} and the ruminal fiber mass (Q_{NDF}), including 27 and 43 averages of the measured variables for sheep and cattle respectively. Variables were scaled to W and the Lucas test applied to both scaled Q_{NDF} and NDFI by assuming steady-state conditions. Robust nonlinear and linear estimation procedures were employed. All variables were scaled to W^1 and the relationship between Q_{NDF} and NDFI yield parameter estimates that violated current assumptions. This result implied that more than one fiber pool based on the RR digesta stratification should be modeled to calculate the nutritive value of forage-based diets.

Introduction

Ruminants that consume forage-based diets typically have two distinguishable solid phases within the ruminoreticulum (RR) compartment: the rumen floating mat (raft), formed by newly ingested particles of the diet, and a pool of small particles dispersed within the fluid phase ventrally to the raft (Hungate, 1966; Sutherland, 1989). Exceptions to this rule occur when feeding behavior is somewhat constrained leading to exclusion of coarse fiber from the diet (Hoffman, 1989; Van Soest, 1996). Despite the digesta stratification, its fiber mass is treated as a single pool in the most accepted paradigm concerning fiber dynamics in the RR. However, an alternative modeling approach was proposed by Ellis et al. (1994) based on the natural stratification of fibrous particles in the RR observed in forage fed ruminants. At this point, our primary objective was to evaluate the steady-state assumptions related to the model that considers the fiber mass in the RR as a single pool.

Experimental Procedures

Data used in the present study were the same gathered by Cannas et al. (2003). Results from 15 studies containing 27 and 43 averages for sheep and cattle, respectively, of body weight (W, kg), dry matter intake rate (DMI, g/d), NDF intake rate (NDFI, g/d), fresh rumen contents (Q_{FC}, g) and either the dry matter (Q_{DM}, g) or the NDF (Q_{NDF}, g) contents of the RR digesta were analyzed. The most important criteria established by those authors was that forages must have constituted at least 25% of the dry matter consumed.

The strategy of scaling variables in relation to W was adopted to reduce size effects on their behaviors and the general power function was employed (see Appendix for details):

$$Y = A \times W^b \qquad \text{(Eq. 1)}$$

In the Eq. 1, A is a scaled constant expressed as the dependent variable unit per unit of W raised to power b. The scaled variable Y, i.e. scaled pool sizes or intake rates, was obtained by the quotient $Y/W^{\hat{b}}$.

The NDF pool size of the rumen (Q_{NDF}) can be considered uniform if, and only if, the Lucas test yields reasonable estimates for the relationship between Q_{NDF} and NDFI according to Eq. 2 (Van Soest et al., 1992):

$$Q_{NDF} = T_{NDF} \times NDFI + M_{NDF} \qquad \text{(Eq. 2)}$$

Where T_{NDF} is the true NDF turnover and M_{NDF} is the metabolic portion of the NDF digesta in the RR. The criteria of linearity, low standard deviations for regression and slope (T_{NDF}), and zero intercept must be held in order to assume that Q_{NDF} behaves as a single uniform pool of fibrous particles.

Nevertheless, to avoid distortions due to size effects, the both scaled NDF pool size (Q_{NDFS}) and NDF intake rate (NDFI) were analyzed according to the linear model (Eq. 2), since it could be demonstrated that scaling of variables do not interfere in the general assumption of linearity, provided that both variables scale with the same power of W (Eq. 3):

$$Q_{NDFS} = T_{NDFS} \times NDFI_S + M_{NDFS} \qquad \text{(Eq. 3)}$$

in which subscript *S* denotes that the variable was scaled to W by an appropriate power. It could be checked that $T_{NDFS} = T_{NDF}$ whether estimates of the powers of W for Q_{NDF} and NDFI are exactly the same, since $T_{NDF} = Q_{NDF}/NDFI$. This property could be considered as an additional criterion ($\hat{T}_{NDF} = \hat{T}_{NDFS}$) to check whether assumptions regarding the Lucas test were not violated.

All statistical analyses were performed with SAS (SAS Inst., Cary, NC). In order to obtain iteratively reweighted nonlinear least-squares estimates of the parameters of Eq. 1, a robust regression criteria published by Beaton and Tukey (1974) was used. Similarly, Eq. 2 and 3 were fitted according to robust linear regression procedures to properly weight for outlier's effects and heterogeneity of variances for higher response levels of Q_{NDF} and Q_{NDFS} (see Appendix for details).

Results and Discussion

The robust nonlinear parameter estimates presented high negative correlations ($r_{A,b} \cong -0.99$) for all variables (pool sizes and intake rates) after fitting Eq. 1. A large variation was observed, particularly in the cattle data set, but b estimates were all different from zero (Table 1). Pool sizes Q_{FC} and Q_{DM} scaled to a power of W lower than one. A larger variation was observed for b of Q_{NDF}, but consistently to the hypothesis that NDF gives a major contribution to the bulky of digesta, the estimate did not differ from unity, i.e. was isometric with respect to W (Van Soest et al., 1992; Van Soest, 1996).

Intake rates had exponents not different from unity (Table 1), indicating that intake rates probably achieved its potential, despite that forages contributed significantly to the NDF of the reported diets (Illius and Gordon, 1991; Ellis et al., 1994). Inferences concerning estimates of A should be done carefully. Besides large variations observed, pool sizes are actually a result of trends in the RR capacity. Such biological rhythm is dictated by homeorhetic mechanisms evolved for survival and reproductive purposes (Mertens, 1996).

Van Soest et al. (1992) emphasized that the Lucas test allows identifying possible heterogeneous pools within the RR digesta. Application of robust regression procedures yielded estimates that violated assumptions regarding uniformity of the pool of fiber particles within the RR. Firstly, a metabolic component was estimated for the fiber fraction (NDF) within the rumen either for the as measured and the scaled NDF pool sizes (Table 2), violating the principle that animals can not secrete fiber in the gastrointestinal tract; it derives entirely from the diet. Another criterion is that the regression line must present a good overall fit to the data; although the robust regression procedure employed yielded precise parameter estimates, the poor R^2 for both the scaled or not variables do not met the quality of fit criteria established by Lucas and co-workers early in 1961 (cited by Van Soest et al., 1992), which means low residual mean square for the regression and a high coefficient of determination (R^2).

Another result that substantially violated intrinsic assumptions related to the single pool model is the fact that the true turnover estimates are statistically distinct because confidence intervals did not overlap (Table 2). If Q_{NDF} and NDFI were scaled to the same power of W, i.e. b = 1 (Table 1), then the scaled true turnover should be the same of the as measured turnover as shown in Eq. 4.

$$T_{NDF} = (Q_{NDF}/NDFI) = (Q_{NDF}/W^1)/(NDFI/W^1) = T_{NDFS} \quad \text{(Eq. 4)}$$

Let us assume that the variables did not scale to the same power of W, instead, Q_{NDF}/W^{α} and $NDFI/W^{\beta}$ are the scaled NDF pool size (Q_{NDFS}) and intake rate (NDFIS), respectively. Let us assign $\Delta = \alpha - \beta$, then the scaled turnover becomes:

$$T_{NDFS} = T_{NDF} \times W^{-\Delta} \quad \text{(Eq. 5)}$$

In fact, the scaled turnover becomes a function dependent on W and not a constant which, by its turn, premise Eq. 2 and 4. The lack of consistency among estimated slopes and powers of W is an additional indication that the single pool model was not sufficient to describe the nature of the fibrous digesta (Tables 1 and 2).

Other factors might also explain this anomalous behavior: different diet compositions, variation within (dairy vs. beef) and between (sheep vs. cattle) species, variation in the physically effectiveness of the NDF, physiological stage, and between study effects. These factors were not considered in the analysis performed, but they might interfere on parameter estimates at a certain degree. Nevertheless, despite large variations observed in the interval estimates for parameter A (Table 1), a reasonable estimate of the scaled NDF pool size under unrestricted feeding conditions was obtained. Although we recognize that the intake rate is rather a behavioral output resulting from complex interactions between the animal and its environment, we found exactly the same estimate of 1.2% of live weight for the NDF intake as suggested by NRC (1996).

The non conformity to the premise concerning the Lucas test should be interpreted as an existing heterogeneous pool of the RR fibrous digesta. The common separation of particles in the ruminant forestomach led to the hypothesis that a sequence of two pools, an unmixing pool formed by particles not eligible to leave the RR because of their resistance to flow (rumen mat or raft), and a second pool located ventrally to the raft: a mixing

The combined kinetic forces of hydration, solubilization, and rumination in the raft enhance accessibility and adhesion to inner feed particles by microbes due to physical breakdown. The propelling forces produced by rumen motility interact with structural anatomy of the particles (three dimensional structure and array of tissues), its chemical composition and intrinsic degradation rates (plant leafs *vs.* stems). The resultant of such interaction is the entrapment of fermentation gases within the food particles increasing their buoyancy. In fact, the net balance among these competing forces is the progressive transfer of matter from the unmixing or non-escapable pool of particles to the mixing or escapable pool of fluid diluted particles. There is not a clear cut between these two pools and migrating particles are actually commingled (Sutherland, 1989; Ellis et al., 1994). Henceforth, a mechanism operating as an ageing chain process takes place as kinetic actions that promote breaking down and flow overcome the buoyancy forces that offer flowing resistance of particles, which urges a more comprehensive approach.

Implications

It is noteworthy that the most accepted paradigm concerning the way that fiber is retained within the ruminoreticulum could yield biased estimates of the flux mechanisms representative of the digestion and passage processes in ruminants eating enough amounts of forage. Models should be developed to accommodate the unmixing/mixing pools concepts as well as an aging chain process to improve current recommendations to yield better estimates of the nutritive value of forage-based diets and ultimately, the prediction of the animal performance.

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Table 1. Nonlinear robust estimates of the parameters regarding body weight (W) scaling to the variables fresh (Q_{FC}), dry matter (Q_{DM}) and neutral detergent fiber (Q_{NDF}) contents (g) of the ruminoreticulum, and to the intake rates (g/d) of dry matter (DMI) and neutral detergent fiber (NDFI).

Variable	Parameter[3,4]	Estimate	Approx. ± SE	Approximate 95% Confidence Limits		Estimated[5] RSD	Reference[6] RSD
				Lower	Upper		
Q_{FC}[1]	A	558	157	245	872	6191	5000
	b	0.74	0.04	0.65	0.82		
Q_{DM}[1]	A	51	23	4	98	1239	1000
	b	0.79	0.07	0.65	0.94		
Q_{NDF}[1]	A	24	21	– 17	64	1107	1000
	b	0.79	0.14	0.53	1.07		
DMI[2]	A	18	17	– 16	51	2565	2000
	b	1.01	0.15	0.72	1.30		
NDFI[2]	A	12	9	– 6	30	1018	800
	b	0.95	0.12	0.71	1.18		

[1] Pool sizes expressed in mass units;
[2] Intake rates expressed in mass units per unit of time;
[3] The parameter A related to pool size variables is expressed in mass units per unit of body weight mass raised to power b;
[4] The parameter A related to intake rates is expressed in mass units per unit of body weight mass raised to power b per unit of time;
[5] Estimated residual standard deviation (RSD), expressed in the same units of the related variable;
[6] Reference value of the RSD as an initial estimate in the robust regression procedure, with a tuning constant of 1.96×3 was assumed as well.

Table 2. Final weighted linear robust least-squares estimates regarding NDF pool size, as measured (Q_{NDF}) and scaled (Q_{NDFS}) to the unity power of body weight (W), as a linear function of NDF intake rate (NDFI) scaled or not to the unity power of W

Variable	Parameter[1,2]	Estimate	± SE	95% Confidence Limits		R^2
				Lower	Upper	
Q_{NDF}	M_{NDF}	700	6	688	712	0.63
	T_{NDF}	0.959	0.001	0.956	0.961	
Q_{NDFS}	M_{NDFS}	4.2	0.3	3.6	4.9	0.37
	T_{NDFS}	0.608	0.03	0.549	0.667	

[1] The parameters M_{NDF} and M_{NDFS} represent metabolic amounts of NDF with the same unit of the as measured NDF pool and scaled to the power one of body weight (valid estimates should not differ from zero);
[2] The parameters T_{NDFS} and T_{NDF} correspond to the true turnovers of NDF respectively scaled or not to W within the ruminoreticulum. It is worthy to note that $T_{NDF} = T_{NDFS}$ when Q_{NDF} and NDFI scales to the same power of body weight (see details in the text).

APPENDIX

A.1) The SAS statements related to the estimation of the reweighted nonlinear least squares estimates presented in Table 1 (observations within parenthesis). Note that Qndf = Q_{NDF} and BW = W.

```
proc nlin data=test best=5 method=marquardt nohalve;
parms a=15 to 30 by 1 b=.5 to 1.5 by .1;
model Qndf=a*BW**b;
resid=qndf-model.qndf;
sigma=1000; (sigma = estimated RSD in Table 1)
c=1.96*3; (c = tuning constant)
w = abs(resid/sigma);
if w <= c then _weight_ = (1-(w/c)**2)**2;
else _weight_ = 0;
output     out = d     r = rbi;
run;
data d;
set d;
sigma = 1000;
b = 1.96 * 3;
w = abs(rbi/sigma);
if w <= c then _weight_ = (1-(w/c)**2)**2;
else _weight_ = 0;
proc print;
run;
```

} these lines establish robust criteria

A.2) The SAS statements related to the estimation of the final weighed least squares estimates presented in Table 2.

```
proc robustreg data=test fwls;
    model qndf = ndfi/diagnostics;
    weight qndf;
    output out=ric2 r=resid sr=stdres;
  run;
```

A.3) If a power scale parameter estimate do not differ from unity, accurate estimates for A could be obtained with the following SAS statement:

```
proc robustreg data=test fwls;
    model Qndf = BW/noint diagnostics; (noint = non intercept model)
    weight Qndf;
    output out=ric2 r=resid sr=stdres;
  run;
```

A.4) Derivation of the “Scaling Function” or the so called “Allometric” equation. We prefer “Scaling Function” because of its scaling purpose between variables and because a given variable could be isometric when a “dependent” variable scales to

the same power of the "independent" variable. We recommend Bioenergetics and Growth, by Samuel Brody (1945), as a further reading on the subject. Let us assume that our independent variable is body weight (W) and a given body part F, for instance the maximum NDF holding capacity of the ruminoreticulum, is our dependent variable, and both are functions of time:

$$\dot{W} = k_1 \cdot W \quad \text{(Eq. 1A)}$$

$$\dot{F} = k_2 \cdot F \quad \text{(Eq. 2A)}$$

After integrating with respect to time, the state trajectory functions or transition functions of W and F could be described by the following equations:

$$\ln(W/W_0) = k_1 \cdot t \quad \text{(Eq. 3A)}$$

$$\ln(F/F_0) = k_2 \cdot t \quad \text{(Eq. 4A)}$$

If we divide Eq. 4A by Eq. 3A, the following result could be obtained:

$$\frac{\ln(F/F_0)}{\ln(W/W_0)} = \frac{k_2 \cdot t}{k_1 \cdot t} \Rightarrow F = F_0 \cdot \left(\frac{W}{W_0}\right)^{\frac{k_2}{k_1}} \quad \text{(Eq. 5A)}$$

If we consider parameter $b = k_2/k_1$ and parameter $A = F_0/(W_0)^b$, we finally arrive to Eq. 1, which scales body parts to the whole:

$$F = A \cdot W^b. \quad \text{(Eq. 6A)}$$