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Technical note

Digestion and passage rates of grass hays by llamas, alpacas, goats, rabbits, and horses

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Abstract

Many studies have suggested that South American camelids (SAC) have greater digestive efficiency than pecoran ruminants, but others have found no difference. In an effort to provide new data on this issue, we investigated the ability of SAC (alpacas and llamas), goats, horses, and rabbits to digest C_3 (*Bromus inermis*) and C_4 (*Cynodon dactylon*) grass hay with nearly equal nitrogen and cell wall concentrations. Dry matter digestibility (DMD) of the C_3 grass hay was not significantly different between SAC and goats. Foregut fermenters (SAC and goats) digested C_3 and C_4 grasses more efficiently than hindgut fermenters (horses and rabbits). SAC digested C_4 grass hays more efficiently than goats, possibly due to their relatively longer particulate matter mean retention times (71 and 54 h, respectively). Apparent nitrogen digestibility was 9% higher for all species with the C_3 grass in comparison to C_4 grass. This suggests that the highly-vascularized bundle sheath cells of C_4 plants prevent efficient utilization of dietary nitrogen.

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1. Introduction

Several studies have suggested that South American camelids (SAC) have superior digestive efficiency compared to pecoran ruminants (Hintz et al., 1973; Foose, 1982; San Martin and Bryant, 1989), while others have reported no difference (Florez, 1973; Hintz et al., 1976; Engelhardt and Schneider, 1977; Warmington et al., 1989). Some of these contradictory results may stem from differences in feed quality. San Martin (1987) observed that llamas are better suited to digesting high-fiber, low-protein forages than sheep, but this advantage disappeared on higher quality diets. Warmington et al. (1989), however, noted no differences in digestive efficiency between llamas and sheep fed low-quality ryegrass straw. Given this array of results, it is probably fair to say that we still know far too little about the costs and benefits of tylopod and pecoran digestive strategies. In this study, we investigated the digestive capacities of SAC, goats, horses, and rabbits on two grass hays, one using the C_3 and the other the C_4 photosynthetic pathway. This allowed us to study the interaction between digestive capacities and plant photosynthetic

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pathways (e.g. Caswell et al., 1973; Heckathorn et al., 1999).

Most temperate grasses utilize the C_3 photosynthetic pathway and most tropical grasses use the C_4 photosynthetic pathway. C_3 plants tend to have higher nitrogen and lower cell wall concentrations than their C_4 counterparts (Wilson and Haydock, 1971; Caswell et al., 1973; Ehleringer and Monson, 1993; Heckathorn et al., 1999). But even if C_3 and C_4 grasses have similar nitrogen and cell wall concentrations, they might nonetheless be nutritionally disparate because C_4 plants (particularly the NAD-me variety) concentrate protein in highly-vascularized bundle sheath cells, which have been shown to be indigestible to insect granivores (Caswell and Reed, 1976) and resistant to bacterial degradation in vitro (Akin et al., 1983; Wilson and Hattersley, 1983). In contrast, protein is dispersed more evenly throughout the highly-digestible mesophyll of C_3 plants. Consequently, even with similar nitrogen and cell wall concentrations, C_4 grasses are predicted to have lower dry matter digestibility (DMD) and apparent nitrogen digestibility (AND) than their C_3 counterparts (Caswell et al., 1973; Ehleringer and Monson, 1993).

We had three primary objectives in this study. First, we examined the digestive efficiency of SAC, pecoran ruminants, and hindgut fermenters. Second, we addressed the possibility that anatomical differences between C_3 and C_4 grass hays lead to differences in DMD and AND. Finally, we studied particulate matter passage rates in SAC and other taxa using stable carbon isotopes as intrinsic markers (Svejcar et al., 1993; Sudekum et al., 1995), as digestive efficiency has been linked to retention of digesta in the gastrointestinal tract (e.g. Foose, 1982; San Martin, 1987; Silanikove et al., 1993; Silanikove, 2000; Van Soest, 1994).

2. Materials and methods

2.1. Digestion trial

Four llamas (*Lama glama*), suri alpacas (*Lama pacos*), boer goats (*Capra hircus*), quarter horses (*Equus caballus*), and New Zealand rabbits (*Oryctolagus cuniculus*) were used in the two grass hay digestion trials. All animals were non-lactating adults. Llamas, alpacas, and horses were obtained from the Brigham Young University herds in Provo, UT. Goats and rabbits were bought from local Utah breeders. Body weight data for all taxa are shown in Table 1. The nutritional compositions of the C_3 and C_4 grass hays (*Bromus inermis* and *Cynodon dactylon*, respectively) were very similar (Table 2). Treatments consisted of 3-week diet acclimation periods followed by 5-day collection periods. The C_3 digestion trial was performed first, followed by a C_4 acclimation period and the C_4 digestion trial. Both the experiments occurred under identical conditions during the same season on the same 20 animals, thus minimizing artifacts due to changing environmental conditions and intraspecific variability (Rymer, 2000). The rabbits were housed in metabolism cages, where the feces fell through a mesh floor. The goats and alpacas were also housed in metabolism crates and fitted with fecal collection bags. Horses and llamas were housed in individual pens and feces were collected from each pen every 4 h. All animals were placed in their respective collection housing 2 weeks prior to the initiation of collection to acclimate them to their surroundings. Water was provided ad libitum throughout the trial. Feed was shredded to limit selectivity, and animals were fed at 12-h intervals. Feed provided was equal to 100% ad libitum intake, which was determined for each animal during the acclimation period on each feed. During each 5 day trial feed intake was recorded, and orts and total fecal output for each animal collected. Fecal collection took place at 4-h intervals to reduce contamination. Rabbit, goat, alpaca, and llama feces were collected, weighed wet and dried at 60 °C. Horse feces were weighed wet, homogenized, and a 10% aliquot was taken and dried at 60 °C. We used one-way analysis of variance to compare digestion data from the C_3 and C_4 hay trials and Fisher's PLSD to compare foregut and hindgut groups and interspecies means within each trial.

2.2. Passage rate trial

The same animals were used in the passage rate study. Four alpacas, goats, and rabbits were placed in metabolic crates 1 week prior to the trial, while the horses and llamas were placed into individual pens. All animals were fed 100% C_3 diets prior to the study. All taxa were then fed a 200 g spike of isotopically distinct

Table 1
Digestibility trial data and standard deviations (±) for rabbits, horses, goats, alpacas, and llamas fed of C_3 and C_4 grass hays with similar nitrogen and cell wall concentrations

	Animal species				
	Rabbit	Horse	Goat	Alpaca	Llama
Body weight (kg)	2 ± 0	453 ± 96	29 ± 4	73 ± 4	109 ± 6
C_3 hay					
Adjusted intake (g/BW$^{0.75}$/day)	116 ± 27[a,b,c]	102 ± 8[a,b,c]	62 ± 15[d,e,b]	29 ± 5[f]	53 ± 5[d,e,b]
Dry matter digestibility (%)	26 ± 10[f]	44 ± 11[f]	61 ± 7[d,e]	57 ± 5[d,e]	53 ± 5[d,e]
Digestible dry matter/BW$^{0.75}$	28 ± 11[e]	42 ± 13[d,b,c]	35 ± 10[b]	16 ± 2[e,a]	27 ± 4[e]
Apparent N digestibility (%)	46 ± 7[f]	59 ± 8[d,a,b]	71 ± 5[d,e]	68 ± 3[d,e]	66 ± 4[d]
Digestible N/BW$^{0.75}$	0.8 ± 0.1[b]	0.9 ± 0.2[a,b,c]	0.6 ± 0.2[e,b]	0.3 ± 0.0[d,e,a]	0.5 ± 0.1[e]
C_4 hay					
Adjusted intake (g/BW$^{0.75}$/day)	38 ± 12[e,a,g]	112 ± 14[f]	68 ± 5[f]	28 ± 8[e,a,c]	49 ± 10[e,a,b]
Dry matter digestibility (%)	45 ± 18[c]	39 ± 7[b,c]	44 ± 8[c,g]	57 ± 1[a]	61 ± 3[d,e,a]
Digestible dry matter/BW$^{0.75}$	18 ± 13[e]	39 ± 7[d,b]	28 ± 6[b]	15 ± 4[e,a,c]	28 ± 6[b]
Apparent N digestibility (%)	49 ± 16[b,c]	41 ± 3[b,c,g]	51 ± 7[c,g]	63 ± 2[d,e,g]	66 ± 3[d,e,a]
Digestible N/BW$^{0.75}$	0.3 ± 0.2[e,a,g]	0.7 ± 0.1[d,b,c]	0.5 ± 0.0[d,b]	0.3 ± 0.1[e,a,c]	0.5 ± 0.1[e,b]

[a] Significantly different from the goat value ($P < 0.05$).
[b] Significantly different from the alpaca value ($P < 0.05$).
[c] Significantly different from the llama value ($P < 0.05$).
[d] Significantly different from the rabbit value ($P < 0.05$).
[e] Significantly different from the horse value ($P < 0.05$).
[f] Significantly different from all other values ($P < 0.05$).
[g] Significantly different from the C_3 value for the species ($P < 0.05$).

C_4 grass hay at the beginning of the experiment, after which they resumed consumption of 100% C_3 grass hay. Since C_3 and C_4 plants have disparate $^{13}C/^{12}C$ ratios, one can trace movement of the C_4 spike through the gastrointestinal tract by analyzing the stable isotope composition of each animal's feces (Svejcar et al., 1993; Sudekum et al., 1995). Rabbit feces were collected every 2 h for the first 24 h, and every 4 h for another 24 h. For all other taxa, feces were collected every 4 h for the first day, every 8 h on the second day, and every 12 h for the following 7 days. Feces for each collection period were dried at 60 °C and a sub-sample homogenized with a mortar and pestle. A 2-mg aliquot was combusted in an automated gas chromatograph (Carlo Erba Instruments, Milan, Italy) and stable isotopes were analyzed using a flow-through inlet system on a continuous flow isotope ratio mass spectrometer (Finnigan, Bremen, Germany). This provided us with carbon and nitrogen isotopes compositions as well as the percentage of carbon and nitrogen in each sample. Carbon isotope data were normalized so that minimum and maximum fecal $^{13}C/^{12}C$ ratios for each animal equaled 0.0 and 1.0, respectively. Carbon isotope excretion curves were then plotted as stable carbon isotope concentrations versus hours since the C_4 spike (Fig. 1) and mean retention times (MRT) were calculated as the area under each excretion curve using NCSS 2001 (Number Cruncher Statistical Systems, Kaysville, UT).

Table 2
Dry matter compositions of the C_3 and C_4 grass hays

Feed properties[a]	Grass hays	
	C_3	C_4
Dry matter (%)	94	95
Nitrogen (%)	1.5	1.5
Acid detergent insoluble nitrogen (%)	0.2	0.3
Acid detergent fiber (%)	41.9	36.8
Neutral detergent fiber (%)	59.7	56.4
Lignin (%)	5.1	4.6
$\delta\ ^{13}C$ (‰)[b]	−26.9	−13.5

[a] Expressed as a percentage of dry matter.
[b] Carbon isotope ratios are expressed as δ values in part per thousand (‰) relative to the PDB standard.

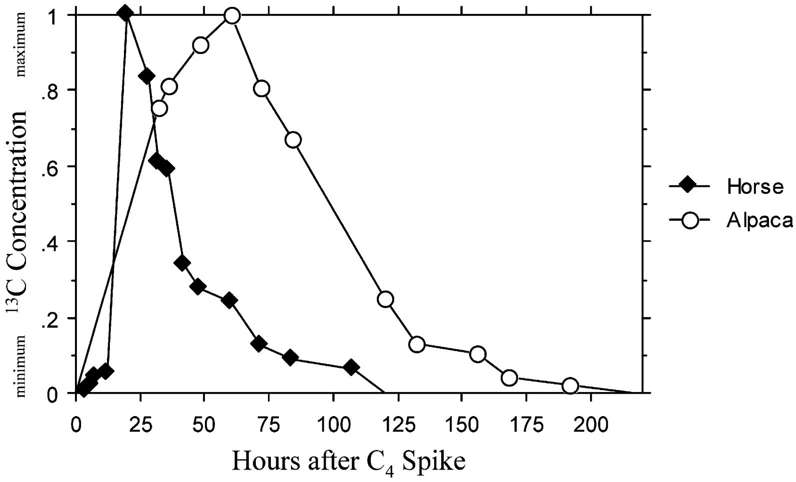

Fig. 1. Stable carbon isotope excretion curves for one horse and one alpaca. Transformed stable isotope concentration data are represented on *y*-axis and hours after the C_4 spike on the *x*-axis.

3. Results and discussion

3.1. Digestibility

The trials with the C_3 and C_4 grasses demonstrated that foregut fermenters (SAC and goats) have higher DMD and AND than hindgut fermenters (horses and rabbits) ($P < 0.001$; Table 1). These results are consistent with earlier studies (e.g. Foose, 1982; Van Soest, 1994). C_3 grass was digested similarly by SAC and goats, although DMD was slightly higher for the goats. Despite this similarity in the digestion efficiency, dry matter intakes relative to metabolic weight were not similar for all of these taxa (adjusted intakes, AI). As a result, the digestible dry matter relative to metabolic weight (DDM/MW, $g_{digested}$/body weight$^{0.75}$/day) was highest for goats and lowest for alpacas. Although horses had an inferior ability to digest the C_3 hay, they had higher DDM/MW due to higher AI than foregut fermenters ($P < 0.05$). Rabbits also compensated for their poorer digestion of the C_3 grass hay by having a higher AI than foregut fermenters ($P < 0.05$).

The C_3 and C_4 hays were digested to a similar extent by llamas and alpacas (Table 1). In contrast, the DMD of C_4 grass by goats was inferior to the DMD of C_3 grass ($P < 0.05$). This result, coupled with no significant changes in the intake levels of all foregut fermenting species, meant that the superior DDM/MW of goats disappeared on the C_4 hay. For horses, there were no significant differences in the DMD or DDM/MW of the two hays. Rabbits, in contrast, digested the C_4 hay better than the C_3 hay, but because their AI decreased their DDM/MW was lower on the C_4 feed.

Apparent nitrogen digestibility (AND) was higher in foregut than hindgut fermenters ($P < 0.01$), and like DMD, there were no statistically significant differences between SAC and goats. Digestible nitrogen relative to metabolic weight (DN/MW) was higher in hindgut fermenters than foregut fermenters, and higher in goats than in SAC due to their relatively higher nitrogen intakes. AND of the C_4 hay was 9% lower than that of the C_3 hay on average ($P < 0.05$; Table 1). This difference was particularly marked in horses and goats, for which AND was ~20% lower on the C_4 grass hay. Thus, even though the DN/MW for horses and goats remained quite high, they appeared to be most affected by the anatomical differences of C_3 and C_4 plants. As with DMD, AND of the C_3 and C_4 grasses was similar in SAC. This, together with the possibility that SAC recycle nitrogen better than most pecoran ruminants (Engelhardt and Schneider, 1977; Warmington et al., 1989), suggests that they are particularly suited for habitats with low nitrogen availability.

3.2. Passage rate

The MRT determined here for llamas, alpacas, goats, horses, and rabbits are 72 ± 14, 71 ± 5, 54 ± 1, 27 ± 5, and 7 ± 2 h, respectively. Our data agree with previous studies that have shown that MRT of SAC are longer than those of goats and sheep (Florez, 1973; San Martin, 1987). Nonetheless, the MRT determined here for llamas and alpacas are higher than those found in some studies (Florez, 1973; Heller et al., 1986a; San Martin, 1987), which probably resulted from the lower-quality diet used here. African camelids (*Camelus dromedarius*) on low-quality roughage diets also have very long MRT (76 h; Heller et al., 1986b). The mean retention time of 71 h for alpacas is conspicuous, however, given that they are 33% smaller than the llamas in this study. Thus, relative to body size, alpaca mean retention times are much longer than those of the llamas, which likely accounts for their very low AI.

4. Conclusions

This study shows that SAC have higher digestive efficiencies than goats on C_4 grass hay, but not on C_3 grass hay. This provides limited support for the hypothesis that SAC have higher digestive efficiencies than pecoran ruminants. Furthermore, these data indicate that nitrogen is more readily available in C_3 than in C_4 plants due to their anatomical differences, even when they have similar nitrogen concentrations. This implies that the wide-scale emergence of C_4 grasses over the last 8 million years would have strongly influenced the evolution of modern grazing herbivores (Cerling et al., 1997). And finally, although llamas and alpacas are generally considered to have identical nutritional requirements when corrected for body size (e.g. San Martin, 1987; Fowler, 1998), our data demonstrate that llamas have much higher DDM/MW than alpacas. This suggests that llamas perform better on low-quality forages than alpacas.

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