Available online at www.sciencedirect.com
SCIENCE DIRECT®
Small Ruminant Research 64 (2006) 162–168
Small Ruminant Research
www.elsevier.com/locate/smallrumres

Digestibility and nitrogen retention in llamas and goats fed alfalfa, C_3 grass, and C_4 grass hays

T.F. Robinson [a,*], M. Sponheimer [b,c], B.L. Roeder [a], B. Passey [d], T.E. Cerling [c,d], M.D. Dearing [c], J.R. Ehleringer [c]

[a] *Department of Integrative Biology, Brigham Young University, Provo, UT 84602, USA*
[b] *Department of Anthropology, University of Colorado at Boulder, Boulder, CO 80309, USA*
[c] *Department of Biology, University of Utah, Salt Lake City, UT 84112, USA*
[d] *Department of Geology & Geophysics, University of Utah, Salt Lake City, UT 84112, USA*

Received 9 July 2004; received in revised form 15 March 2005; accepted 16 April 2005
Available online 1 July 2005

Abstract

The objective of this experiment was to determine the relative digestive capabilities and N retention between goats and llamas fed three forages. Four llamas (2 yrs; 125 ± 7.3 kg BW) and four Boer-cross goats (2 yrs; 53 ± 8.4 kg BW) were housed in metabolism crates and fed alfalfa (*Medicago sativa*; ALF), temperate C_3 grass (*Festuca arundinacea*; C3G) and tropical C_4 grass (*Cynodon dactylon*; C4G) hays. Each forage was fed for 21 d during which time the animals were adapted to the forage, followed by a 5 d period of urine and feces sample collection. Dry matter intake species differences, when adjusted to metabolic body weight (kg $BW^{0.75}$; MW), were noted for ALF and C3G ($P<0.01$), while the goats showed a difference between all three forages ($P<0.05$; 61.6, 31.0 and 46.2 g/(d $kg^{0.75}$) for ALF, C3G and C4G, respectively), the llamas showed a difference between the grasses (40.4, 52.1 and 38.5 g/(d $kg^{0.75}$) for ALF, C3G and C4G, respectively). Digestible DM relative to MW (DDM/MW) was higher for ALF and C4G for the goats versus the llamas ($P<0.03$; 42.5 and 29.0 g/(d $kg^{0.75}$) for goat ALF and C4G and 27.9 and 23.2 g/(d $kg^{0.75}$) for the llama ALF and C4G, respectively). Llamas had a higher DDM/MW for the C3G, 19.6 and 28.9 g/(d $kg^{0.75}$) than goats. Both animal species were in positive N balance for all three forages; llamas and goats retained more N on the high-protein ALF, 0.60 and 0.22 g/(d $kg^{0.75}$), respectively, than they did on either of the grasses ($P<0.05$; 0.15 and 0.04 g/(d $kg^{0.75}$) for C3G and 0.35 and 0.14 g/(d $kg^{0.75}$) for C4G). Unexpectedly, however, both species retained more N on C4G than on C3G. These results demonstrate that, under these circumstances, llamas do not have a higher digestive efficiency than goats, and goats retained more DM and N than llamas. Thus the goats appear to be more efficient on these forages than the llamas. Feeding strategy and morphology difference may account for these findings.

Keywords: Digestibility; N balance; Alfalfa; Grass hays; Llamas; Goats

* Corresponding author. Tel.: +1 801 422 6172; fax: +1 801 422 0090.
E-mail address: todd_robinson@byu.edu (T.F. Robinson).

0921-4488/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.smallrumres.2005.04.018

1. Introduction

There have been many questions regarding the relative digestion efficiencies of pseudoruminant llamas (three compartment stomach) and pecoran ruminants (true ruminants; four compartment stomach) such as goats and sheep (San Martin and Bryant, 1989; Warmington et al., 1989; Sponheimer et al., 2003). Some have suggested that llamas and their close relative, the alpaca, have superior digestive capabilities compared to pecoran ruminants (Hintz et al., 1973; San Martin and Bryant, 1989), while others have found no differences between these taxa (Hintz et al., 1976). Dulphy et al. (1997) and Warmington et al. (1989) found no difference in DMD between llamas and sheep fed a high CP diet, but suggested that llamas are more efficient on low-quality feeds because they lose less urinary N than do ruminants. Under confined laboratory conditions camelids have been reported to have a higher efficiency in extracting energy and protein from forages than pecoran ruminants (Warmington et al., 1989; San Martin and Bryant, 1989).

Grasses can be classified by the photosynthetic pathway they use. In C_3 plants, the first photosynthetic products have 3-carbon structures, while the first products of C_4 plants have 4-carbon structures. C_4 grasses are found in all tropical grasslands and are dominant in warm-season temperate grasslands. C_4 forage has thinner leaves, more bundle sheaths and smaller interveinal distances (Heckathorn et al., 1999). This generally equates to higher cellulose and higher lignin content, and as a result, a decrease in digestibility compared to C_3 grasses (Minson, 1971). A more detailed description of C_3 and C_4 photosynthesis can be found in Ehleringer and Cerling (2002).

This experiment was conducted to investigate the relative digestive capabilities and N retention of llamas (*Lama glama*) and goats (*Capra hircus*) under laboratory conditions fed a dicot forage alfalfa (*Medicago sativa*), a temperate monocot grass (tall fescue, *Festuca arundinacea*). In addition we wanted to determine taxa differences in digestive capabilities between monocots using a C_3 photosynthetic pathway grass (tall fescue) and a tropical C_4 photosynthetic pathway grass (coastal Bermuda, *Cynodon dactylon*) of similar protein and fiber content.

2. Materials and methods

Four llamas (2 yrs old; 125 ± 7.3 kg BW) and four Boer-cross goats (2 yrs old; 53 ± 8.4 kg BW) were obtained from the Brigham Young University herds in Provo, Utah. The animal metabolism room was maintained at 18 °C and lighting was on a 12:12 h on:off cycle. Prior to starting the experiment each animal was introduced to the metabolism crates for fourteen d, during which time they were exercised daily, fed ad libitum grass hay (mid-bloom tall fescue, *Festuca arundinacea*) and ad libitum water. The experiment consisted of every animal being fed each of the three forages during three treatment periods. The three forage hays fed were a mid-bloom alfalfa (*Medicago sativa*; ALF), a mid-bloom tall fescue (*Festuca arundinacea;* C3G) and mid-bloom Bermuda grass (*Cynodon dactylon*; C4G). Forage chemical analysis was performed at a commercial lab (DHI Forage Testing Laboratories, Dairy One, Inc., Ithaca, NY) using wet chemistry procedures for CP, ADF, NDF, lignin, NSC, fat and ash (Table 1). Each forage hay was chopped to a 5 cm fiber length, thoroughly mixed, then stored to reduce any variation when fed during the experiment. The forage treatments were tested during the same season in the same eight animals, thereby minimizing artifacts due to changing environmental conditions and intraspecific variability (Rymer, 2000). All animals were fed each experimental forage for 21 d prior to a 5 d collection period. Feed was provided at 12-h intervals at approximately 100% ad

Table 1
Composition data for mid-bloom alfalfa hay (*Medicago sativa*), a mid-bloom tall fescue hay (*Festuca arundinacea*) and mid-bloom coastal Bermuda grass hay (*Cynodon dactylon*)

Components	Forage hay (% DM[a])		
	Alfalfa	Tall fescue	Bermuda
CP (%)	20.5	10.4	10.3
ADF (%)	36.6	36.6	28.5
NDF (%)	51.5	60.4	63.0
Lignin (%)	6.5	5.2	5.6
Non-structural carbohydrates (%)	27.2	15.6	18.2
Crude fat (%)	3.7	2.7	1.5
Ash (%)	10.8	11.5	9.2

[a] Composition determined by DHI Forage Testing Laboratories, Dairy One, Inc., Ithaca, NY using wet chemistry procedures and are expressed as a percent of DM. Dry matter content was 92, 93 and 93% for the alfalfa, fescue and Bermuda hays.

libitum intake, as determined during each animal's 21 d acclimation period. On the day before each collection period, animals were fitted with a receptacle harness system for total fecal and urine collection. During each 5 d collection period feed intake, feed refusal, total fecal and urine output were determined for each animal. Feed refusal, feces, and a forage grab sample were collected daily and dried at 60 °C. At the end of each forage collection period, these daily dried samples were combined and ground through a Wiley mill (1 mm screen, Arthur A. Thomas Co., Philadelphia, PA). Urine was collected into flasks containing 50 ml of 12 N HCl and the volume measured daily. Individual urine samples for a forage treatment were combined, and an aliquot frozen for future analysis. Nitrogen content of feces, urine and feed was determined by combustion elemental analysis (LECO Corp., St. Joseph, MI). Biological value of N was calculated to be N retained as a percent of N absorbed.

Analysis of variance was determined by general linear model using the SAS procedure GLM (SAS, Inst., Cary, NC) to compare main effects of species, forage and species by forage interaction. Data are expressed as least squares means at a level of significance of ($P < 0.05$).

3. Results

3.1. Digestibility

Dry matter intake (DMI) was different between species and forages ($P < 0.02$ and 0.05, respectively; see Table 2) with the llamas consuming more than the goats across the three forages. The goats consumed more ALF than either C3G or C4G ($P < 0.05$) and llamas consumed more C3G than ALF or CG4. When adjusted to metabolic body weight (kg $BW^{0.75}$; MW) species differences were noted for ALF and C3G ($P < 0.01$), but not for C4G. The goat's adjusted DMI was greater for ALF compared to the grass forages ($P < 0.05$), while C3G was higher than C4G for the llama's ($P < 0.05$); ALF was not different from the grasses.

There were no differences in the ability of the goats and llamas to digest ALF, C3G and C4G hays (see Table 2). The DMD of C3G and C4G were not different to the ALF when fed to the goats (64.5, 62.7 and 68.9%, respectively). Dry matter digestibility was higher for ALF than C3G or C4G in the llamas ($P < 0.05$), 68.9–61.6 and 59.5%, respectively. Digestible DM was adjusted for metabolic weight (DDM/MW) to represent the amount of DM retained (g/(d MW)) by the animal. ALF and C4G DDM/MW were higher for the goats than the llamas ($P < 0.03$), while llamas had a higher DDM/MW for the C3G. Goat DDM/MW was 42.5 g/(d MW) for ALF, decreasing to 19.6 and 29.0 g/(d MW) for C3G and C4G; all were different ($P < 0.05$). Llama DDM/MW was 27.9, 28.9 and 23.2 g/(d MW) for ALF, C3G and C4G, respectively; ALF was not different from the grasses, while C3G was different from C4G ($P < 0.05$).

3.2. Nitrogen balance

Nitrogen intake and adjusted N intake (g/(d MW)) followed DMI for all three forages (see Table 2). Fecal N excretion on a MW (FNE/MW) basis was different ($P < 0.04$) for all three forages between the goats and llamas, where the goats had a higher FNE/MW for ALF and C4G than the llamas. Goat FNE/MW was different ($P < 0.05$) between each of the forage treatments (0.43, 0.26 and 0.17 g/(d MW) for ALF, C4G and C3G, respectively). Llamas FNE/MW was not different between the three forages, ranging from 0.23 to 0.27 g/(d MW). Urine N excretion adjusted for MW (UNE/MW) was not different between the two species, but forage differences were noted within each species for all three forages. Goat and llama UNE/MW was highest for ALF ($P < 0.05$), 1.00 and 0.85 g/(d MW), respectively. UNE/MW for goat C3G and C4G were 0.15 and 0.20 g/(d $kg^{0.75}$), while llama UNE/MW was 0.26 and 0.48 g/(d MW). Urine N expressed as a percent of total N excreted adjusted for MW (UPE) was different across species and forage ($P < 0.01$ and $P < 0.05$, respectively). Llama UPE was higher than that of goats across all three forages and highest for ALF and lowest for C4G (76.8, 64.1 and 53.5%/MW for ALF, C3G and C4G, respectively). Goat UPE followed the same pattern (69.6, 54.1 and 35.8%/MW for ALF, C3G and C4G, respectively).

Both species were in positive N balance for all three forage trials (see Table 2). No difference was significant between the species, though the goats retained numerically more N than the llamas on all three forages. Llamas and goats retained more N on the high-

Table 2
Digestibility and N balance data for goats and llamas consuming three different hays; mid-bloom alfalfa hay (*Medicago sativa*), a mid-bloom tall fescue (*Festuca arundinacea*; C_3 grass hay) and mid-bloom coastal Bermuda (*Cynodon dactylon*; C_4 grass hay)

	Species		S.E.M.	Species *P*
	Goat	Llama		
Alfalfa hay				
Dry matter intake (g/d)	1211	1512	79	0.02
Adjusted intake (g/(d kg$^{0.75}$))	61.6	40.4	2.7	0.01
Dry matter digestibility (%)	68.9	68.9	2.3	NS
Digestible DM/MW (g/(d kg$^{0.75}$))	42.5	27.9	2.0	0.03
N intake (g/day)	39.7	49.6	1.9	0.01
Adjusted N intake (g/(d kg$^{0.75}$))	2.02	1.33	0.05	0.01
N digestibility (%)	78.8	80.7	1.9	NS
Fecal N excreted (g/(d kg$^{0.75}$))	0.43	0.25	0.02	0.04
Urine N excreted (g/(d kg$^{0.75}$))	1.00	0.85	0.05	NS
Urine as percent of total N excreted (%/kg$^{0.75}$)	69.6	76.8	2.7	0.01
N retention (g/d)	11.7	8.3	1.2	NS
Adjusted N retention (g/(d kg$^{0.75}$))	0.60	0.22	0.04	0.01
Biological value (%)	29.6	17.0	4.8	0.01
C_3 grass hay				
Dry matter intake (g/d)	608[a]	1758[a,c]	79	0.01
Adjusted intake (g/(d kg$^{0.75}$))	31.0[a]	52.1[c]	2.7	0.01
Dry matter digestibility (%)	64.5	61.6[a]	2.3	NS
Digestible DM/MW (g/(d kg$^{0.75}$))	19.6[a,c]	28.9[c]	2.0	0.03
N intake (g/day)	10.1[a]	29.3[a,c]	1.9	0.01
Adjusted N intake (g/(d kg$^{0.75}$))	0.52[a,c]	0.78[a]	0.05	0.01
N digestibility (%)	67.8[a]	66.1[a]	1.9	NS
Fecal N excreted (g/(d kg$^{0.75}$))	0.17[a,c]	0.27	0.02	0.04
Urine N excreted (g/(d kg$^{0.75}$))	0.15[a,c]	0.26[a,c]	0.05	NS
Urine as percent of total N excreted (%/kg$^{0.75}$)	54.1[a,c]	64.1[a,c]	2.7	0.01
N retention (g/d)	2.9[a,c]	1.4[a,c]	1.2	NS
Adjusted N retention (g/(d kg$^{0.75}$))	0.15[a,c]	0.04[a]	0.04	0.05
Biological value (%)	30.3[c]	4.5[c]	4.8	0.01
C_4 grass hay				
Dry matter intake (g/d)	900[a]	1436[b]	79	0.01
Adjusted intake (g/(d kg$^{0.75}$))	46.2[a]	38.5[b]	2.7	NS
Dry matter digestibility (%)	62.7	59.5[a]	2.3	NS
Digestible DM/MW (g/(d kg$^{0.75}$))	29.0[a,b]	23.2[b]	2.0	0.03
N intake (g/day)	14.8[a]	23.7[a,b]	1.9	0.01
Adjusted N intake (g/(d kg$^{0.75}$))	0.76[a,b]	0.63[a]	0.05	NS
N digestibility (%)	65.7[a]	63.7[a]	1.9	NS
Fecal N excreted (g/(d kg$^{0.75}$))	0.26[a,b]	0.23	0.02	0.04
Urine N excreted (g/(d kg$^{0.75}$))	0.20[a,b]	0.48[a,b]	0.05	NS
Urine as percent of total N excreted (%/kg$^{0.75}$)	35.8[a,b]	53.5[a,b]	2.7	0.01
N retention (g/d)	6.9[a,b]	5.3[b]	1.2	NS
Adjusted N retention (g/(d kg$^{0.75}$))	0.35[a,b]	0.14	0.04	0.01
Biological value (%)	46.3[a,b]	20.4[b]	4.8	0.01

NS: no differences ($P > 0.05$); S.E.M.: standard error mean.
[a] Different from alfalfa ($P < 0.05$).
[b] Different from C_3 grass hay ($P < 0.05$).
[c] Different from C_4 grass hay ($P < 0.05$).

protein ALF than on either of the grass hays ($P<0.05$), and both species retained more N on C4G than on C3G ($P<0.05$). Nitrogen retention relative to MW (Nret/MW) was higher in goats than llamas for both grass hays ($P<0.01$). Alfalfa Nret/MW was higher in goats than in llamas ($P<0.06$). For all three forages within species ALF Nret/MW was highest followed by C4G then C3G; significance was noted for goats between the three forages, while only C3G was different from ALF. Digestibility of N was not significant between species, but a forage effect ($P<0.05$) was apparent between ALF and the two grasses; 79.8% for ALF to 66.9 and 64.7% for C3G and C4G, respectively. Biological value (BV) of N was lower ($P<0.01$) for the llamas than the goats across all three forage treatments. Goat BV was higher ($P<0.05$) for C4G than ALF or C3G, while BV for the llamas was the same for ALF and C4G and lower ($P<0.05$) for C3G.

4. Discussion

The three forage hays used in this study were chosen for specific reasons; the alfalfa hay was chosen for its high crude protein and digestibility. The temperate grass (tall fescue, *Festuca arundinacea*) using the C_3 photosynthetic pathway and the tropical grass (coastal bermuda, *Cynodon dactylon*) using the C_4 photosynthetic pathway where chosen because they had similar crude protein and fiber content. Although both grass hays had similar fiber and protein concentrations, the latter would be expected to have lower N availability because C_4 grasses concentrate protein in highly-vascularized bundle sheath cells, which have proven to be a deterrent to insectivorous and bacterial degradation (Caswell and Reed, 1976; Wilson and Hattersley, 1983; Heckathorn et al., 1999).

Several studies have reported that camelids have superior digestive capabilities to pecoran ruminants (Hintz et al., 1973; San Martin and Bryant, 1989; Warmington et al., 1989). In this study, however, we found no evidence of this. The llamas and goats digested alfalfa DM and the two grass hays equally well when expressed on a percentage basis, although the llamas had a higher digestibility of the alfalfa than the two grass hays. However, when digestible DM retained was expressed on a MW basis the goats retained more on the alfalfa and the C_4 grass than the llamas; conversely the llamas retained more on the C_3 grass than the goats. This observation is associated with DM intake and represents the same pattern. The goats consume more on a MW basis resulting in a higher retention of DM when compared to the llama. This retention or extraction of DM can proxy for energy consumed and demonstrate that the goats have a greater capacity to consume more energy. Goats are classified as intermediate to concentrate selectors, while llamas are classified as intermediate feeders to grazers (Van Soest, 1994; Hoffman, 1985). Domingue et al. (1991) compared Red deer, goats and sheep digestibility. Sheep are classified in the same category as llamas, while the Red deer and goat are classified the same as the goats. They found that the goats and deer were better at digesting the forages used in the experiment than the sheep. They summarized that goats chewed the *Medicago sativa* forage to smaller particle size than the sheep, increasing surface area for microbes to attach allowing for a greater microbial breakdown of the fiber. Our findings may be attributed to this difference in particle size. The alfalfa and C_4 hays had higher lignin content than the C_3 hay. Although the diets in this study were ground to avoid sorting of coarse and fine material, it was observed that the goats ate more of the fine material, leaving more of the coarse, and the llamas consumed more of the coarse, leaving more of the fines. Based on their feeding strategies this would be expected and also may account for DDM/MW differences. The higher capacity for forage intake at the same digestibility will result in the goat extracting more nutrients on a MW basis than the llama. Under the circumstances our animals were under, it does not appear that the llama digests DM more efficiently than the goat. Regardless, these results do suggest that when considering digestive capabilities of taxa, one cannot do so without also considering their feeding classification.

The animals in this study were in late stage of growth, where we would not expect great differences in N retention. Because of the intense nature of this study, the animals were not weighed in a manner that would provide data to evaluate protein weight gain based on N retention. The N retention data indicate that the goats retained relatively more N than the llamas. Given the stage of growth and the fact that llamas recycle urea N more than sheep (Hinderer and Engelhardt, 1975), the llamas' N requirement may have been met at a lower level, and the lower N retention was due to excretion of excess N in urine and the low BV. The forage difference in N retention of the llamas compared to goats was due to the loss of relatively more urinary N; fecal N losses relative to N intake were identical for both species. Couple this response to the higher BV for goats consuming each of the different forages, and it appears that the goats have a better biological utility of the N absorbed given their stage of growth, instead of a better ability to access it. Nitrogen recycling by the llama could also account for the differences.

The high N retention for both species on the alfalfa hay was expected, but the greater N retention for C4G than C3G ran counter to our expectations. Considerable attention has been paid to the potential importance of the biochemical and anatomical differences between C_3 and C_4 plants (Wilson and Hacker, 1987; Wilson et al., 1991; Ehleringer and Cerling, 2002). Tropical C_4 plants typically have lower N and higher cell wall concentrations than C_3. The concentration of protein in the highly protected bundle sheath cells of C_4 plants should reduce their DM and N digestibility even further (Wilson and Haydock, 1971; Ehleringer and Monson, 1993). In this experiment, where the grass hays were similar in chemical composition, we found the goats and llamas digested the C_4 and C_3 grasses equally well. Both species digested the grass N the same, but C4G resulted in a higher BV than the C3G. This finding was surprising given the evidence that C_4 N is well protected and unavailable. One possible explanation for this is, that the amino acid balance of C4G was superior to that of C3G, resulting in the biological availability being higher.

5. Conclusion

Much of the literature suggests that camelids are more efficient at digesting forages than pecoran ruminants. Data presented here compare taxa with intermediate/concentrate selector and intermediate/grazer feeding patterns and show that goats are capable of consuming more and retaining more DM and N on a MW basis than the larger llama. Digestive physiology may play a part, but the fact remains that the llama can subside on less forage with less N. While C_4 grasses are expected to be of poorer quality than their C_3 counterparts, this may not always be the case as shown by our data. Further research in this area is needed, as the wide-scale emergence of C_4 plants since the late Miocene period has been suggested to be a driving force in the evolution of modern grazing herbivores (Ehleringer and Monson, 1993; Cerling et al., 1998).

References

Caswell, H., Reed, F.C., 1976. Plant-herbivore interactions: the indigestibility of C_4 bundle sheath cells by grasshoppers. Oecologia 26, 151–156.

Cerling, T.E., Harris, J.M., MacFadden, B.J., 1998. Carbon isotopes, diets of North American equids, and the evolution of North American C4 grasslands. In: Griffiths, H. (Ed.), Stable Isotopes and the Integration of Biological, Ecological, and Geochemical Processes. Bios Scientific Publishers, Oxford, pp. 363–379.

Domingue, B.M., Francoise, Dellow, D.W., Wilson, P.R., Barry, T.N., 1991. Comparative digestion in deer, goats and sheep. N. Z. J. Agric. Res. 34, 45–53.

Dulphy, J.P., Dardillat, C., Jailler, M., Ballet, J.M., 1997. Comparative study of forestomach digestion in llamas and sheep. Reprod. Nutr. Dev. 37, 709–725.

Ehleringer, J.R., Cerling, T.E., 2002. C_3 and C_4 photosynthesis. In: Munn, R.E. (Ed.), Encyclopedia of Global Environmental Change. The earth system: biological and ecological dimensions of global environmental change, vol. 2. Wiley, NY, pp. 186–190.

Ehleringer, J.R., Monson, R.K., 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annu. Rev. Ecol. Syst. 24, 411–439.

Heckathorn, S.A., McNaughton, S.J., Cleman, J.S., 1999. In: C4 Plant, Biology, Sage, R.F., Monson, R.K. (Eds.), C_4 Plants and herbivory. Academic Press, San Diego, CA, pp. 285–312.

Hinderer, S., Engelhardt, W.V., 1975. Urea metabolism in the llama. Comp. Biochem. Physiol. 52, 619–622.

Hintz, H.F., Schryver, H.F., Halbert, M., 1973. A note on the comparison of digestion by new-world camels, sheep and ponies. Anim. Prod. 16, 30–35.

Hintz, H.F., Sedgenrick, C.J., Schryver, F., 1976. Some observations of a pelleted diet by ruminants and non-ruminants. Int. Zoo Yearb. 616, 54–57.

Hoffman, R.R., 1985. Digestive physiology of the deer—their morphophysiological specialization and adaptation. In: Fennessy, P.F., Drew, K.R. (Eds.), Biology of Deer Production, vol. 22. The Royal Society of New Zealand, Wellington, Bulletin, pp. 393–407.

Minson, D.J., 1971. Influences of lignin and silicon on a summative system for assessing the organic matter digestibility of *Panicum*. Aust. J. Agric. Res. 22, 589–598.

Rymer, C., 2000. The measurement of forage digestibility in vivo. In: Givens, D.I., Owens, E., Axford, R.F.E., Omed, H.M. (Eds.), Forage Evaluation in Ruminant Nutrition. CABI Publishing, New York, NY, pp. 113–134.

San Martin, F., Bryant, F.C., 1989. Nutrition of domestic South American llamas and alpacas. Small Rumin. Res. 2, 191–216.

Sponheimer, M., Robinson, T., Roeder, B., Hammer, J., Allyffe, L., Passey, B., Cerling, T., Dearing, D., Ehleringer, J., 2003. Digestion and passage rates of grass hays by llamas, alpacas, goats, rabbits, and horses. Small Rumin. Res. 48, 149–154.

Van Soest, P.J., 1994. Nutritional Ecology of the Ruminant, second ed. Comstock Publishing, Ithaca, NY.

Warmington, B.G., Wilson, G.F., Barry, T.N., 1989. Voluntary intake and digestion of ryegrass straw by llama × guanaco crossbreds and sheep. J. Agric. Sci. 113, 87–91.

Wilson, J.R., Haydock, K.P., 1971. The comparative response of tropical and temperate grasses to varying levels of N and phosphorus nutrition. Aust. J. Agric. Res. 22, 573–587.

Wilson, J.R., Hattersley, P.W., 1983. In vitro digestion of bundle sheath cells in rumen fluid and its relation to the suberized lamella and C_4 photosynthetic type in *Panicum* species. Grass Forage Sci. 38, 219–223.

Wilson, J.R., Hacker, J.B., 1987. Comparative digestibility and anatomy of some sympatric C_3 and C_4 arid zone grasses. Aust. J. Agric. Res. 38, 287–295.

Wilson, J.R., Deinum, B., Engels, F.M., 1991. Temperature effects on anatomy and digestibility of leaf and stem of tropical and temperate forage species. Neth. J. Agric. Sci. 39, 31–48.