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Abstract

The effect of browse level in the diet on the in vivo dry matter digestibility (DMD) in sheep and the DM degradation of peanut hay in the rumen of cattle-fed tree forage-based diets were investigated in order to detect the occurrence of digestive interactions between diet components. Selected browse species *Acacia albida* pods, *Pithecellobium dulce, Adansonia digitata* and *Calotropis* ***procera*** leaf samples were collected in the central regions of Senegal, sundried and stored in LNERV animal bams for in vivo trials. Classical in vivo balance trials were performed for each tree forage sample. The proportion of browse in the applied diet varied between 0 and 75% of DM. Regression and difference procedures were both tested to estimate the DMD of the browse component of the diet. DMD capacity in the rumen of three young Gobra bulls fed the browse-based diets was estimated by measurement of the in *sacco* dry matter degradation profile of a standard sample, peanut hay. For each sample, large variations were observed when the browse DMD was calculated by difference. Both total ration DMD and rumen DM degradation capacity were significantly ($p<0.001$) influenced by browse level in the diet. However, non-linear response of total diet DMD to increasing levels of browse was observed only in A. ***digitata*** and *P. dulce* indicating occurrence of digestive interactions in those species. Rumen DM degradation capacity varied according to plant species which played a major role in the observed digestion profile. Results suggest that the digestion of tree forages-based diets may be influenced by digestive interactions but the large variations observed in plant species show their importance. Optimal DM degradation occurred at 15–30% of browse level in the diet for both *A. albida* and ***A. digitata*** while for *P. dulce* it was at 50%. Corresponding browse digestibility was of 50%, 47.1%, 51.3% and ***60.7%*** DM for A. ***albida, A. digitata,*** l? ***dulce*** and C. ***procera*** respectively. Fnrther work using the

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regression method in a wider range of browse species could help confirm between-species variations.

Keywords: Browse plants; In vivo dry matter digestihility: Rumen DM degradation; Sheep; Digestive interactions; Tropical regions

1. Introduction

In vivo dry matter digestibility is a basic measurement for the evaluation of energy utilisation of animal feeds. This method may be labour-intensive and time-consuming, but the importance of its application is often emphasised by many research workers.

The application of the in vivo method to evaluate browse digestibility needs some precautions as their chemical composition is characterised by the occurrence of secondary compounds which may be toxic for ruminants. Condensed tannins are well known for their negative effect on rumen microbial activity and consequently, on energy and nitrogen metabolism (McLeod, 1974; D'Mello, 1992; Bernays et al., 1989; Leinmuller et al., 1991; Reed et al., 1990). Toxic amino acids including mimosine are one of the major constraints to legumes incorporation in ruminant diet (Lowry. 1989). Other toxic compounds include cyanogenetic glycosides and alkaloids which may cause deleterious effects in livestock (Conn, 1973; Culvenor, 1973; James et al., 1992). Therefore, the occurrence of these chemical compounds in tree forages limits their ad libitum use by ruminants. This mises the crucial question of their restricted incorporation in ruminant diet. Thus, the selection of appropriate browse level in the diet is problematic. Previous results have shown marked effects of browse level on in vivo DMD of tree forage-based rations (Fall, 1993; Fall et al., 1996; Miranda, 1989; Dick and Urness. 1981). Linear and non-linear relationships were found between browse proportion and in vivo DMD of diets involving different browse species. A linear relationship shows additivity of different diets components while a curvilinear relationship indicates non-additivity of the different ingredients which is also visualised by differences in browse digestibility when calculated by difference. This implies the occurrence of digestive interactions or associative effects as described in rations involving graded levels of concentrates (Wainmann et al., 1981; Sauvant and Giger, 1989; Berge and Dulphy, 1991).

The aim of the present study was to investigate the occurrence of digestive interactions in tree forage-based diets.

2. Material and methods

2.1. *Experiment 1: Measurements of in vivo DMD of tree forages-based diets*

In vivo triais were conducted in the ISRA (Senegalcsc Institute of Agricultural Research) station of LNERV (National Laboratory for livestock and Veterinary Research) appreciated by an analysis of variance. The significance of differences was appreciated by an independent analysis of variance for each incubation time in each plant species.

3. Results

3.1. Estimation of BDMD by difference

In vivo DMD of studied browse species is presented in Table 2.

Average ration dry matter intake was ***54.9, 53.0, 53.4, 53.3*** g/kg $BW^{0.75}$ for ***A. albida*** pods, ***A. digitata*** leaves, ***P. dulce*** and C. ***procera*** leaves-based diets respectively. Therefore, feed restriction allowed similar dry matter intake for all diets.

Total crude protein content of the diet (12.5% DM in average) was not a limiting factor for studied diets. It was similar between diets and browse species except for ***P. dulce*** leaves (CP= 19.1% DM) which has higher nitrogen content than the other browse species.

TRDMD averaged 49.6, 47.7, 51.0 and 55.7 respectively for ***A. albida*** pods, A. ***digitata, P. dulce*** and C. ***procera*** leaves-based diets. There was little between animal variations (2>rsd>0.4).

Calculated by difference, BDMD varied markedly between 3 1% to 68%, 40% to 100%, 24% to 65% and 0% to 51% DM for ***A. albida*** pods, ***C. procera, P. dulce*** and ***A. digitata*** leaves respectively. The highest standard deviations (>10) were observed in the lowest browse proportion (15% DM) in the diet. Between-animal variations decreased as the proportion of browse level increased. Within a browse species, there were marked

Table 2
Influence of the browse proportion in the diet (% DM) on the total diet and browse in vivo digestibility (% DM) in sheep

Trial	1	2	3	4	5
Browse level % DM	0	15	30	50	75
Diet composition					
Browse	0 (0)	15 (0)	30 (0)	50 (0)	75 (0)
Peanut cake	15.2 (0.5)	12.9 (0.1)	10.5 (0)	7.5 (0)	3.1 (0.0)
Rice straw	84.7 (0.5)	72.1 (0.1)	59.5 (0)	42.5 (0)	21.3 (0)
Total CP content % DM	12.1 (0)	12.0 (0.9)	12.3 (1.3)	12.8 (2.1)	13.5 (3.2)
Intake g DM/kg MBW[a]	52.5 (0.3)	53.4 (2.3)	55.2 (1.0)	54.4 (1.2)	52.8 (2.1)
Digestibility % DM**					
Total diet					
A. albida	46.4 (1.9)	49.5 (0.7)	47.1 (1.1)	50.2 (0.7)	51.2 (1.4)
A. digitata		45.3 (0.9)	49.1 (0.7)	47.5 (0.7)	49.0 (0.6)
P. dulce		47.8 (0.7)	52.2 (0.8)	52.7 (1.3)	51.4 (0.4)
C. procera		53.1 (1.6)	50.0 (0.5)	58.0 (0.5)	61.1 (1.1)
Browse					
A. albida		48.01 (0.1)	43.0 (7.1)	50.7 (2.9)	51.6 (3.8)
A. digitata		19.6 (12.8)	47.7 (4.7)	45.0 (3.0)	48.6 (1.7)
l? dulce		35.6 (9.5)	57.9 (5.5)	55.6 (5.1)	52.0 (1.2)
C. procera		70.3 (22.6)	52.6 (3.7)	67.6 (2.3)	65.3 (2.8)

( ) Standard deviation.
* MBW: Metabolic Body weight.

Table 3
Influence of the browse proportion on the diet digestibility: Analysis of variance

Browse species	P	R^2	c v	SME	Significance	N
All species	0.000 1	0.38	6.1	3	****	128
Acacia albida	0.24	0.36	4.7	2.3	N S	32
Adansonia digitata	0.0009	0.66	3.4	1.6	**	32
Pithecelobium dulce	0.0013	0.63	3.7	1.9	*	32
Calotropis procera	0.0001	0.87	4.1	2.2	***	32

Significance: * $p<0.05$; ** $p<0.01$; *** $p<0.001$; **** $p<0.0001$.
NS: not significant.
SME: Standard error of mean.

between-animals and between-diets variations owing to a poor accuracy of the calculation method.

3.2. Estimation of hrowse DMD by regression

The relationships between browse level in the diet and TRDMD are described in Table 3, and Fig. 1. TRDMD fluctuates significantly according to browse proportion ($p<0.0001$) and species ($p<0.0001$) in the diet. An independent analysis of variance for each species shows significant influence of browse level on TRDMD for A. *digituta* ($p<0.001$), *P dulce* ($p<0.01$) and C. *procera* ($p<0.0001$) while *A. albida*-based diets did not give a significant response ($p>0.05$).

Table 4
Relationships between browse level and in vivo DMD: Stepwise regressions

Btowse species	Step	Stepwise regressions*	S	SEM**
A. albida	1 linear	$y=48.94+0.02x$	N S	2.3
	2 quadratic	$y=49.58-0.054+0.001x^2$	N S	
	3 cubic	$y=49.78-0.138+0.004x^2-0.003x^3$	N S	
	4 quarctic	$y=49.58+0.268x-0.0281x^2+0.0007x^3-0.000005x^4$	N S	
A. digitata	1 linear	$y=48.09+0.002x$	N S	1.6
	2 quadratic	$y=48.82-0.086x+0.001x^2$	*	
	3 cubic	$y=49.20-0.241x+0.007x^2-0.00005x^3$	N S	
	4 quarctic	$y=49.58-1.051x+0.071x^2-0.0051x^3+0.00001x^4$	***	
l? dulce	1. linear	$y=49.32+0.042x$	**	1.9
	2 quadratic	$y=48.74+0.111x-0.0009x^2$	N S	
	3 cubic	$y=49.33-0.130x+0.008x2-0.00008x^3$	*	
	4 quarctic	$y=49.59-0.675x+0.051x^2-0.001x^3+0.000007x^4$	*	
C. *procera*	1 linear	$y=49.29+0.152x$	****	2.2
	2 quadratic	$y=49.86+0.084x+0.0009x^2$	N S	
	3 cubic	$y=50.05+0.008x+0.004x^2-0.00003x^3$	N S	
	4 quarctic	$y=49.59+0.994x-0.074x^2+0.002x^3-0.00001x^4$	***	

* y=In vivo total ration DMD; x=browse proportion in the diet.
**Standard error of mean.

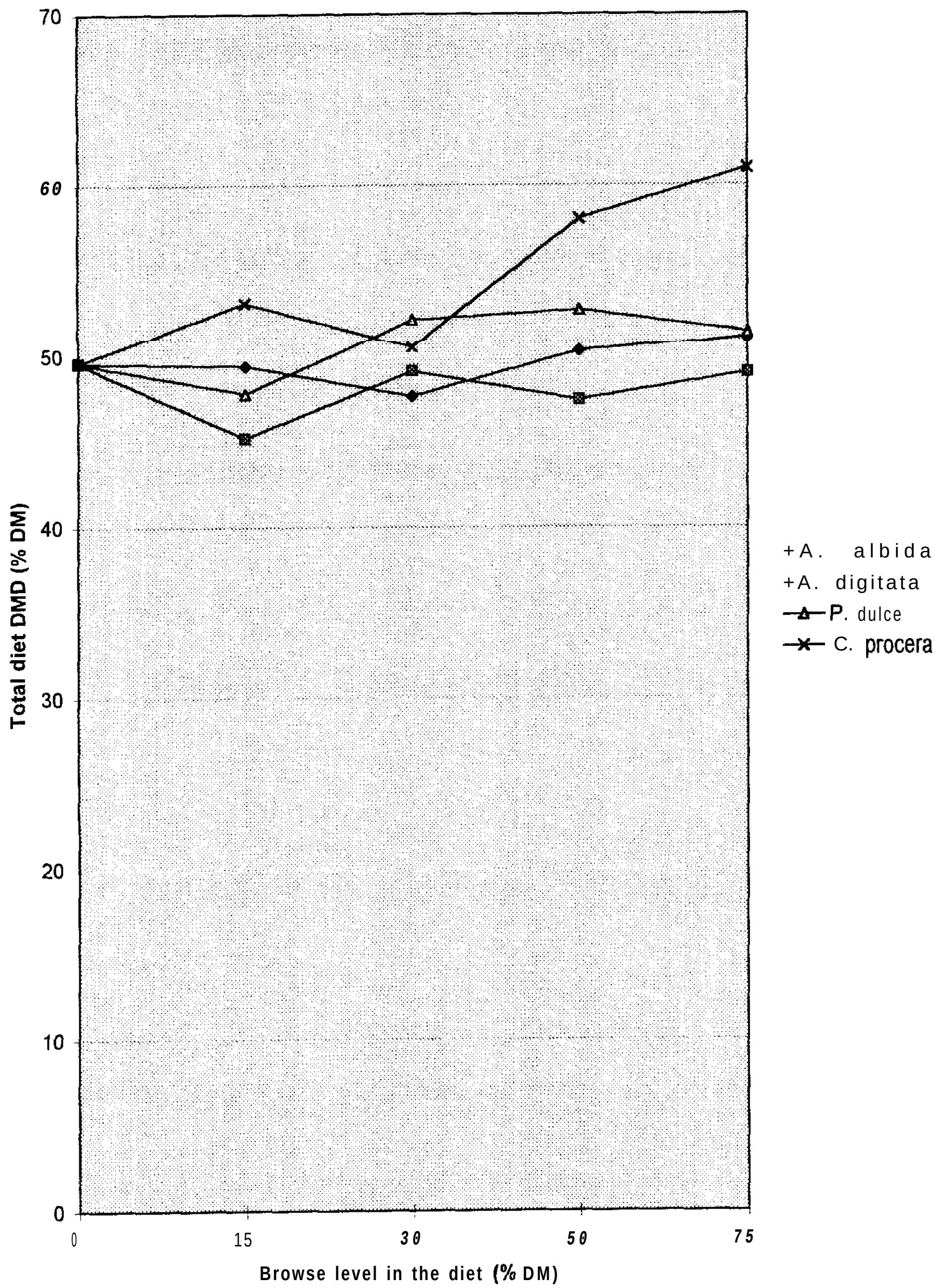

Fig. 1. Influence of browse level on the total diet in vivo DMD.

Table 5
In situ dry matter disappearance of peanut hay (% DM) in zebu cattles fed different hrowse proportions in the diet

Browse species	Incubation time (h)	Browse level in the diet (% DM)				
		0	15	30	50	75
A. albida	4	32.6"	32.4"	32.5"	30.3"	30.4"
		0.5	1.5	0.3	0.6	0.8
	24	57.6"	57.9"	55.2"	52.7[b]	53.1[b]
		3.8	2.6	3.3	5.4	5.8
	48	64.4"	63.5"	64.5"	62.8[b]	61.3[b]
		0.8	0.2	0.4	0.6	1.5
	72	65.7"	64.6"	65.6[a]	62.3'	63.1"
		1.4	0.1	0.5	0.6	0.6
A. digitata	4	32.8"	33.2"	30.9"		
		0.3	1.5	0.7		
	24	4X.2"	53.6"	50.4"		
		1.8	5.3	5.1		
	48	60.2'	63.1"	59.4"		
		2.3	2.5	2.7		
	72	65.6"	66.9"	63.1[a]		
		0.7	1	0.6		
P. dulce	4	32.6"	34.2[b]	35.9[b]	33.2"	
		0.4	0.6	1.4	1.2	
	24	57.6"	49.1[b]	56.9"	61.2"	
		3.3	3.7	3.9	0.9	
	48	64.4"	63.1"	61.5[a]	64.5"	
		0.6	1.2	3.1	0.3	
	72	65.7[a]	63.7"	66.5"	64.5"	
		1.1	1.1	0.6	0.4	

Standard deviation.
Mean values followed by the different superscripts within the same line are significantly different ($p<0.05$).

Stepwise regressions are presented in Table 4. A significant non-linear quadratic relationship was observed for ***A. digitata*** ($p<0.05$). In ***P. dulce*** both linear ($p<0.01$) and non-linear ($p<0.02$) relationships were significant while for ***C. procera,*** the linear regression was most adequate ($p<0.0001$) to describe the relationship between TRDMD and browse proportion in the diet. For ***A. albida***, regressions between browse level and TRDMD were not significant ($p>0.05$).

Optimal browse level corresponding to maximum diet digestibility was of 15%, 30%, 50% and 15% DM (Fig. 1) while corresponding browse digestibility was 50%, 47.1%, 51.3% and 60.7% for ***A. albida*** pods, ***A. digitata, P. dulce*** and ***C. procera*** leaves respectively.

3.3. DMD profile of peanut hay in the rumen of Gobra bulls fed graded levels of tree forages

The degradation profile of peanut hay incubated in the rumen of zebu bulls fed graded level of tree forages is presented in Table 5. Average peanut hay dry matter disappearance

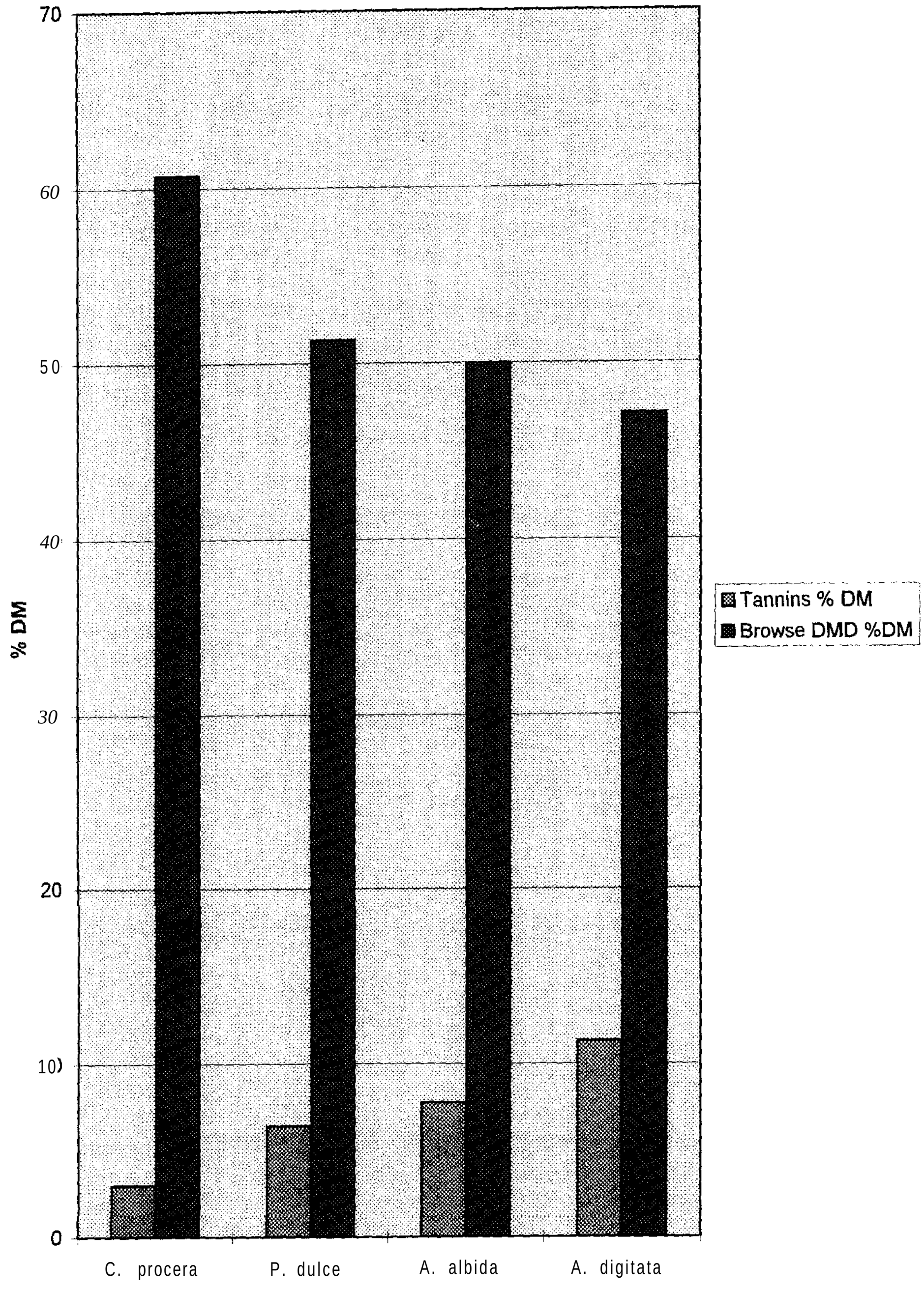

Fig. 2. Tannin content and in vivo digestibility of tree forages

was 52.370, 53.3%, 54.3%. 55.0% and 51,070 DM for 0%, 15%, 30%, 5070 and 75% DM browse level respectively. It was significantly influenced by browse level in the diet ($p<0.001$), animal ($p<0.05$) and incubation time ($p<0.0001$). Peanut hay DM disappearance was higher in the control as compared to browse-based diets. At 24 h incubation time, maximum peanut hay DM disappearance was observed at the browse proportion of 15% both for *A. albida* pods and *A digitata* leaves and 50% for *P. dulce* leaves. Results are in agreement with in vivo observation regarding optimal level for *A. albida* and *P. dulce* while a higher value (50%) was identified for *A. digitata*

3.4. Tannin concentration in tree forages

Condensed tannin content in browse were 7.8%, 1 1.3%, 6.5% and 3.1% DM respectively for *A. albida* pods, *A. digituta, P. dulce* and C. *procera* leaves. Tannin influence on in vivo DMD of diets was highly significant. Tannin concentration allowed a classification of studied species as the highest tannin content corresponded to the lowest digestibility (Fig. 2).

4. Discussion

In vivo DMD of browse-based diets showed marked variation when browse digestibility was calculated by the difference method. These variations raise the question of the browse level that can be considered to assess browse-specific digestibility.

Optimal rumen DM degradation capacity and diets digestibility at low browse proportions (15–30% DM) would suggest its adoption as a standard level of browse in ruminant diets. However, a poor DMD accuracy has been observed with high standard deviations (SD>10), when BDMD was evaluated by the difference from low browse level diets. This result is in agreement with that reported by Sauvant and Giger (1989) for concentrate-based diets and by Fall (1993) for browse-based rations. This suggests that the difference method to determine browse DMD may not be appropriate for diet with a low level of browse. That result is confirmed by the significant influence of browse proportion in the diet on the rumen DM degradation capacity measured as dry matter disappearance of peanut hay in the rumen of zebu cattle fed graded levels of tree forages. However, all browse species do not show the same variation trends. *A. albida* and C. *procera* showed linear relationships between browse level and TRDMD. Digestibility response was curvilinear for *A. digitata* while *P. dulce* showed both linear and non-linear responses. Therefore, animal response to browse-based diet seems to be complex and the influence of browse level in the diet may be variable according to plant species.

The highest tannin concentration in A. *digituta* (11.3% DM), more than double of the critical level (5% DM) reported by McLeod (1974), may explain the occurrence of digestive interactions in that species. Specificity of *A. digitata* may also be due to the occurrence of an emollient which may cause transit acceleration in the ruminant digestive tract as observed in human food containing *A digitata* leaves commonly consumed in West Africa.

Although the occurrence of digestive interaction is not demonstrated for all studied species, large variations were observed in browse DMD within the same sample when the difference method was applied. That method, assuming the additivity of different ingredients in the diet, may not be relevant for all browse species. It suggests the application of the regression method to test the occurrence of digestive interaction.

Browse proportions were different in the preliminaty study (Fall, 1993) but there is a confirmation of the non-linear response of TRDMD to increasing browse level in the diet for ***A. digitata*** and l? ***dulce*** leaves although linear response was more significant ($p<0.01$) than non-linear one ($p<0.02$) in that last species.

The influence of browse proportion is not often taken into account in the evaluation of the digestibility of tree forages-based diets. Single and high browse proportions are often applied in in vivo tria1 studies (Table 6). However, potential toxicity of many browse species would recommend to check the role of browse level in the diet. Nastis and Malechek (198 1), Villena and Pfister (1990) and Dick and Urness (1981) studying digestibility of rations based on ***Quercus gamhelii,*** *Quercus havardii* and ***Quercus*** *gambelii* leaves respectively, a found negative and linear effect of browse level on the ration DMD. Those observations do not support the occurrence of digestive interactions in browse-based diets. Interactions between the diet components may have been masked by the high initial level (40%) of browse as curvilinearity is often observed at low browse proportion in the diet (30>L<15%; Fall. 1993). In contrast, digestive interactions have been evidenced by Miranda (1989), Preston and Leng (1987) and Traoré et al. (1995) when assessing in vivo DMD and performances of animals fed with rations based on *Prosopis sp* pods, ***Gliricidia*** *sepium* and ***Leucaena leucocephala*** leaves respectively. The non-linear regression equation was calculated and optimal browse proportions of 40%, 30% and 30% DM were identified respectively for *Prosopis* pods, ***Leucaena*** and *Glyricidia* leaves.

The occurrence of digestive interactions or associative effects between forage basa1 diet and concentrates has been widely reported (Frederiksen, 1973; Kromann, 1973; Giger and Sauvant, 1983; Sauvant and Giger, 1989; Berge and Dulphy, 1991). They are attributed to cell wall components (Berge and Dulphy, 1991). Their digestibility is decreased by soluble carbohydrates leading to a drop in rumen pH and cellulolytic activity for diets with high levels of concentrate. Concentrate physical form can also be involved in the occurrence of digestive interactions. Their fine consistency may cause transit acceleration in the digestive tract reducing particle rumen residence time and thus, cell wall degradation in the rumen.

Studied browse species are rather coarse and often not subject to physical treatment; thus, transit modifications cannot be held responsible for the occurrence of digestive interactions except for ***A. digitata*** leaves in which an emollient has been identified and used as human food. Cell wall components are more important sources of energy as compared to soluble carbohydrates in browses (Fall and Michalet-Doreau, 1995). So the cell wall fraction may have a negative influence in browse digestibility as generally described in conventional feestuffs (Van Soest, 1982), particularly in browse plants (Wilson, 1977; Craig et al.. 199 1; Rafique et al., 1992). Potentially toxic compounds may also be involved in the occurrence of digestive interactions in browse-based diets. ***A. digitata.*** higher than the other species in tannin, was the most affected by digestive interactions. Condensed tannins reduce the digestibility of carbohydrates. Their negative effect has been widely reported (McLeod, 1974; Mangan, 1988; Lowry, 1989; Leinmuller

Table 6
In vivo digestibility of tropical tree forages: A review

Browse species	Plant part	stage	Animal	Browse level % DM	CP % DM	RDMD* % DM	ROMD** % DM	Authors
C. montanus	Dry leaves		Goat	30-60	8–12	—	54.2	Boutouba et al., 1990
A. canescens				30-60		—	52.2	
Mixture of species			Cattle	40-60	11	54	—	Arthun et al., 1992
A. breviscipa		Wet season	Sheep	22-38	9-11	44	—	Coppock and Reed, 1992
A. tortilis	Fruits			22-38		50		
A. tridentata			Goat	30	8		59.1	Nunez-Hernandez et al., 1989
Q. grisea				30	8	—	45.6	
C. montanus				30	8	—	51.8	
J. monosperma				30	8	—	58.2	
C. lanata				30	8	—	51.1	
A. cunata				30	8	—	54.1	
A. cyanophylla	Dry leaves	Vegetative	Sheep	80	13	64	—	Bhattacharya, 1989
H. persicum		Vegetative		80	10	52		
A. halimus		Vegetative		50	18	54		
S. coccinea +	Dried and ground leaves							
C. corymbulosus 50: 50				42	10.5	44		Rafique et al., 1992
C. montanus +								
A. canescens 50: 50				42	10.5	43	—	Rafique et al., 1991
M. indica	Fresh leaves		Goat	85	6.5	55		Akbar and Alam, 1991
S. asper				85	6.5	61.9		Akbar and Alam, 1991

* RDMD: ration dry matter digestibility
** ROMD: ration organic matter digestibility

et al., 199 1; Bernays et al., 1989). Tannins can kill microbes and depress rumen microbial activity. They can also inhibit forage digestion through the formation of insoluble complexes with long chain cell wall carbohydrates such as cellulose and hemicellulose (Bernays et al., 1989). They may act as enzyme inhibitors by inactivation of protein enzymes responsible for cell wall degradation (McLeod, 1974; Lohan et al., 1981). They can also bind muco proteins in the digestive tract reducing gut wall permeability and nutrients absorption consequently.

In browse-based diets, the negative effect in rumen DMD capacity has been identified as two mechanisms that can be involved in digestive interactions for studied species.

Although the in vitro effect of plant tannins on browse digestibility has been in evidence, demonstration of the mechanism in vivo is not often reproducible and conflicting results are reported. Barnes et al. (1991) have established a negative relationship between ration digestibility and tannin content in *Acacia berlandieri* while Dick and Urness (1981) were not able to show a similar relationship in *Quercus gambelii*.

There is a large diversity in animal response to high tannin diets. The animal response is determined by the plant species and the type of tannins, its concentration in the diet and the physiological capacity of animal species to adapt to high tannin levels in the diet (McLeod, 1974; Hagennann et al., 1992). Tannin-resistant animal species are reputed to secrete saliva rich in hydroxyproline which can inactivate tannins by precipitation during chewing (Burrit et al., 1987; Robbins et al., 1987). This adaptation capacity can offset the depressing effect of tannin up to a certain level corresponding to the tannin-binding capacity of secreted proline-rich saliva. Beyond that level, one can observe tannin-binding activity on proteins in general, digestive enzyme in particular and also carbohydrates. This thesis is supported by anatomic observations which showed larger salivary glands in browsers as compared to grazers.

5. Conclusion

The in vivo DMD of diets based on selected tree forages in the present study varied according to the diet composition and particularly to browse proportion in the diet. However, the non-linear response of total diet DMD to graded level of browse in the diet was clearly demonstrated only for one species *A. digitatu*. The digestion profile of *P.* dulce-based diets was significantly non-linear but explained more by a linear relationship. Results suggest that digestive interactions may occur in browse-based diets but the browse species is a major variation factor.

The in vivo DMD of browse-based diets appears to be a relative value. It can be evaluated taking into account the browse level and species which seems to be a major source of variation. In consequence the regression method, including graded browse levels in the diet, seems to be more appropriate than the difference method to test occurrence of digestive interactions.

TO improve the use of tree forages in tropical feeding systems, there is a need to evaluate their nutritive value taking into account the ration type in which they are included. Their digestibility, markedly influenced by the occurrence of secondary compounds, raises the question of browse limitation in ruminants diets. Low levels of incorporation varying from 15–50% of the diet give a higher ration digestibility and therefore avoid ruminants intoxication.

Further work with a wider range of browse species is needed to confirm the influence of plant species and to elucidate the role of intake and basa1 diet type in the occurrence of digestive interactions in browse-based diet for sheep.

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