

**PREDICTION OF INTAKE OF TROPICAL FORAGES IN DAIRY CATTLE
BASED ON STUDIES FROM FIBRE DIGESTION KINETICS**

BY

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ABSTRACT

Two experiments were conducted simultaneously to estimate the physical fill of tropical forages and the maximum intake capacity of mature non-pregnant crossbred heifers kept under zero grazing system. The experiments were carried out at Magadu Dairy Research Farm, Department of Animal Science and Production, Sokoine University of Agriculture. The objectives were to describe the tropical forages in terms of their rumen degradability characteristics, digestion and passage rates of fibre and their resultant rumen pool sizes in order to estimate the physical fill and potential intake of tropical forages. The study was planned to test the hypothesis that in the tropics where ruminants are fed forages of high fibre content and low digestibility, the physical fill is the major factor in regulation of feed intake.

Five forages [Signal grass (*Brachiaria brizantha*) hay (BH), Maize (*Zea mays*) silage (MS), Lucerne (*Medicago sativa*) hay (LH), Lucerne grass hay (LGH) and urea-treated rice (*Oryza sativa*) straw (UTRS)] were fed to 10 mature non-pregnant rumen fistulated dairy heifers in two 5 x 5 Latin square designs. In experiment 1 (Expt.1) the forages were fed as a sole diet with only minerals and vitamins supplementation to form five diets. Diet 1 = BH + minerals and vitamins (BH), Diet 2 = MS + minerals and vitamins (MS), Diet 3 = LH + minerals and vitamins (LH), Diet 4 = LGH + minerals and vitamins (LGH), Diet 5 = UTRS + minerals and vitamins (UTRS). In experiment 2 (Expt.2) the forages were supplemented with urea (20 g d⁻¹/100 kg body weight) and 200 g d⁻¹ fishmeal (FM). Diet 1 = BH + minerals and vitamins (UNBH), Diet 2 = BH + minerals and vitamins + urea + FM (SBH), Diet 3 = MS + minerals and vitamins + urea + FM (SMS), Diet 4 = LH + minerals and vitamins + urea + FM (SLH) and Diet 5 = UTRS + minerals and vitamins + urea + FM (SUTRS).

Parameters measured were similar in both experiments. These were voluntary feed intake (VFI) and faecal output by total collection method for seven days, whereas rumen pH and NH_3 were measured at an interval of 2 h for 24 h. *In situ* degradability was carried out in a standard procedure and in both experiments. Rumen pool sizes were measured by rumen evacuation technique (RET) during the last seven days of the experiments. Fractionation of the NDF into digestible (DNDF) and indigestible (INDF) was done using the *in situ* long time (30 days) incubation of feeds, rumen content and faeces. The parameters were used together with rumen pool sizes to derive rate of digestion and passage of NDF, DNDF and INDF. Passage rate of NDF was also estimated using chromium mordanted fibre (CR-MF).

The chemical composition, the degradability characteristics, digestion and passage rates and the obtained rumen pool sizes varied substantially between the tropical forages studied. The crude protein (CP) ranged from 64-151 g kg^{-1} DM, NDF ranged from 615 – 770 g kg^{-1} DM and ash content ranged from 93 – 180 g kg^{-1} DM.

There was a marked difference ($P < 0.0001$) between forages in the rate and extent at which these forages were degraded in the standard procedure and in experiments 1 and 2 for DM, N and NDF. The lag times were short (0 – 9 h) and not different ($P > 0.05$). In the standard procedure the NDF had *b* value of 47, 58, 70, 72 and 76 % DM for LH, LGH, BH, UTRS and MS respectively. The rate constant *c* for NDF when forages were incubated in the standard diet was 2.9, 2.9, 3.6, 3.7 and 8.8 % h^{-1} for BH, UTRS, LGH, MS and LH respectively. The rate constant *c* for NDF when forage were incubated in diets for expt.1 was 2.0, 3.2, 3.8, 5.0 and 6.9 % h^{-1} for MS, UTRS, BH, LGH and LH respectively, whereas that of expt.2 was 2.6, 2.9, 3.0, 3.6, and 9.1 % h^{-1} SMS, SBH, UNBH, SUTRS and SLH respectively.

The forage dry matter intake (DMI) were different ($P < 0.01$) and the animals consumed 4.2, 5.1, 6.3, 6.5 and 6.7 kg d⁻¹ of MS, BH, UTRS, LH and LGH respectively in expt.1. Supplemented forage diets in expt.2 were not different ($P > 0.05$) for all other nutrients intake except N and water. Forage DMI in expt.2 was 4.4, 4.8, 4.8, 5.9 and 6.4 kg d⁻¹ for SMS, UNBH, SBH, SLH and SUTRS respectively. Water intake was 10, 22, 23, 30 and 31 l d⁻¹ for MS, BH, UTRS, LH and LGH respectively in expt.1 and 14, 21, 23, 26 and 30 l d⁻¹ for SMS, UNBH, SBH, SLH and SUTRS respectively in expt.2.

The rumen pool sizes of NDF (kg) in expt.1 were different ($P < 0.01$) and were higher in animals fed LGH (5.2) and lowest in MS (3.8) compared to those fed BH (4.8) and UTRS (4.5). In expt.2 the NDF pool sizes (kg) were also different ($P < 0.002$) highest in animals fed SBH (4.9) and lowest in animals fed SMS (3.3) compared to those fed UNBH (4.0) with similar values in SLH and SUTRS (4.3).

The passage rates (k_p) measured using CR-MF and RET showed high variability between forages and between the two methods in both experiments. The passage rates estimated by RET for NDF differed ($P < 0.03$) between the forage diets and were 1.78, 1.63, 1.54, 1.53 and 1.36 % h⁻¹ for UTRS, LGH, BH, LH and MS respectively in expt.1 and 2.02, 1.50, 1.41, 1.38 and 1.32 % h⁻¹ for SUTRS, UNBH, SBH, SMS and SBH respectively in expt.2 ($P < 0.05$). The k_p measured using CR-MF was higher than k_p derived from RET and varied from 2.26 – 3.24 % h⁻¹ in expt.1 ($P > 0.42$) and 2.22 – 3.86 % h⁻¹ in expt.2 ($P < 0.003$).

There were differences in Fill (day) when calculated using k_p obtained from RET – total NDF in expt.1 ($P < 0.045$) and expt.2 ($P < 0.046$). In expt.1 the Fill (day) values were 1.84, 1.77, 1.55,

1.41 and 1.35 for MS, LH, BH, LGH and UTRS respectively. Fill (day) values were 1.91, 1.65, 1.64, 1.55 and 1.09 for SBH, UNBH, SLH, SMS and SUTRS respectively in expt.2. Fill values were not different when calculated using k_p from CR-MF in both experiments. Fill values calculated using an assumed passage rate of 2 % h⁻¹ as a constant value were also not different in expt.1 ($P>0.35$) and expt.2 ($P>0.09$).

The predicted NDF intake (PNDFI) across forages were over-estimated when fill calculated from passage rate estimated from CR-MF was used and under-estimated when passage rate obtained from RET was used. A similar trend to that obtained in PNDPI was observed for predicted DM intake (PDMI) for forages in expt.1 and 2. The accuracy of PDMI from PNDPI from passage rates obtained from other NDF fractions-RET was generally poor for both experiments, except for RET-total NDF. The best prediction was obtained from RET-total NDF ($P<0.0001$) with $R^2 = 0.70$ (RMSE = 0.83) in expt.1 and $R^2 = 0.75$ (RMSE = 0.71) in expt.2.

It was concluded that the most important limitation to tropical forage intake is the physical fill of NDF in the rumen. The results have demonstrated that intake of tropical forages can adequately be described from physical fill based on degradability characteristics, rumen pool size and passage rate of NDF measured by RET. The use of NDF parameters as predictors of VFI is recommended as a realistic estimate of forage DMI because NDF was found to be distinct from microbial and endogenous materials. It can further be concluded that PDMI of tropical forages fed to cross-bred dairy heifers can be calibrated in the equation $DMI (kg d^{-1}) = 1.19 + 1.10 PDMI$ (RMSE = 0.83) in expt.1 and $DMI (kg d^{-1}) = 0.98 + 1.16 PDMI$ (RMSE = 0.71) in expt.2.

DECLARATION

I, DYNES MUZE MGHENI, do hereby declare to the SENATE OF SOKOINE UNIVERSITY OF AGRICULTURE that the thesis presented here is my own original work and that to the best of my knowledge has not been submitted for a degree award to any other University.

Signature.....

Date.....*25th October, 2000*

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DEDICATION

To God my Heavenly Father whom I trust, honour, worship and adore. For my God is omniscient (all knowledge) and His grace was sufficient for me and His power made perfect in my weakness (II Corinthians 2:8b) that I could do all things through Him who strengthens me (Philippians 4:13). To Jesus Christ whom I love as my Lord, Healer, Saviour and Redeemer. To the fellowship of the Holy Spirit which gave me the FRUIT of patience and perseverance (Galatians 5:22) that strengthened and encouraged me throughout my study and forever more. Amen.

TABLE OF CONTENTS

	Page
ABSTRACT.....	ii
DECLARATION.....	vi
COPYRIGHT.....	vii
ACKNOWLEDGEMENT.....	viii
DEDICATION.....	x
TABLE OF CONTENTS.....	xi
LIST OF TABLES.....	xv
LIST OF FIGURES.....	xix
LIST OF APPENDICES.....	xx
LIST OF ABBREVIATIONS.....	xxi
1. INTRODUCTION.....	1
2. LITERATURE REVIEW.....	8
2.1 Historical background.....	8
2.2 Factors regulating VFI in ruminants.....	9
2.2.1 Descriptions of forage characteristics when VFI is limited by physical fill.....	9
2.2.1.1 Definition of fibre and chemical composition.....	10
2.2.1.2 Fibre digestion kinetics.....	14
2.2.1.3 Factors influencing digestion rate of individual fractions of fibre.....	17
2.2.1.4 Fibre kinetics of passage.....	23
2.2.1.5 Description of chemical composition influencing VFI	26
2.2.1.6 Description of rumen degradation characteristics and its limitation to VFI.....	27
2.2.1.7 Influence of level of feeding on rumen retention time, rumen pool sizes and intake... ..	29

2.2.1.8	Nutrients and water requirements and its effect on VFI.....	31
2.2.1.9	Effect of fishmeal and urea supplementation on fibre utilisation and VFI.....	34
2.2.2	Descriptions of animal characteristics when VFI is limited by physical fill.....	37
2.2.3	Metabolic control of VFI.....	40
2.2.4	Physical and metabolic control of VFI.....	42
2.2.5	Environmental factors that influence VFI.....	43
2.2.6	Learning, diet selection and animal's maximum comfort and appetite related to regulation of VFI.....	45
2.3	Prediction of VFI.....	47
2.3.1	Prediction of intake from chemical composition and digestibility.....	47
2.3.2	Prediction of intake from degradability characteristics.....	48
2.3.3	Prediction of intake based on physical fill.....	49
2.3.4	Prediction of VFI based on models developed from regression analysis and mathematical modelling.....	53
2.3.4.1	Simple regression analysis models.....	54
2.3.4.2	Multiple regression analysis models.....	54
2.3.4.3	Mathematical modelling.....	56
2.4	Methods for measuring parameters used for prediction of VFI when limited by physical fill.....	58
2.4.1	Chemical composition.....	59
2.4.2	Measurement of apparent total tract digestibility and faecal output.....	61
2.4.3	<i>In sacco (in situ)</i> methods.....	62
2.4.4	Studies on digestion and passage kinetics of fibre.....	63
2.4.4.1	Rumen evacuation technique.....	63

2.4.4.2	Marker techniques.....	69
2.4.4.3	Use of mathematical models.....	70
2.5	General conclusion from the literature reviewed.....	74
3	MATERIALS AND METHODS.....	76
3.1	Objectives of the study and experimental design.....	76
3.2	Materials.....	78
3.2.1	Animals and their management.....	78
3.2.2	Forages:Processing, physical form, chemical and agronomic description.....	78
3.3	Methods.....	81
3.3.1	Measure of VFI (Experiments 1 and 2).....	81
3.3.2	Faecal output.....	82
3.3.3	<i>In sacco</i> degradability.....	84
3.3.4	Measure of rumen pool size of DM and NDF.....	85
3.3.5	Determination of indigestible NDF (INDF).....	86
3.3.6	Determination of passage rate of chromium mordanted fibre (CR-MF).....	87
3.3.7	Collection of rumen fluid for pH and NH ₃ measurements.....	88
3.3.8	Chemical analysis.....	88
3.3.9	Calculations.....	89
3.3.10	Statistical analysis.....	98
3	RESULTS.....	100
4.1	Health of the animals.....	100
4.2	Chemical composition.....	100
4.3	<i>In sacco (in situ)</i> degradability.....	102
4.4	Intake of DM, OM, NDF, CP and water.....	109

4.5	Body weights of the animals.....	109
4.6	<i>In vivo</i> digestibility coefficients.....	111
4.7	Rumen fermentation.....	114
4.7.1	Rumen pH.....	114
4.7.2	Rumen NH ₃ concentration.....	114
4.8	Rumen pool sizes.....	118
4.9	Rate of digestion and passage.....	121
4.10	Rumen physical fill, mean rumen retention time (MRRT) and effective degradability (ED) calculated using four different passage rates in expts.1 and 2..	124
4.10.1	Rumen physical fill-(fill (day)).....	124
4.10.2	Mean rumen retention time (MRRT).....	124
4.10.3	Effective degradability of forage NDF.....	127
4.10.4	The relationship between <i>in vivo</i> and ruminal digestibility (ED).....	127
4.11	Effect of FM and urea supplementation.....	127
4.12	Predicted intake.....	135
5	DICUSSION.....	129
5.1	Description of forage characteristics.....	135
5.2	Description of animal characteristics, rumen environment and intake parameters..	164
5.2.1	Rumen fermentation.....	165
5.2.2	Feed intake and animal performance.....	166
5.3	Prediction of intake.....	173
6	CONCLUSIONS AND RECOMMENDATIONS.....	180
6.1	Conclusions.....	180
6.2	Recommendations.....	182
	REFERENCES.....	184
	APPENDICES.....	202

LIST OF TABLES

Table no.	Page
2.1	Composition, solubility and nutritional characteristics of the main plant cell wall components.....12
2.2	Fibre (NDF) and CP contents for selected tropical grass, legume and crop residue forages.....13
2.3	Influence of declining level of NDF intake and varying proportions of concentrate, starch and sucrose on intake and digestion kinetics of fibre in dairy cows.....20
2.4	Influence of varying proportions of concentrate, starch and sucrose on rumen environment (pH, NH ₃ and VFA).....22
2.5	Influence of level of feeding and varying proportions of concentrate, pure starch and sucrose on rumen retention time and intake of DM and NDF.....30
2.6	Daily nutrient requirements for growing dairy females given as a guide line under average conditions.....33
2.7	Prediction of voluntary dry matter intake (VDMI) of feeds using chemical composition, digestibility and degradability characteristics of forages.....48
2.8	Prediction coefficients from the general model $Y_i = \alpha + \beta X_i$ and showing their accuracy and error of prediction from the equation NDFI = Rumen pool size/Fill and DMI = 1/proportion of NDF in the feed DM multiplied by the predicted NDFI (Madsen et al., 1994).....51
2.9	Important factors to consider in predicting VFI.....53
3.1	Arrangement of the two 5x5 Latin Squares in experiments 1 and 2.....77
3.2	Composition of the vitamins and minerals (MINOVIT SUPER, PHARMVITA and MACLIK SUPER).....83

3.3	Composition of the concentrate fed to rumen fistulated heifers in the standard nylon bag technique.....	84
4.1	Chemical composition of tropical forages and nitrogen supplements (fishmeal and urea) used in experiments 1 and 2.....	101
4.2	Degradability constants of dry matter (DM), nitrogen (N) and neutral detergent fibre (NDF) for tropical forages and FM conducted in a standard procedure.....	103
4.3	Degradability constants of dry matter (DM), nitrogen (N) and neutral detergent fibre (NDF) for tropical forages incubated during experiments 1 and 2.....	104
4.4	Measured intake (kg d ⁻¹) of total and forage DM, OM, N, NDF and water (l d ⁻¹) in experiments 1 and 2.....	110
4.5	Initial (ILBW) and final (FLBW) live and corrected body weights (kg) and body weight changes (LBWC), total (TDMI) and forage (FDMI) dry matter intake expressed as a percentage or 0.75 exponent of FLBW (Experiments 1 and 2).....	112
4.6	<i>In vivo</i> apparent digestibility coefficients (ADC) of DM, OM, NDF, N and ash for the tropical forage based diets without or with FM and urea supplementation and potential rumen (PRD) and maximum rumen (MRD) digestibility in experiments 1 and 2.....	113
4.7	Effect of feeding tropical forage based diets without or with FM and urea supplementation on pH and NH ₃ concentration in ruminal fluid (Experiments 1 and 2).....	115
4.8	Rumen pool sizes (kg) of wet digesta, DM, NDF, DNDF and INDF evacuated at three different times and as an average of the three rumen evacuations (Experiment 1).....	119

4.9	Rumen pool sizes (kg) of wet digesta, DM, NDF, DNDF and INDF evacuated at three different times and as an average of the three rumen evacuations (Experiment 2).....	120
4.10	NDF fractions intake, mean rumen pool sizes, faecal output, rate of passage measured using chromium mordanted fibre (CR-MF), derived kinetics for NDF, DNDF and INDF and passage rate calculated from <i>in vivo</i> digestibility (ADC) and rumen degradability characteristics (RDC) of NDF (Experiment 1).....	122
4.11	NDF fractions intake, mean rumen pool sizes, faecal output, rate of passage measured using chromium mordanted fibre (CR-FM), derived kinetics for NDF, DNDF and INDF and passage rate calculated from <i>in vivo</i> digestibility (ADC) and rumen degradability characteristics (RDC) of NDF (Experiment 2).....	123
4.12	Physical fill (Fill) of NDF in the rumen as estimated using degradation characteristics (RDC) and passage rates (k_p) estimated from chromium mordanted fibre (CR-MF) rumen evacuation technique (RET) or assumed passage rate of 2 % h ⁻¹ in experiments 1 and 2.....	125
4.13	Mean rumen retention time (MRRT) of NDF as estimate from passage rates (k_p) estimated from chromium mordanted fibre (CR-MF) and rumen evacuation technique (RET) in experiments 1 and 2.....	126
4.14	Effective degradability (ED) of NDF calculated using degradation characteristics (RDC) and passage rates (k_p) from chromium mordanted fibre (CR-MF), rumen evacuation technique (RET) or assumed passage rate of 2 % h ⁻¹ in experiments 1 and 2	128

4.15	Predicted NDF intake (PNDFI) estimated from rumen pool sizes of NDF and Fill calculated from passage rates (k) measured using chromium mordanted fibre (CR-MF), rumen evacuation technique (RET), derived passage rates of NDF, DNDF and INDF or assumed passage rate of $2\% \text{ h}^{-1}$ (Experiments 1 and 2).....	130
4.16	Predicted DM intake (PDMI) estimated from predicted NDF intake (PNDFI) in Table 12 and the proportion of NDF in the forage DM (Experiments 1 and 2)...	131
4.17	The accuracy of predicting forage DM intake (FDMI) using rumen pool size of NDF and Fill and that of NDF digestibility (NDFD) using effective digestibility (ED) of NDF calculated from passage rates estimated from different methods in experiments 1 and 2.....	132
4.18	Effect of supplementation on some major variables.....	133
4.19	Calculated R^2 obtained from simple regression analysis of the measured and predicted LSMeans (Table 4.16) dry matter intake instead of individual observations.....	134

LIST OF FIGURES

Figure No.	Page
2.1 The relationship between the ambient temperature, heat production and feed intake in cattle (Madsen, 1983).....	44
2.2 The relationship between actual and predicted intake of NDF (Source:Stensig <i>et al.</i> , 1994b).....	51
2.3 Hypothetical diagrammatic presentation of simple model of fibre disappearance from the rumen, where k_d is the fractional rate of digestion and k_p is the fractional rate of passage.....	66
2.4 Hypothetical diagrammatic presentation of feed intake, particle size reduction and rate of digestion and passage assuming a two pool model.....	67
2.5 Relationship between ruminal digestibility (feed-ileum) and effective degradability (ED) of NDF (Source: Stensig <i>et al.</i> , 1994a).....	72
4.1 Degradation of DM for the forages incubated according to the standard procedure (A), or in the different forage diets in experiments 1 (B) and 2 (C).....	106
4.2 Degradation of CP for the forages incubated according to the standard procedure (A), or in the different forage diets in experiments 1 (B) and 2 (C).....	107
4.3 Degradation of NDF for the forages incubated according to the standard procedure (A), or in the different forage diets in experiments 1 (B) and 2 (C).....	108
4.4 Diurnal pH fluctuations in the rumen of animals fed forage diets in experiments 1 (A) and 2 (B).....	116
4.5 Diurnal NH ₃ fluctuations in the rumen of animals fed forage diets in experiments 1 (A) and 2(B).....	117

LIST OF APPENDICES

Appendix No.	Page
1	Ambient temperature (temp) and humidity (RH) for July, August and September (1997) as recorded daily from the Meteorological Station SUA main campus, Morogoro.....202
2	Ambient temperature (temp) and humidity (RH) for October and November (1997) as recorded daily from the Meteorological Station SUA main campus, Morogoro.....203
3	LSM means dry matter (DM), nitrogen (N) and neutral detergent fibre (NDF) degradability values at different incubation times of tropical forages done in a standard procedure (% DM).....204
4	LSM means dry matter (DM) degradability values at different incubation times as incubated in animals fed tropical forages in experiments 1 and 2 (% DM).....205
5	LSM means nitrogen (N) degradability values at different incubation times as incubated in animals fed tropical forages in experiments 1 and 2 (% DM).....206
6	LSM means neutral detergent fibre (NDF) degradability values at different incubation times as incubated in animals fed tropical forages in experiments 1 and 2 (% DM).....207
7	Livebody weights (kg) of the animals as weighed at beginning of the experiments and at the end of each period (1-5) regardless of their forages diets (Experiment 1).....208
8	Livebody weights of the animals as weighed at beginning of the experiments and at the end of each period (1-5) regardless of their forage diets (Experiment 2)208
9	LSM means, rumen pH and ammonia (NH ₃) diurnal variations measured in animals fed tropical forage-based diets (Experiment 1)209
10	LSM means, rumen pH and ammonia (NH ₃) diurnal variations measured in animals fed tropical forage-based diets supplemented with FM and urea (Experiment 2)210

ABBREVIATIONS

AOAC	-	Association of Official Agricultural Chemists
ARC	-	Agricultural Research Council
BH	-	<i>Brachiaria</i> hay
cm	-	Centimetre
CP	-	Crude protein (N x 6.25)
CR-MF -	-	Chromium mordanted fibre
CWC	-	Cell wall constituents
d	-	Day
DM	-	Dry matter
DMD	-	Dry matter digestibility
DMI	-	Dry matter intake
DNDF	-	Digestible neutral detergent fibre (NDF)
ED	-	Effective degradability
FLBW	-	Final live body weight
FM	-	Fish meal
g	-	Gram
h	-	Hour
ILBW	-	Initial live body weight
INDF	-	Indigestible NDF
kg	-	Kilogram
LH	-	Lucerne hay
LGH	-	Lucerne grass hay
LSMeans	-	Least Square Means

LW	-	Liveweight
mg	-	Milligram
MJ	-	Mega-joule
ml	-	Millilitre
MS	-	Maize silage
mm	-	Millimetre
MRRT	-	Mean rumen retention time
NAFCO	-	National Agricultural Food Company
N	-	Nitrogen
NDF	-	Neutral detergent fibre
NDFI	-	NDF intake
NH ₃	-	Ammonia
NRC	-	National Research Council
NA	-	Not analysed
OM	-	Organic matter
OMD	-	Organic matter digestibility
PDMI	-	Predicted DMI
RNDFD	-	Rumen NDF digestibility
RFC	-	Rapid fermentable carbohydrates
RET	-	Rumen evacuation technique
PNDFI	-	Predicted NDF intake
SBH	-	Supplemented <i>Brachiaria</i> hay
SLH	-	Supplemented Lucerne hay
SMS	-	Supplemented maize silage

SUTRS -	-	Supplemented urea treated rice straw
SEM	-	Standard error of the LSM means
TDN	-	Total digestible nutrients
TSH	-	Tanzanian shillings (1 US \$ = TSH 804 year 2000)
UNBH	-	Unsupplemented <i>Brachiaria</i> hay
UTRS	-	Urea treated rice straw
VDMI	-	Voluntary dry matter intake
VFI	-	Voluntary feed intake
VFA	-	Volatile fatty acids

1 INTRODUCTION

Smallholder dairy cattle production in Tanzania has grown very fast in the past two decades. Although this trend has been mostly in urban and peri-urban areas, other highly populated rural areas have experienced similar growth. This has been in response to high demand for milk due to growth in industries and other institutions that created employment and attracted shift of the population from rural to urban areas. Thus, urban growth made people to move from economic deprivation to an improved financial position. The shift increased their consumption of animal protein foodstuffs like milk, meat and eggs. One can therefore confidently predict that the demand for animal protein foods will increase in response to improvements in economic prosperity.

Increased demand for animal products like milk motivated fast growth of small-scale dairy production enterprises in urban and peri-urban parts of Tanzania. The system became attractive because it gives regular income to families. Nkya *et al.* (1998) reported that grazing tended to give higher milk production due to increased intake than zero-grazed animals. However, the former has no future due to strict enforcement of urban by-laws on animal keeping that forbid grazing of animals. Mlozi *et al.* (1989) and Msangi *et al.* (1998) reported similar views. However, smallholder dairy sector is not only important in urban and peri-urban areas, but also carried out in highly populated areas as a means of integrating crop and animal production systems. Mdoe *et al.* (1993) reported that smallholder dairy sector contributes substantially to the national economy and well being of women who mostly look after the animals. This may tempt one to predict that the sustainability of smallholder dairy production in peri-urban and high populated areas will depend on zero-grazed (cut and carry) system.

Viewed from a global perspective, the position of future food supply looks fairly dire. Thomas (1998) predicted that population growth over the next 25-30 years will grow to a level that will demand an increase of a two to three times the present level of food production. Milk being among the important food products this trend can be expected also in Tanzania as it is part of the global growing population.

Despite this high-predicted demand for milk, the level of production of the dairy cattle in Tanzania is still lower than their genetic potential (Msangi *et al.*, 1998). Studies carried out in Morogoro, Tanzania (Nkya *et al.*, 1998) reported that the major constraint hindering increased milk production under smallholder dairy production was low dry matter intake especially during the dry season.

Forage contributes a substantial amount of energy in dairy production. The symbiotic relationship between the host animal and the microbial system effects fibre digestion by microbial fermentation. Studies on fibre kinetics have reported that the extent and rate of digestion and passage out of the rumen is rather slow (Tamminga *et al.*, 1989; Huhtanen *et al.*, 1995; Stensig and Robinson, 1997; Stensig *et al.*, 1998b). This accounts for the major factor that limits voluntary feed intake (VFI) of fibre due to the physical limitation of indigestible fibre fraction in the rumen (Jarrige *et al.*, 1986; Kristensen and Ingvarsten, 1986; Rayburn and Fox, 1993; Madsen *et al.*, 1994).

Despite these shortcomings forage based diets are and will continue to be the cheapest feed for ruminants. Ørskov (1998) suggested that, for economic and environmental reasons, ruminants should be maintained on fibrous feeds as far as possible, so as to avoid direct competition with humans for scarce food resources. Since forages are the most abundant and important source of dietary fibre maximisation of their intake capacity by the animals is the key to successful high

animal productivity in ruminants. It is apparent therefore that knowledge of the amount of food that the animal can consume is a fundamental aspect of nutrition since it accounts for the inputs of all nutrients that determines the efficiency of livestock production. This information can be obtained by either actual measurements of VFI or by use of prediction models. Measurement of VFI is expensive and laborious, whereas prediction is cheap and simple but difficult to achieve the precision required.

Measurement or prediction of VFI is difficult due to the complexity of the mechanisms that regulate VFI. These mechanisms includes physical, metabolic and the interaction between animals, feeds and the environment. In animal nutrition, models attempts to relate physical, metabolic and environmental factors that regulate VFI. A model therefore will be a simplified symbolic representation of a system such as animal metabolic pathway and important interactions of different nutrients and the environment. Based on the factors that regulate VFI, various prediction models have been proposed. Although they have some weaknesses, they are of practical use (simple, accurate and economical) as they include the most important physical and metabolic factors that affect VFI (Ingvarsten, 1994; Forbes, 1995a).

Models for prediction of VFI in ruminants have used information from chemical composition, digestible energy, crude fibre (Jarrige *et al.*, 1986) and degradation characteristics (Ørskov *et al.*, 1988; Shem *et al.*, 1995). In other studies some models included passage rates (Von Keyserlingk and Mathison, 1989; Carro *et al.*, 1991), whereas, some models included rumen pool size of NDF and fill (Stensig *et al.*, 1994b). Prediction systems based on fill-system have been developed and successfully used in France (Jarrige *et al.*, 1986) and in Denmark (Kristensen and Ingvarsten, 1986).

Simple and multiple regression analysis to predict VFI have been developed using data obtained from experiments describing food and animal characteristics. The models form the basis for most feed evaluation systems (NRC, 1989; ARC, 1990). In the United Kingdom, Rook and Gill (1990) used simple and multiple linear least square regression analysis to relate VFI of grass silage by beef cattle to animal and food factors. The major problem with this type of analysis is the possibility of collinearity among the independent variables leading to unstable estimates of the regression coefficients. That is, the estimates can change markedly as a result of a small change in the estimated variable. Such estimates lead to poor prediction in the independent data sets and can be difficult to interpret/explain in terms of the underlying biological processes.

In the United States, the NRC (1989) developed more complex models that take into account both animal and food characteristics. The models were further improved when the base intake was corrected for management and environmental factors and gave a more flexible system (Rayburn and Fox, 1993) than when only animal and food characteristics are included in the model.

Mathematical models (modelling) composed of sets of equations describing part or whole systems of an animal have been used to predict VFI. Recently, the Karoline Model (Danfær, 1998) was developed in Denmark, into a dynamic, mechanistic model of the digestive tract of a dairy cow. The model has been tested and was able to explain intake and production response (Danfær, 1998) with acceptable precision.

A number of reviews (Ingvarsen, 1994; Dulphy and Dermarquilly, 1994; Forbes 1995a; Udén, 1998) showed that a lot of progress has been made in developing models for prediction of VFI. The authors noted further that most models for prediction of VFI are still inaccurate because

important animal, food and environmental factors and possible interactions are inadequate and where possible should be modified as more information become available.

Appropriate methods for evaluating tropical feeds for ruminants and their potential limitations have been well presented by Madsen *et al.* (1997). The authors concluded that inspite of the fact that a lot of work has been done to describe tropical feed characteristics in terms of their energy and protein values (Kimambo *et al.*, 1994, Mgheni *et al.*, 1996, Mbwile and Udén, 1997; Mero and Udén, 1998) more experiments should be made to establish the potential feed intake of tropical feeds. Ørskov (1998) had similar views.

A system based on the physical fill of feed in the rumen seems appropriate as the dominant limitation for intake in ruminants is physical fill of partly digested plant fibre in the rumen. The use of degradation characteristics and passage rates of NDF in the rumen is a potentially useful method to predict the physical fill of fibrous feeds. The method for estimating rumen fill proposed by Madsen *et al.* (1994) has shown to reflect variation in intake. The variation indicates that the method can be reliable and useful tool in understanding and predicting changes in intake. The variations have been associated with changes in rate of degradation and passage rate assuming physical regulation of intake. Methods for estimating the various input parameters for predicting intake were well covered by Stensig *et al.* (1994a) and use of NDF parameters (degradability characteristics, passage rates and rumen pool size) were preferred to that of DM, because this fraction was distinct from microbial and endogenous material. Stensig *et al.* (1994b) found a high correlation ($R^2 = 0.82$) between the actual and predicted VFI when grass cubes and maize silage were fed *ad libitum* to dairy cows.

Several animal and feed factors have been found to influence intake apart from degradation rates and passage. Fermentation qualities (DM, pH, NH₃, VFA and lactic acid) that affect silage taste (Bal *et al.*, 1997) depress VFI if not at optimal level. High feeding level and/or concentrate supplementation (Robinson *et al.*, 1987; Huhtanen and Jaakkola, 1993) depress fibre digestion and consequent VFI. The proportion of starch and/or sugar in the diet (Robinson *et al.*, 1987; Stensig *et al.*, 1998a) influence VFI of forage based diets. For example production level of growing animals (Shem *et al.*, 1995), lactating or dry cows (Holden *et al.*, 1994) will have a different intake capacity for forage based diets. It is therefore cautioned that many of the input factors to the model may be costly, difficult and even impossible to achieve the required accuracy and precision. It is therefore fairly dire to choose which animal and feed factors to include in the model taking into account its contribution to the accuracy of the model including the importance of individual feed analysis and their cost.

Prediction of VFI in Tanzania using degradability characteristics (Shem *et al.*, 1995) and assumed rumen pool size of microbial free DM and passage rate (Kimambo *et al.*, 1994) have been reported. Work done by Kimambo *et al.* (1996) to measure rumen pool of DM (in steers) was inconclusive because intake was carried out in different animals (heifers) and therefore it was not possible to test the precision of the estimates. Further work by Mgheni *et al.* (1998) in heifers measured rumen pool size of DM and degradability characteristics as predictors of VFI. However, due to microbial contamination in the DM pool size that was not accounted for and use of a constant passage rate (2 % h⁻¹) to calculate fill, poor correlation ($R^2 = 0.28$) was obtained.

The use of degradability characteristic, rumen pool sizes and measured passage rate to predict VFI has showed some promising results in Tanzania (Mgheni *et al.*, 1998) and elsewhere (Stensig *et al.*, 1994b). The method is even more suitable in a situation where resources to

generate large body of data or to carry out large experiments that would integrate physical, metabolic and environmental factors that influence VFI under a defined feeding system is difficult and expensive. It is, therefore, natural to study first the most limiting factors that are believed to control VFI in the tropics such as physical fill of feeds. The results will form the basis for future inclusion of more and suitable variables that can improve the precision of the model and explain the biological and production response of the complex processes that regulate intake.

The present study was, therefore, carried out to obtain quantitative information on digestion and passage kinetics of individual tropical forage fibre and rumen pool size of neutral detergent fibre (NDF) as predictors of VFI in mature and non-pregnant crossbred dairy heifers kept under stall feeding (zero grazing) system.

The study had the following specific objectives:

- (a) To describe rumen degradation parameters (*in situ*), rumen pool size, digestion (*in vivo*) and passage rate of NDF as predictors of VFI.
- (b) To evaluate different methods for estimating passage rate.
- (c) To develop a system that can predict VFI in dairy cattle fed tropical forages *ad libitum* with or without urea and fishmeal supplementation and discuss its limitation in feed evaluation.

2 LITERATURE REVIEW

2.1 Historical background

Prediction of voluntary food intake (VFI) in cattle has been given much attention through many decades. Flatt (1987) noted that the need to determine levels of VFI was recognised in 2500 BC when the Egyptians force-fed stock and recorded that animal performance was influenced by VFI. Review by Poppi (1996) recognised that interest in developing systems for prediction of intake has been increasing over the past 200 years.

The background for this interest is the great impact VFI has on animal performance. Ørskov and Ryle (1990) noted that knowledge of feed values is often of little interest without knowledge of the amount the animals can consume. Madsen *et al.* (1997) also noted that feed evaluation is basically a description of feed in terms that allow for a prediction of the performance of the animals offered the feeds. Ørskov (1998) stressed also the need to develop new systems that incorporate VFI as an important component in feed evaluation. The systems should be able to describe the feed in terms of its energy, protein and fat values. The adequacy of the system should further be able to describe the feed in terms of its carbohydrate composition (sugars, starch and cell wall fractions), physical structure (long form, chopped, hay, silage and straw), minerals and vitamins profiles and describe any toxic and/or anti-nutritional factors.

Initially, systems for predicting intake were based on chemical composition and digestibility (*in vivo* or *in vitro*) of feeds alone. The systems have received criticisms since VFI is not only limited by chemical composition and total digestibility alone, but also digestion and passage rates (Mertens, 1993; Stensig *et al.*, 1998a), physical fill (Madsen *et al.*, 1994; Forbes, 1995b) and production level (Holden *et al.*, 1994). Also the interaction between the diets (Robinson *et al.*, 1987; Huhtanen and

Jaakkola, 1993; Stensig and Robinson, 1997) animal factors (Holter *et al.*, 1990) and the feeding environment (Forbes, 1985; Madsen, 1983; Young, 1987) have great influence on VFI. Several reviews (Ingvarsen, 1994; Dulphy and Damarquilly, 1994; Forbes, 1995a; McDonald *et al.*, 1995; Illius and Jessop, 1996) showed several theories on regulations of feed intake and described their weaknesses. There was a general agreement that VFI is the most important factor determining animal performance and yet the prediction of VFI is the weakest point of all methods or models of diet formulation.

2.2 Factors regulating VFI in ruminants

Causes of differences in VFI in ruminants and particularly forage intake are many. Dulphy and Damarquilly (1994) noted that regulation of feed intake is primarily controlled by short-term mechanism. McDonald *et al.* (1995) described the long-term regulation of intake based on the previous body condition of the animal. Metabolic control of VFI and how food and animal factors integrate physically or metabolically to control VFI in ruminants under a specified feeding environment is also given but detailed review is beyond the scope of this study.

2.2.1 Descriptions of forage characteristics when VFI is limited by physical fill

Naturally, ruminants live in symbiotic relationship with the microbial population in the rumen for survival on fibre diets. Frequent failure of animals to achieve maximum nutrient intake capacity would be the consequence of constraints imposed on the intake process. In animals fed predominantly forage based diets a physical constraint (physical rumen fill) is primarily held responsible for the variations in forage intake. The objective of this review is to study the literature findings that describe forage characteristics, particularly the fibre fraction, which influence VFI by physical fill in the rumen.

There is an overwhelming amount of literature to support the theory that when ruminants are fed forage-based diets, VFI is most likely to be limited physically. Several reviews (Jarrige *et al.* 1986; Ingvarlsen, 1994; Madsen *et al.*, 1997) revealed that the most limiting factor of VFI in ruminants is the physical fill of indigestible feed residues in the reticulo-rumen. In the tropics, the diet of ruminant animals including dairy animals is basically based on fibrous forages especially during the dry season (Sarwatt *et al.*, 1989; Mgheni *et al.*, 1993; Mbwile and Udén, 1997; Mero and Udén 1998; Nkya *et al.*, 1998). Tamminga and Williams (1998) reported that ruminants evolution and adaptation have been developed for utilisation of forages than most animal species over the last 60 million years. This adaptation process in tropical and other ruminants of the world have evolved a complex set of stomach compartments in which digesta are stored for many hours for microbial fermentation. It is likely that this long period of storage makes the rumen fill of the stomach a potential limiting factor to VFI. A review that ought to support this theory is therefore given.

2.2.1.1 Definition of fibre and chemical composition

In literature the word cell wall constituents/carbohydrates (CWC), fibre and/or neutral detergent fibre (NDF) have been used interchangeably. Thus, several definitions have been given. Flint and Forsberg (1995) defined the plant cell wall structure as a complex of cellulosic microfibrils embedded in a matrix of interwoven hemicellulosic polymers and insoluble protein. Jung and Allen (1995) defined plant CWC as the complex biological structure containing many different molecules, whereas fibre is an analytical product. In terms of classification of plant carbohydrates, Van Soest (1994) defined CWC as structural polysaccharides, primarily pectins, hemicelluloses, and celluloses and further classified them in terms of their solubility and availability to metabolism. Van Soest *et al.* (1991) defined the fibre fraction to be the insoluble

fraction in feed that includes the crosslinked matrix of the plant cell wall and that it is analysed most conveniently as NDF, which includes cellulose, hemicellulose, and lignin as the major components. Jung and Allen (1995) described the development of plant CWC and showed that the primary cell wall is deposited initially and it contains cellulose, hemicellulose and pectins. Lignin becomes part of the cell wall during formation and thickening of the secondary cell wall. In addition to the cell wall components, a review by Flint and Forsberg (1995) showed that there is the salient waxy cuticle layer at the surface which protects against microbial penetration and the pectin material which glue cells to one another. The summary of the description of the main components of the CWC in terms of its composition, solubility and nutritional characteristics are given in Table 2.1 and the NDF and CP contents in selected tropical forages are given in Table 2.2.

Carbohydrates are the main products and storage of photosynthetic energy in plants. Van Soest (1994) estimated that carbohydrates constitute roughly 50-80 % of the DM in forages and cereals mostly in a form of structural carbohydrates (NDF). This high proportion of NDF in tropical forage DM, give in most forages less than 20-50 % to constitute other carbohydrates and other feed fractions (Table 2.2).

It is evident that tropical forages (C⁴ plants) have a relatively high fraction of NDF content compared to temperate (C³ plants) legumes and grass forages (NRC, 1989; Van Soest, 1994; Strudsholm *et al.*, 1995). Table 2.2 demonstrates a high variation in tropical forages in both CP and NDF contents depending on the type of species, degree of maturity, physical form and method of processing/preservation. There is a general agreement by all authors that legumes have higher CP content but lower NDF content than grasses and crop residues.

Table 2.1 Composition, solubility and nutritional characteristics of the main plant cell wall components

Component	Composition	Solubility	Nutritional characteristics
Cellulose	Major component. Present as microfibrils hydrogen bonded to arabinoxylans, xyloglucans and glucomannans that are cellulose like in conformation. Also present as glucose polymer bound together (β 1-4) in linear chains with a high degree of polymerisation. Exist mainly in a crystalline form.	Soluble only in strong inorganic acids.	Slowly fermentable and partly available.
Hemi-Cellulose	Various sugars (mainly arabinoglucuronoxylan) bound together by different kinds of bonds at different position of carbon, hydrogen and oxygen atoms. It is amorphous and has a lower degree of polymerisation than cellulose.	Soluble in acids or in alkaline solutions. Insoluble at neutral pH.	Slowly fermentable and partly available.
Pectin	Amorphous polysaccharide rich in galacturonic acid. The distinction between pectin and hemicellulose is not clear.	Soluble in neutral and alkaline solutions.	Rapidly fermentable and almost completely available.
β-glucan	Like cellulose a glucose polymer, but with a mixture of β 1-3 and β 1-4 linkages which gives an amorphous structure.	Partially soluble in neutral and soluble in alkaline solutions.	Rapidly fermentable and almost completely available.
Lignin	Not well defined but polymerisation of monolignol precursors that leads to lignin formation. A variety of cross links occur between lignin and other polysaccharides. Lignin also forms direct ester linkages between acids and their corresponding alcohols that may involve glucose. Various degrees of polymerisation through cross-linkages (glucosidic links) with phenolic acids and other cell wall components.	Insoluble even in strong inorganic acids. Soluble in alkaline solutions.	Indigestible.
Protein	Protein linked to the cell wall carbohydrates. Lignin associated protein may act as a focus for lignin polymerisation	Variable.	Slowly fermentable and partly available.

Source: Van Soest (1994), Giger-Reverdin (1995), Flint and Forsberg (1995).

Table 2.2 Fibre (NDF) and CP contents for selected tropical grass, legume and crop residue forages

Type of forage	Stage of growth, physical form or preservation method	CP (% DM)	NDF (% DM)	Reference
Crop residues:				
Rice straw	Untreated straw	4.7	78.1	Tuen <i>et al.</i> (1991)
Rice straw	Soaking (40g urea l ⁻¹)	10.9	79.0	Tuen <i>et al.</i> (1991)
Rice straw	Untreated straw	4.4	72.1	Mgheni <i>et al.</i> (1993)
Rice straw	50g kg ⁻¹ urea-treated	11.6	78.1	Mgheni <i>et al.</i> (1993)
Rice straw	20g kg ⁻¹ urea on straw	10.9	74.0	Mgheni <i>et al.</i> (1993)
Rice straw	Untreated straw	4.1	68.2	Djajanegara & Doyle (1989)
Rice straw	60g kg ⁻¹ urea-treated	8.2	66.3	Djajanegara & Doyle (1989)
Maize husks	Maize stover fraction	1.9	90.4	Kimambo <i>et al.</i> (1994)
Maize stover	Green Kilima (K)	7.3	77.3	Shem <i>et al.</i> (1995)
Maize stover	Dry Kilima (K)	4.1	88.1	Shem <i>et al.</i> (1995)
Maize stover	30g kg ⁻¹ urea on Kilima	7.9	84.0	Shem <i>et al.</i> (1995)
Maize stover	50g kg ⁻¹ urea-treated K	8.1	83.5	Shem <i>et al.</i> (1995)
Maize stover	Untreated	2.4	77.9	Tolera & Said (1997)
Banana leaves	Banana plant leaves	12.7	65.9	Shem <i>et al.</i> (1995)
Banana pseudostems	After banana fruit is cut	3.8	40.5	Shem <i>et al.</i> (1995)
Canadian wonder	Bean straw (legume)	6.6	83.6	Shem <i>et al.</i> (1995)
Belabela bean	Bean straw (legume)	4.8	86.4	Shem <i>et al.</i> (1995)
Grasses:				
<i>Brachiaria brizantha</i>	Full boom	9.5	79.8	Kimambo <i>et al.</i> (1994)
<i>Brachiaria brizantha</i>	1 month post bloom	7.3	79.1	Kimambo <i>et al.</i> (1994)
<i>Hyparrhania rufa</i>	Full boom	3.9	84.7	Kimambo <i>et al.</i> (1994)
<i>Hyparrhania rufa</i>	1 month post bloom	3.1	80.9	Kimambo <i>et al.</i> (1994)
<i>Pennisetum purpureum</i>	Full boom	6.6	78.5	Kimambo <i>et al.</i> (1994)
<i>Pennisetum purpureum</i>	1 month post bloom	3.2	79.9	Kimambo <i>et al.</i> (1994)
<i>Cynodon dactylon</i>	Full boom	11.8	80.0	Kimambo <i>et al.</i> (1994)
<i>Cynodon dactylon</i>	1 month post bloom	6.1	81.9	Kimambo <i>et al.</i> (1994)
<i>Cenchrus ciliaris</i>	Full bloom	11.4	NA	Mgheni <i>et al.</i> (1996)
<i>Panicum maximum</i>	Full bloom	10.8	NA	Mgheni <i>et al.</i> (1996)
<i>Tripsacum spp</i>	Not specified	10.9	78.4	Shem <i>et al.</i> (1995)
<i>Setaria grass</i>	Not specified	9.0	78.8	Shem <i>et al.</i> (1995)
<i>Chloris gayana</i>	Hay	4.4	86.6	Shem <i>et al.</i> (1995)
<i>Chloris gayana</i>	Green	6.7	83.5	Shem <i>et al.</i> (1995)
Legumes:				
<i>Rynchosia spp</i>	Full bloom	16.0	51.4	Kimambo <i>et al.</i> (1994)
<i>Rynchosia spp</i>	1 month post bloom	12.9	60.1	Kimambo <i>et al.</i> (1994)
<i>Mucuna spp</i>	Full bloom	16.8	63.5	Kimambo <i>et al.</i> (1994)
<i>Desmodium incinatum</i>	Before full bloom	16.3	NA	Mgheni <i>et al.</i> (1996)
<i>Pueraria phaseoloides</i>	Full bloom	15.1	NA	Mgheni <i>et al.</i> (1996)
<i>M. astropurpureum</i>	8 weeks & sun dried	13.1	59.8	Mero and Udén (1998)
<i>Neonotonia wightii</i>	8 weeks & sun dried	12.6	61.3	Mero and Udén (1998)
<i>Sesbania scabra</i>	2m tall & sun dried	12.6	59.3	Mero and Udén (1998)
<i>Desmodium intortum</i>	Hay	13.2	53.2	Tolera and Said (1997)
<i>Sylosanthes guianensis</i>	Hay	14.8	49.3	Tolera and Said (1997)
<i>Macrotyloma axillare</i>	Hay	8.9	54.9	Tolera and Said (1997)

NA=Not analysed

Van Soest (1994) noted that cellulose is the most abundant carbohydrate in the world, amounting to 20-40 % of the DM of all higher plants. Its availability when fed to the animal will depend on the degree of lignification. Lignin is completely indigestible. The review by Van Soest (1994) further showed that lignin/cellulose ratio ranged from 0.08-0.20 in temperate grasses, 0.11 - 0.24 in tropical grasses, 0.10 - 0.26 in straws and 0.18 - 0.30 in alfalfa. Hemicellulose is more associated with lignin than any other polysaccharide. Lignin content has been reported to be the major component of the CWC that limit VFI of tropical forages (Van Soest, 1994).

Forage CWC is and will continue to be major dietary components for ruminants. Mertens (1993) suggested that in order to be able to predict the nutritive value of forages under different feeding situations it is important to study the quantitative expression of the kinetics of digestion and passage rates of forage NDF and their response to feed intake and composition. It is therefore fairly dire to develop a system that will describe tropical forages NDF constituents in terms of their feed intake potential.

2.2.1.2 Fibre digestion kinetics

In mammals fibre digestion can only occur by microbial fermentation influenced by several factors. Intrinsic and extrinsic attributes of the forage fibre and the animal itself influence the rumen fibrolytic activity. The ability of the animal to utilise the plant CWC will depend on the degree of lignification (Van Soest, 1994) and microbial attachment (Flint and Forsberg, 1995). Microbial attachment is important not only to achieve domain over the substrate but also to avoid being washed out of the rumen. Mertens (1993) reported that the matrix of the CWC requires multitude of enzymatic complexes to effect digestion, and because it involves attachment, enzymatic induction and hydrolysis through microbial fermentation, the process is slow.

Various authors have indicated that lignin is the major component of plant CWC that limit digestion (Van Soest *et al.*, 1991; Flint and Forsberg, 1995). Digestion is limited by shielding the polysaccharides from enzymatic hydrolysis (Jung and Allen, 1995). Lignin, therefore, affects mainly the potential extent of digestion and is poorly related to the rate of digestion of the CWC (Mertens, 1993). The extent to which the lignin fraction affects digestion will, however, vary with plant species and stage of growth. Review by Van Soest (1994) showed that in general legumes contain roughly twice as much lignin and are less digestible than grasses at the same stage of growth, but the rate of digestion was higher in legumes than grasses.

Straws in particular have been characterised to have a CWC content that is highly associated to lignin and hence relatively low in digestion and poorly eaten by the animals. Tuen *et al.* (1991) reported acid detergent lignin (ADL) content of 187 and 192 g kg⁻¹ DM in rice straw, whereas lower values of ADL of 27 and 32 g kg⁻¹ DM (Djajanegara and Doyle, 1989) and 35 and 33 g kg⁻¹ DM (Mgheni *et al.*, 1993) for untreated and urea-treated rice straw respectively.

In grasses and legumes more quantitative studies have been reported for CWC. Weiss and Shockey (1991) reported much higher NDF digestibility (72%) for orchardgrass (CP content of 22 % and NDF content of 52 %) than for alfalfa (48 %) which had lower NDF content (40 %) and similar CP contents (22 %). It is evident that the grass was more digestible than alfalfa because the fibre fraction of these forages was more digestible than that of alfalfa. Similar results were reported by Holden *et al.* (1994). Stensig and Robinson (1997) reported a markedly higher indigestible NDF (INDF) content and a markedly faster rate of degradation of the digestible NDF (DNDF) fractions in alfalfa than in timothy grass silage. The results confirms the views of Mertens (1993) and Stensig

and Robinson (1997) that there is a need to incorporate more quantitative information about the specific characteristics of various NDF sources to improve models of intake prediction.

Differences in rate of digestion between species on the other hand may be related to differences in the degree of lignification in grasses and legumes (Van Soest, 1994). Variation in digestion kinetics due to effect of plant maturity is related to the secondary thickening of the cell wall which makes it less fragile to mechanical breakdown and microbial penetration (Mertens, 1993). However, the effect of plant maturity on fibre digestion is often confounded by lignin because lignin content increases with plant cell wall development (Flint and Forsberg, 1995).

Cutins (waxes and polymerized hydroxyl fatty acids) are other intrinsic attributes of forages that limit fibre digestion. Van Soest (1994) noted that cutins are a protective and indigestible part of the epidermis that covers all higher plants. This attribute protects feed particles against microbial invasion and create poor attachment to the feed particles (Flint and Forsberg, 1995). Tannins and other phenolic acids are other examples of plant components that may limit CWC digestion (Van Soest 1994; Jung and Allen, 1995). Some species of tropical legumes have been reported to contain anti-nutritional factors such as tannins, oestrogens and indospicine compounds that limit their utilisation (Shayo and Udén, 1998). Tannins for example have the ability to precipitate protein in aqueous media thereby affecting digestibility of proteins (Hagerman *et al.*, 1992).

In tropical forages Shayo and Udén (1998) observed that browse shrubs contain high levels of tannins and proteins bound to the CWC with NDF-CP values varying 0.06-0.7 of the total protein. Other tropical forages with high protein content like *Leucaena leucocephala* (241.9 g kg⁻¹ CP; 72.3 g kg⁻¹ PBV; and 36.1 g kg⁻¹ AAT) have been evaluated to have high potential as protein source for

dairy animals (Mgheni *et al.*, 1994a) but its nutritional value is limited due to presence of the anti-nutritional factor, mimosine, a toxic amino acid.

2.2.1.3 Factors influencing digestion rate of individual fractions of fibre

Fibre utilisation is not only influenced by the intrinsic attributes of forages but also to a considerable extent by extrinsic factors influencing fibrolytic activity in the rumen. The rumen retention time, the rate at which long particles are broken down, and the proportion of rapidly fermentable carbohydrates in the diet have been reported to influence fibre digestion and finally intake. In high producing cows, reduced fibre digestion has always been associated with reduced rumen pH. When concentrate diets high in rapidly fermentable carbohydrates (RFC) are fed to high producing dairy cows, a lot of volatile fatty acids (VFA) are produced at a higher rate than the rate at which they are absorbed through the rumen wall and result in decreased pH (Moulds *et al.*, 1983; Huhtanen and Khalili, 1991; Stensig and Robinson, 1997).

Lactic acid production is characteristic of high starch diets and it is under such conditions that lactate fermenters (*Selenomonas ruminantium* and *Streptococcus bovis*) flourish (Van Soest, 1994). Lactate is usually rapidly fermented, but at high production rate it may accumulate and results in markedly decrease rumen pH. Lactic acid is a stronger acid than the VFA causing a depression in VFI. Review by Ørskov and Ryle (1990) and Van Soest (1994) showed that cellulolytic, hemicellulolytic and pectinolytic rumen micro-organisms are all inhibited by low pH. The flow of saliva is stimulated by eating and rumination and negatively related to high concentrate intake (Nørgaard, 1993). Hence the negative effect of feeding RFC may further be increased if the rumen buffering capacity is decreased as a result of low saliva production. However, under normal circumstances the rumen is highly buffered by partial CO₂ pressure, saliva production,

concentration of VFA salts and ammonia, rate of absorption and passage of digesta out of the rumen.

Studies on rumen environment have demonstrated that there is a critical level of rumen pH below which the rumen fermentation activity is impaired. The rate of degradation of forages is optimal when pH is maintained at 6.7 ± 0.15 and below 6.0-6.1 cellulolysis is inhibited (Mould *et al.*, 1983). A similar range of optimal conditions for cellulolysis activities have also been reported (Silva and Ørskov, 1988; Djajanegara and Doyle, 1989; Mgheni *et al.*, 1994b) in ruminants fed forage based diets.

Other possible conditions of rumen environment that influence fibre digestion have been suggested. Mould *et al.* (1983) alleviated the pH by infusion of bicarbonate buffers and observed that depression of fibre digestion that was not attributed to effect of pH was the result of feeding high grain diets suggesting that some strains of bacteria preferred RFC rather than cellulose. Stritzler *et al.* (1998b) reported that the higher the energy level of supplementation, the lower the digestion of the CWC. However, feeding of RFC should be done with caution. Results obtained from rumen evacuation technique (Table 2.3) demonstrated a decreased intake, total tract digestibility, and rate of digestion with the increased amount of RFC and level of feeding.

The capture of carbohydrate energy into metabolites useful to the host animal is greater when propionic acid is produced than acetic acid, whereas generation of hydrogen and hence of methane (a waste product) is greatest when acetic acid is formed (Ørskov and Ryle, 1990). Thus, in forage based diets the available energy utilisation is normally inefficient, whereas addition of concentrate

change the fermentation pattern and reduce the utilisation of the fibre in forages (Mould *et al.*, 1983).

Interpretation of the results (Mould *et al.* 1983) relative to individual fibre source was, however, not clear in those studies (Mould *et al.*, 1983, Robinson *et al.*, 1987). This was because concentrates used were not fibre free since fibre composition of the diet changed depending on the amount of RFC in the diet (Weiss and Shockey, 1991). To avoid this confounding effect, Stensig and Robinson (1997) suggested that fibre free concentrate is useful when digestion and passage kinetics of specific forage fibres are measured.

Use of fibre free (pure starch and sucrose), Stensig *et al.* (1998a) demonstrated that intake of DM, digestion rate and passage did not differ between diets with lower proportion of RFC in the diet. At high proportion of starch in the diet the rate of digestion as well as passage of NDF decreased. In this study (Stensig *et al.*, 1998a) reported that digestion rate of NDF decreased by 6.8 and 17.5 % respectively in relation to an increase in starch and sucrose in the diet (Table 2.3). Other workers (Robinson *et al.*, 1987; Huhtanen and Khalili, 1991) reported similar findings. A reduced rate of digestion of fibre will result into high degree of rumen fill, which can be an important factor in limiting VFI of forages.

Table 2.3 Influence of declining level of NDF intake and varying proportions of concentrate, starch and sucrose on intake and digestion kinetics of fibre in dairy cows

Item	Orchardgrass		Alfalfa			Reference	
	Level of concentrate in the diet						
	20 %	40 %	60 %	20 %	40 %		60 %
DM intake (kg d ⁻¹)	17.1	20.5	21.8	21.3	22.4	23.2	Weiss and Shockey (1991)
NDF intake (kg d ⁻¹)	7.8	7.8	6.8	7.5	6.8	5.9	
NDF digestibility (%)	73.3	72.5	72.4	48.3	49.9	45.7	
	Concentrate level (g DM kg ⁻¹ diet DM)						
	250	500	750	250	500	750	Huhtanen and Jaakkola (1993)
NDF	0.045	0.041	0.026	0.052	0.047	0.032	
DNDF	0.074	0.073	0.044	0.089	0.077	0.051	
	Alfalfa		Orchardgrass				
	D	L	D	L			
Intake DM (kg d ⁻¹)	6.51	19.17	5.81	16.32			Holden <i>et al.</i> (1994)
NDF intake (kg d ⁻¹)	2.58	7.61	2.46	6.71			
DM digestibility	0.73	0.68	0.78	0.74			
NDF digestibility	0.60	0.46	0.74	0.63			
Digestion rate (<i>k_d</i> h ⁻¹)	0.079	0.096	0.083	0.077			
	Alfalfa		Timothy				
	Level of concentrate (kg d ⁻¹)						
	8	12	8	12			Stensig and Robinson (1997)
Intake (kg d ⁻¹):							
Total DM	22.8	23.4	23.1	23.6			
Silage DM	15.8	12.9	16.2	13.2			
NDF	7.62	6.38	8.16	6.9			
DNDF	4.17	3.56	6.16	5.18			
INDF	3.45	2.82	2.00	1.61			
	Digestibility (WTAD):						
OM	59.9	70.3	69.8	69.8			Stensig and Robinson (1997)
NDF	31.1	37.5	56.3	47.4			
DNDF	67.3	63.7	70.1	62.5			
N	73.9	78.9	76.5	73.8			
Digestion rate ((<i>k_d</i> h ⁻¹)	0.041	0.035	0.031	0.024			
	STARCH		SUCROSE				
	20	30	20	30			Stensig <i>et al.</i> (1998a)
Intake (kg d ⁻¹):							
DM	15.5	15.9	15.3	16.9			
N	0.498	0.506	0.71	0.523			
NDF	4.69	4.11	4.50	4.26			
DNDF	4.18	3.69	4.05	3.86			
INDF	0.51	0.41	0.45	0.40			
	Digestibility (WTAD):						
OM	75.3	77.07	74.5	74.6			Stensig <i>et al.</i> (1998a)
N	66.3	69.1	62.0	59.6			
NDF	67.4	66.2	69.3	62.9			
DNDF (ileum-D)	63.3	64.4	64.0	57.6			
Digestion rate (NDF)/h	0.019	0.018	0.019	0.016			
Digestion rate (DNDF)/h	0.024	0.022	0.024	0.021			

The abbreviations in Table 2.3 are DM = Dry matter, OM = organic matter, N = nitrogen, NDF = Neutral detergent fibre, DNDF = digestible NDF, INDF = indigestible NDF, ileum-D = feed-ileum digestibility, WTAD and where digestibility is not indicated whole tract apparent digestibility, D = dry cows and L = lactating cows.

Decreased fibre digestion can be explained by several factors that occur in the rumen during fibre metabolism. The rumen bacteria, protozoa and fungi ferment the available food constituents (polysaccharides, sugars, and protein) in the rumen thereby generating the ATP they need for maintenance of homeostasis, and for growth (Nolan, 1993; Flint and Forsberg, 1995). Fermentation also generates intermediate products like phosphates, pyruvates and peptides that are used for synthesis of cell constituents to replace those continually flowing to the small intestine of the host.

In ruminants the major end products of the rumen fermentation process are the volatile fatty acids (VFA), ammonia and microbial cells. Ørskov and Ryle (1990) reported that rumen content usually include about 10^{10} - 10^{11} bacteria/ml, and up to 75 % being associated with feed particles. The VFA mainly consists of acetic acid, propionic acid and butyric acid. Sometimes lactic acid is also produced (Stensig *et al.*, 1998a) that resulted in depressed pH with increased starch and sucrose in the diet. The VFA are mostly absorbed from the rumen through the rumen wall. Major products of rumen fermentation as influenced by different proportion of concentrates, starch and sucrose are given in Table 2.4.



Table 2.4 Influence of varying proportion of concentrate, starch and sucrose on rumen environment (pH, NH₃ and VFA)

Item	Orchardgrass			Alfalfa			Reference
	Level of concentrate in the diet						
	20 %	40 %	60 %	20 %	40 %	60 %	
Acetic acid (% DM)	67.3	66.8	63.9	66.5	65.1	63.5	Weiss and Shockey (1991)
Propionic acid (% DM)	16.1	16.2	18.6	17.4	17.4	18.9	
Butyric acid (% DM)	11.4	12.1	12.4	9.8	11.2	11.7	
	Alfalfa			Timothy			
	Level of concentrate (kg d ⁻¹)						
VFA (mol/100 mol)	8	12	8	12			Stensig and Robinson (1997)
Acetic acid	67.5	65.6	65.1	63.1			
Propionic acid	18.6	20.2	21.8	22.8			
Butyric acid	8.9	9.2	9.8	10.5			
NH ₃ (mg/100)	23	22.0	26.0	21.9			
pH	6.49	6.33	6.43	6.38			
	Starch		Sucrose				
VFA (mol/100 mol)	20	30	20	30			Stensig <i>et al.</i> (1998)
Acetic acid	60.1	55.9	57.4	53.9			
Propionic acid	22.3	26.6	22.9	24.5			
Butyric acid	12.6	12.6	15.2	17.9			
Lactate (mM l ⁻¹)	1.7	2.6	1.2	5.9			
NH ₃ (mg/100)	12.8	13.0	9.8	13.5			
pH	6.31	6.20	6.43	6.19			
	Type of diet						
Diets ¹	1	2	3	4			Mgheni <i>et al.</i> (1994b)
pH	6.7	6.7	6.7	6.7			
NH ₃ -N (mg l ⁻¹)	214	215	76	91			
VFA (mM l ⁻¹):							
Acetate	54.6	51.6	54.5	50.9			
Propionate	12.6	12.8	13.2	13.1			
Butyrate	4.1	4.3	5.2	5.1			

¹Diets:

Diet 1 = rice straw sprayed with urea (20 g kg⁻¹) + rice bran

Diet 2 = rice straw sprayed with urea (20 g kg⁻¹) + rice bran + fishmeal

Diet 3 = urea-treated rice straw (50 g kg⁻¹) + rice bran

Diet 4 = urea-treated rice straw (50 g kg⁻¹) + rice bran + fishmeal

2.2.1.4 Fibre kinetics of passage

Ruminant animals are unique anatomically and physiologically compared to non-ruminants. During eating, feed particles enter the cranial sac of the rumen and the heavy particles may sink directly through the rumen mat into the reticulum or the cranial sac of the rumen (Van Soest, 1994). Light particles that float are slowly forced into the dorsal sac by contraction of the reticulum and the cranial sac. Small particles that contain bubbles of gas will float and not sink to the liquid phase in the lower part of the reticulum where passage occurs. From the dorsal sac the feed is slowly turned, squeezed and kneaded by the rumen pillars.

As the functional specific gravity of the feed particles increases, they sink into the ventral sac of the rumen (Welch, 1986). On contraction of the ventral sac the liquid which carries feed particles enters the cranial sac as the result of downward motion of the cranial pillar of the rumen and returns to the reticulum by contraction of the cranial sac (Van Soest, 1994). Finally feed particles which have been adequately communicated may pass out of the reticulum and into the omasum while larger particles are remasticated (Faichney, 1993). Studies with plastic particles (Welch, 1986) reported that particles with specific gravity between 1.2 and 1.4 in most cases have been observed to pass rapidly out of the rumen.

Feedstuffs enter the rumen as a continuous distribution of particle sizes. The shape and distribution is dependent on the previous physical form like chopping or long form, grinding, drying and chewing activity by the animal (Nørgaard, 1993; Poore *et al.*, 1993). Particles greater than the threshold size must be reduced before they can pass out from the rumen. A review by Allen and Mertens (1988) showed this threshold size to be variable but has been reported to be that which will

pass through sieves of 1-2 mm for sheep and 2-4 mm for cattle. In another review by Van Soest (1994) particle size reduction was showed to be primarily due to rumination and fermentation.

During successive meals, particles exit in a continuous range of sizes from very small, e.g. bacteria cells, to pieces of plant material up to several centimetres long that can be found in the rumen when diets of long hay are given. Reviews by Faichney (1993) and Van Soest (1994) showed variable particle size distribution when animals were given chopped/ground and pelleted hay, long hay or just grazing, and whether sieved from samples collected from the faeces or rumen digesta from different species. The sizes varied from 0.91-1.2 mm for both cattle and sheep. Although it is difficult to measure under in vivo condition, the rate of particle size reduction is of major importance in the alleviation of rumen fill and consequently, feed intake. A review by Allen and Mertens (1988) reported that fractional rates of clearance from the rumen have been found to range from less than 0.01 h^{-1} for large particles ($>2-4 \text{ mm}$) to greater than 0.05 h^{-1} for small particles ($<0.5 \text{ mm}$) in steers fed long hay.

Particle size reduction has a great impact on functional specific gravity of feed particles. As particle size is reduced the functional specific gravity increases and consequently tend to sink and have greater probability of passing out of the rumen. In practice selective retention tend to retain course particles that are reduced to finer particles after rumination and digestion. These fine particles have a delayed passage, with their retention time being an inverse function of the rate of passage. During breakdown of feed particles by the rumen microbes, gas bubbles are formed and can markedly decrease the functional specific gravity of the feed particles (Udén, 1988). Further evidence (See review by Van Soest 1994) has shown that the rate at which ingested forage is fermented in the rumen influences the functional specific gravity that facilitates passage out of the rumen.

Hence for newly ingested feeds, long particle size and a combined effect of gas production prevent passage from the rumen. As particle sizes are reduced and gas is eliminated by hydration, passage rate is increased. It is evident that if particle size reduction and specific gravity have been used to describe the escapable and non-escapable rumen fibre fraction their influence on passage rate and, thus, fibre utilisation cannot be ruled out.

Various workers have reported variations in passage rates of NDF. Stensig *et al.* (1998a) reported low values for NDF (1.3-1.6 % h⁻¹) in grass silage close to those reported by Stensig and Robinson (1997) for timothy NDF (1.8 % h⁻¹) and lower than those reported in other studies (Robinson *et al.*, 1987) at the same production level. Although the physical characteristics of the ingested feed particles, such as particle size and density, are important in determining the size of particles that can pass out of the rumen per unit time, they may not be the only factors that limit passage. Mathison *et al.* (1995) showed that passage for the majority of feed particles in the rumen was not limited by either size or functional specific gravity and concluded that there was ample evidence that the animal controls digesta flow out of the rumen. Review by McDonald *et al.* (1995) showed that stretch and tension receptors present in the reticulo-rumen probably control passage as they have been found to control intake by sending messages to the hunger and satiety centres situated in the hypothalamus

There is an overwhelming amount of literature to support the positive relationship between passage rate and level of feeding in fibre based diets. Passage rate usually increases with increasing level of feeding. Colucci *et al.* (1990) reported that the passage rates of chromium mordanted alfalfa were 1.34, 1.58 and 2.16 times faster at *ad libitum* intake of about 20 kg OM d⁻¹ than that at maintenance level of about 6.4 kg OM d⁻¹ for diets of low, medium and high

concentrate respectively. Similarly, Robinson *et al.* (1987) observed that the rumen rate of passage for fibre determined by rumen evacuation technique was 1.6 faster for cows eating 20.9 kg DM d⁻¹ than for cows eating 5.3 kg DM d⁻¹ of diet containing 66:33 concentrate to grass hay ratio. In contrast, Robinson *et al.* (1987) reported passage rate to decrease as the proportion of starch increases in the same diets. Recent work by Stensig and Robinson (1997) and Stensig *et al.* (1998a) reported similar results.

2.2.1.5 Description of chemical composition influencing VFI

Chemical composition of feeds and their relation to VFI have been studied extensively. Feed dry matter (DM) has been used to relate all nutrient uptake. Silage of low DM (<20 %) are consumed in low amounts due to high intracellular water content, whereas silage of high DM (>30 %) have been reported (Bal *et al.*, 1997) to be consumed in high amounts. Sarwatt *et al.* (1989) attributed low intake of maize silage to be due to low DM content, whilst too dry feeds like straws (Djajanegara and Doyle, 1989) may have similar effect.

Nitrogen content of forages has been reported to influence VFI in ruminants. Shem *et al.* (1995) reported low DM intake (2.2-4.7 kg d⁻¹) of tropical forages in steers and attributed this to low CP (38-127 g kg⁻¹) in these feeds. Evaluation of tropical grasses and legume forages showed that both rate of degradation and potential rumen digestibility were influenced markedly by the CP content in tropical forages (Kimambo *et al.*, 1994; Shem *et al.*, 1995; Mgheni *et al.*, 1996).

High NDF content as given in Table 2.2 for tropical forages may also suggest that fill of the NDF fraction may be an important factor that limit VFI and CP utilisation as this fraction may be associated with lignin (Van Soest, 1994). Shem *et al.* (1995) reported low intake in steers and

attributed this to high NDF content of tropical forages. Mbwire and Udén (1997) showed a poor relationship ($R^2 = 0.30$ with $SD=0.5$) between lignin and age of maturity of Rhodes grass (*Chloris gayana* cv. Kunth) but showed that stage of maturity in this grass had high relation to CP ($R^2 = 0.81$ and $SD= 1.4$) in vitro digestibility ($R^2 = 0.87$ with $SD = 1.9$) but relatively lower relationship to NDF content ($R^2 = 0.68$ and $SD = 1.3$). The results showed that in Tanzania there is abundance of rapidly growing grasses during the rainy season but the grasses are associated with rapid decline in feeding value with age of maturity. The situation becomes worse during the dry season when all the grasses are considered to be of poor quality. It is evident that at this stage of growth or season the intake will be low and the most important intake regulation will be the physical fill of NDF fraction in the rumen.

2.2.1.6 Description of rumen degradation characteristics and its limitation to VFI

Studies on rumen degradability characteristics and their influence on VFI of forages have been investigated extensively and their results used to predict forage intake (Ørskov *et al.*, 1988; Von Keyserlingk and Mathison, 1989; Carro *et al.*, 1991; Kimambo *et al.*, 1994; Shem *et al.* 1995; Fonseca *et al.*, 1998). Use of degradability characteristics to explain differences obtained in VFI may be somewhat limited because some feeds do not fit the degradation model (Ørskov and McDonald; 1979) and that the parameters *a*, *b* and *c* are inter-related. Shortcomings of the *in situ* nylon bag technique have been described by several authors (Madsen *et al.*, 1997; Hvelplund and Weisbjerg, 1998; Tamminga and Williams, 1998; Adesogan *et al.*, 1998) and indeed the results obtained have been ambiguous and inconsistent.

It is important to use parameters that have been estimated with reasonable degree of accuracy. The use of degradability characteristics is questionable when it comes to testing the applicability and the precision of the model. Although the correlation between predicted and observed may be high (Ørskov *et al.*, 1988; Shem *et al.*, 1995), the results may be difficult to interpret in terms of underlying biological processes. With poor quality roughages, however, degradation characteristics can be used indirectly to characterise and rank feeds in terms of their feeding value potential (Preston, 1995). Ørskov and McDonald (1979) described the degradation of feedstuffs using the following model:

$$p = a + b (1 - e^{-ct})$$

where,

p = is the degradable fraction at time t

a = is the intercept (immediately soluble fraction, and for NDF near zero, as NDF is not water soluble)

b = is the insoluble but potentially degradable fraction

c = is the degradation rate constant (h^{-1}) at which b is degraded

t = is the incubation time (h)

The soluble fraction is mainly contained within the plant cell contents. The soluble fraction contributes to the weight and specific gravity of the feed, but once released into the rumen fluids right after ingestion, it contributes very little to the fill. In contrast b , the insoluble but potentially degradable fraction will occupy space in the rumen for some time before it is fully degraded or passed out of the rumen. It follows that $[1 - (a + b)]$ will be a measure of the absolute indigestible fraction in the feed. The indigestible fraction will occupy space until is passed out of the rumen.

Hence rate of digestion in the rumen (c) and passage rates (k) are means by which physical fill of the feed is reduced as the feed passes out or is digested and absorbed from the rumen. If the assumption that physical fill limits VFI holds true, then the degradability characteristics combined with passage rate should be able to describe the physical fill of feeds as an important factor that limit VFI.

2.2.1.7 Influence of level of feeding on rumen retention time, rumen pool sizes and intake

Several authors have reported the influence of feeding level on rumen pool sizes, digestion and passage rates (Robinson *et al.*, 1987; Huhtanen and Khalili, 1991; Holden *et al.*, 1994). Each rate expresses the fraction of the rumen component pool that is digested (rate of digestion) or passed (rate of passage) from the rumen, per unit time. Weisbjerg *et al.* (1990) demonstrated that passage of feeds out of the rumen depends on the level of feeding. At high level of feeding passage rate is increased and digestion decreased and vice versa. Similar findings were reported in dairy cows when intake was influenced by the proportion of concentrate, starch or sucrose (Table 2.3).

Source of fibre in forages can have an influence on response by animals when tested at different levels of feeding (Poore *et al.*, 1993). Holden *et al.* (1994) reported a high passage rate (0.030 vs 0.027 h⁻¹), low digestion rates (0.08 vs 0.10 h⁻¹), high mean rumen retention time (90 vs 64 h) and low NDF intake (2.6 vs 7.6 kg d⁻¹) in dry cows compared to lactating cows fed alfalfa diet and a similar trend in orchardgrass (Table 2.3 and 2.5).

Table 2.5 Influence of level of feeding and varying proportion of concentrate, pure starch and sucrose on rumen pool sizes, rumen retention time and intake of DM and NDF

Item	Diets (Experiment 1) ^a			Diets (Experiment 2) ^a			Reference
	C	H	M	C+C	H+C	M+C	
Rumen pool sizes (kg):							
DM	8.71	9.11	6.46	9.90	11.67	9.09	Stensig <i>et al.</i> (1994a)
NDF	4.11	5.28	3.84	5.08	6.50	5.10	
Total digesta	70.9	78.8	60.1	77.1	94.7	70.4	
	Level of feed intake (kg d⁻¹)						
Intake (kg d⁻¹):	24.0	19.5	15.0	10.5	6.0		
OM intake	19.0	15.4	12.0	8.4	4.8		Robinson <i>et al.</i> (1987)
DM-pool (kg)	11.4	9.1	8.1	6.3	4.3		
NDF-pool (kg)	6.0	4.1	3.5	2.4	1.6		
Total digesta (kg)	81.6	75.4	75.4	72.4	59.5		
	Level of starch (% in the concentrate)						
Intake (kg d⁻¹):	8	14	20	26	32		
OM intake	12.1	11.9	11.9	11.9	11.8		Robinson <i>et al.</i> (1987)
DM-pool (kg)	8.1	7.6	7.4	8.5	7.6		
NDF-pool (kg)	3.9	3.4	3.2	3.7	3.3		
Total digesta (kg)	76.2	73.1	69.3	72.4	73.2		
	Grass silage			Dried grass			
Rumen pool sizes (kg):	Concentrate level (g DM kg⁻¹ diet DM)						
	250	500	750	250	500	750	Huhtanen and Jaakkola (1993)
DM	3.42	3.25	3.61	3.71	3.45	3.49	
NDF	1.88	1.65	1.89	1.91	1.75	1.85	
DNDF	1.13	0.93	1.13	1.13	1.07	1.15	
INDF	0.74	0.71	0.76	0.78	0.67	0.69	
	Alfalfa		Orchardgrass				
	D	L	D	L			
Intake DM ((kg d ⁻¹)	6.51	19.17	5.81	16.32			Holden <i>et al.</i> (1994)
NDF intake (kg d ⁻¹)	2.58	7.61	2.46	6.71			
MRRT (h)	89.9	64.2	82.3	81.1			
Digestion rate (k_d h ⁻¹)	0.079	0.096	0.083	0.077			
	STARCH		SUCROSE				
	20	30	20	30			Stensig <i>et al.</i> (1998a)
Rumen pool sizes (kg):							
DM	10.42	10.01	10.26	9.89			
NDF	5.81	5.65	5.73	5.58			
DNDF	4.54	4.50	4.57	4.48			
INDF	1.27	1.15	1.16	1.10			
Total digesta	87.2	81.8	86.0	84.6			

^aDiets were C= grass cubes, H= clover grass hay and M= maize silage (Experiment 1) and Experiment 2 consists of the same forages as in Experiment 1 but supplemented with 6 kg of rolled barley and 1 kg of soybean meal to give three rations C + S, H + S and M + S, where S indicates supplements.

It seems from these results (Table 2.5) that alfalfa and orchardgrass diets that were equal in NDF were not equal in intake and digestibility. It is evident that the source of fibre was important in explaining the differences observed in the rumen parameters measured and intake. In contrast, Stensig and Robinson (1997) reported that DM intake was not affected by source of forage fibre in cows fed alfalfa or timothy silage. Huhtanen and Jaakkola (1993) reported that the type of forage had no effect on rumen pool size of all the dietary constituents measured. Stensig and Robinson (1997) reported that rumen pool sizes of total digesta decreased as the level of concentrate in the diet increased, but there were no differences in the DM pool sizes. The influence of level of feeding and supplementation on rumen pool sizes of NDF and DM from various workers, obtained from rumen evacuation, is given in Table 2.5. These results suggest that changes in gut fill were related more to differences in intake than to passage rate. The results may also suggest that reduced passage rate of NDF in high concentrate or starch diets can partially be compensated for by an increased NDF retention time in the rumen of animals at low level of feeding and increase digestibility.

2.2.1.8 Nutrients and water requirements and its effect on VFI

The basic urge to consume feed is the tendency of the animal to realise a genetically determined capacity for growth and/or milk production. The genetic capacity corresponds to the maximum rate at which tissues can utilise nutrients. The nutrient intake an animal requires to express this genetic capacity is only attained if the nature of the feed, environmental condition and health status are all conducive to it. This requires the presence of feed with high nutritive value in terms of digestibility, protein content, minerals and vitamin, proper physical form and without anti-nutritional factors. In other words, a feed or diet of high intake potential to meet the expected production level without altering the animal's metabolism and health.

Table 2.6 gives the nutrient requirements for small-breed growing heifers as predicted by the NRC (1989). Feeding standards are just guidelines to the users and extrapolating them to different feeding situations from where they were developed may not necessarily results into the expected production levels. It is therefore important to be able to estimate with a certain degree of accuracy that an animal which is, for example, fat and has a high body weight will require more feed than a thinner animal for maintenance requirement but once that requirement is met the animal will require relatively less feed. The situation is even more pronounced in thin animals in the tropical regions where due to less feed intake during the dry season, the animal's forage intake during the rainy season is high for compensatory growth. In high producing cows, however, the animals' requirement is below intake of forage and the animal will eat trying to satisfy requirements for milk production. This will, however, be limited by the rumen capacity due to physical fill and the animal will stop eating even though the requirement is high (Forbes, 1977). The situation is much more critical in early lactation when all high producing animals are in negative energy balance.

Adequate water supply is necessary all the time in order to achieve maximum intake capacity for tropical forage. Water is also vital to the life of organism. McDonald *et al.* (1995) noted that animals will die more rapidly if deprived of water than when deprived of food. Animals obtain water from three sources viz: drinking water, water present in its food and metabolic water. Of these sources, drinking water contributes the largest amount in most feeding situations especially in high producing dairy cows (NRC, 1989; ARC, 1990).

Table 2. 6 Daily nutrient requirements for growing dairy females given as a guide line under average conditions

Live weight (kg)	Gain (g)	DM intake (kg)	Energy				Protein			Minerals			Vitamin		
			NEM (Mcal)	NEG (Mcal)	ME (Mcal)	DE (Mcal)	TDN (kg)	UPI	DPI	CP	Ca	P	A	D	
200	400	4.24	4.57	1.26	10.38	12.16	2.76	201	217	513	19	13	8.48	1.32	
200	500	4.60	4.57	1.60	11.25	13.19	2.99	217	251	562	20	13	8.48	1.32	
200	600	4.96	4.57	1.95	12.14	14.23	3.23	232	286	611	20	14	8.48	1.32	
250	400	5.24	5.41	1.41	12.36	14.57	3.30	185	305	629	21	15	10.60	1.65	
250	500	5.68	5.41	1.80	13.38	15.78	3.58	197	346	681	21	16	10.60	1.65	
250	600	6.12	5.41	2.20	14.43	17.01	3.86	209	389	735	22	16	10.60	1.65	
300	400	6.34	6.20	1.56	14.38	17.06	3.87	176	395	761	22	16	12.72	1.98	
300	500	6.87	6.20	1.99	15.57	18.48	4.19	184	445	824	23	17	12.72	1.98	
300	600	7.40	6.20	2.43	16.79	19.92	4.52	192	495	888	23	17	12.72	1.98	
350	400	7.57	6.96	1.71	16.50	19.71	4.47	173	490	909	23	17	14.84	2.31	
350	500	8.20	6.96	2.18	17.87	21.35	4.84	178	548	985	23	18	14.84	2.31	
350	600	8.85	6.96	2.66	19.28	23.03	5.22	183	608	1 062	23	18	14.84	2.31	
400	400	8.98	7.69	1.84	18.77	22.58	5.12	177	592	1 078	24	18	16.96	2.64	
400	500	9.74	7.69	2.35	20.36	24.50	5.56	181	661	1 169	24	19	16.96	2.64	
400	600	10.52	7.69	2.87	21.98	26.45	6.00	183	730	1 263	24	19	16.96	2.64	

Source: NRC, (1989).

NEM= net energy for maintenance, NEG = net energy for gain, ME = metabolizable energy, DE = digestible energy, TDN = total digestible nutrients,

UPI= undegradable protein intake, DPI = degradable protein intake and CP = crude protein.

2.2.1.9 Effect of fishmeal and urea supplementation on fibre utilisation and VFI

Ad libitum intake of forages in dairy cattle may not be sufficient to meet the requirements of the animal for growth or lactation especially in early lactation. In ruminants knowledge of feeding and supplementation strategies is required in two levels. First level is the required amount of nutrient supply for optimum microbial synthesis in the rumen and secondly at the level of digestion and absorption in the small intestine and lower digestive tract. At both levels nutrients are required to supply energy primarily in a form of adenosine triphosphate (ATP) as precursors for synthesis of fat, protein and carbohydrates (NRC, 1989; ARC, 1990).

Tropical forages especially crop residues have been reported to have low protein content and this limits their utilisation (Mgheni *et al.*, 1993; Kimambo *et al.* 1994; Shem *et al.*, 1995; Ndemanisho *et al.*, 1998). Kimambo *et al.* (1994) using the prediction model of Madsen *et al.* (1994) reported low intake of tropical forages due to low rate of degradation. The authors suggested that N was bound to the CWC and suggested that these feeds must be highly supplemented to the level that can support animal production. Positive response in intake and growth rates have been reported when tropical forages low in protein were supplemented with *Leucaena leucocephala* leaves and/or cotton seed cake (Ndemanisho *et al.*, 1998) urea and/or fishmeal (Djajanegara and Doyle, 1989; Tuen *et al.*, 1991; Mgheni *et al.*, 1993; Shem *et al.*, 1995). The reasons for this response were either increased digestibility (Djajanegara and Doyle, 1989), increased rate of degradation (Mgheni *et al.*, 1993) and increased passage rate (Shem *et al.*, 1995). In the untreated rice straw, urea supplementation *per se* did not seem to improve their utilisation as there was not enough digestible carbohydrates to supply energy for the synthesis of protein (Djajanegara and Doyle, 1989; Mgheni *et al.*, 1993).

Lack of response when poor quality forages are supplemented with urea without energy supplements may be explained by high accumulation of NH_3 found in the rumen of sheep when rice straw was supplemented with 20 g kg^{-1} DM straw (Mgheni *et al.*, 1994b) suggesting that the rate of production of rumen ammonia was higher than the rate at which it was utilised by the rumen microbes. In temperate regions, Weisbjerg *et al.* (1998) observed that urea supplementation to rations deficient in rumen degradable protein improved rumen metabolism and efficiency of microbial protein and also observed recycling of excess nitrogen to the rumen at low rumen ammonia levels.

Fishmeal (FM) and protected proteins have also been used to improve utilisation of tropical forages. Mgheni *et al.* (1993) reported that supplementation of FM to both urea-treated or untreated rice straws had a profound effect on growth rate of dairy goats but not on intake. This may suggest that FM might have caused a metabolic control of VFI as less straw was consumed when FM was provided. However, explanation of the results on the positive response by the animals in terms of markedly improved growth performance when a small amount of FM is supplemented to roughages low in protein has been inconsistent. Ørskov (1991) noted that in growing animals, deposited fat can be used to fuel protein deposition when FM was supplemented to straw based diets to produce lean meat that has a better market quality. Mgheni *et al.* (1993) observed a marked improvement in growth performance of dairy goats (3.3 to 13 g d^{-1}) fed untreated rice straw and 37 to 49 g d^{-1} when fed urea treated rice and attributed this to the use of fat to fuel protein deposition as suggested by Ørskov (1991). This was because there was neither improvement in intake (Mgheni *et al.*, 1993) nor degradation of the straws (Mgheni *et al.*, 1994a) with or without FM supplement. Silvia *et al.* (1988) reported similar results on studies on manipulation of the rumen environment by supplementation. Stritzler *et al.* (1998a) found that inclusion of FM to make the total diet CP of 10

and 14 % DM improved degradability of DM, OM and CWC. Supplementation of forage-based diet with FM increased the ammonia and VFA concentrations but not rumen pH and passage rate. Despite these positive responses of FM supplementation in Tanzania (Mgheni *et al.*, 1993), their use as a supplement to ruminants may be limited due to high cost of FM (1.24 US \$ kg⁻¹) compared to other protein supplements like cotton seed cake (0.12 US \$).

Protected proteins can also be used in a strategic protein supplementation programme to ruminants. Protected proteins could have an added quality of providing protein that escape rumen degradation and increase the size of amino acids pool absorbed from the small intestine. Economically, protected proteins may be too expensive to use in ruminants. Moiro *et al.* (1998) fed protected protein at low levels of inclusion to low quality tropical hay in an attempt to monitor N recycling and increased intestinal protein digestibility. In the same study low DM intake and digestibility were observed due to low level of ammonia in the rumen. It was concluded that although the protected protein was digested in the small intestine at the same efficiency as the unprotected protein, the recycling of the absorbed nitrogen into the rumen was not sufficient to offset the deleterious effect of low rumen degradable protein supply in the diet.

Animals normally eat the amount of food that satisfies their energy requirements. There are some circumstances however, when insufficient is eaten, resulting in loss of body weight or decrease in the productive process, such as growth or milk secretion. Under-feeding is often seen in ruminants where highly fibrous bulky food is offered as in the case of most feeds in the tropics (Preston, 1995) that makes supplementation important. Forbes (1995b) noted that a food with severe imbalance of nutrients would be eaten in smaller quantities than one that provides a mixture of nutrients that is well balanced for metabolism of the animal eating the food.

2.2.2 Descriptions of animal characteristics when VFI is limited by physical fill

Breed, age, sex, and physiological status of animals (pregnancy and lactation, especially late and early lactation) have been found to influence VFI. Different breeds have been found to have different rumen volume (Mould *et al.*, 1982), intake capacity and passage rate (Ingvarlsen and Weisbjerg, 1993). It is generally considered that the capacity of the reticulo-rumen and passage of digesta (Madsen *et al.*, 1994; Dado and Allen, 1995) limit VFI of forages.

Large breeds with inherently large rumen have the ability to accommodate more fermenting materials in the rumen at any time than small breeds with inherently small rumen. Relative to body weight Mould *et al.* (1982) observed much larger ruminal volumes in Zebu cattle in Bangladesh than in Friesian cattle. Dado and Allen (1995) noted that animals challenged to high fibre adapted to higher fill than those fed high levels of concentrates. Ingvarlsen and Weisbjerg (1993) found a higher intake capacity (15-20 %) in Danish Friesians and Danish Red cattle than in Jersey cows. Most feeding systems recognise the intake capacity for different breeds and growth rate (French and Danish fill systems, the NRC, ARC and the Cornell system) as reviewed by Ingvarlsen (1994).

The age of the animal will have a great impact on the rumen volume as reported in several reviews (Ørskov and Ryle, 1990; Van Soest, 1994; Forbes, 1995a). Ruminant calves are almost like non-ruminants in their digestive system and as the animal grows and starts to eat forages its rumen develops and adapts to the use of forages until full intake capacity is achieved.

Sex and animal category (heifers, bulls or steers) have been reported to influence intake. The Cornell system estimates intake to be 3 % higher in heifers than in bulls and steers (Rayburn and Fox, 1993), whereas the NRC (1989) feed requirements predicted higher DM intake in growing

males than females at the same body weights. In the French (Jarrige *et al.*, 1986) and Danish (Ingvarstsen *et al.*, 1992) systems intake capacity of heifers is 9 and 10 % higher, respectively, at 200 kg live weight, similar at 400 kg, and approximately 3 % lower at 55 kg live weight compared to bulls and steers.

Animal live weight (LW) is an important variable that influences intake capacity in most feeding systems. It has been included as an independent variable as percentage of live weight, constant intake ($W^{0.75}$) or raised to other power other than 0.75 (NRC, 1989). Also the natural logarithm (\ln) of LW (Ingvarstsen *et al.*, 1992) or combination of the above (Rook *et al.*, 1990a) has been used. The argument for these differences is the accuracy obtained when fitted to the model. Review by Ingvarstsen (1994) showed that, although most models related to LW have a constant food intake ($W^{0.75}$) because of the concept that maximal relative food capacity is related to basal metabolism. The best relationship was obtained when VFI was expressed on the basis of LW raised to the power of 0.6. Calculation on the food intake capacities (Ingvarstsen *et al.*, 1992) showed that in Holstein Friesian bulls fed concentrates *ad libitum*, the intake capacity was 96 g kg $W^{0.75}$ at 100 kg LW, a maximum of 106 g at 170 kg, and declined to 86 g at 500 kg live weight. Intake is underestimated at LW between 125-350 and overestimated at LW above 375 kg when a constant intake per kg $W^{0.75}$ is assumed. Ingvarstsen (1994) suggested that the best fit is obtained when intake to \ln (LW) is used for cattle above 100 kg LW, probably because this relationship allows higher intake in the interval in which marginal growth is the highest.

Pregnancy, lactation (stage of lactation, milk yield and composition) and parity have been shown to influence intake capacity of animals. Different trimesters of pregnancy have been reported to influence intake. These differences have been associated to increased intake during late pregnancy



as the LW increased due to rapid growth of foetus during the last trimester of pregnancy (NRC, 1989) but other intake regulations (e.g. reduced rumen capacity and hormonal changes) counteract the requirement. Ingvarlsen *et al.* (1992) reported that food intake capacity is depressed by 1.53 % per week from the 26th gestation week and generally depresses during the last six weeks of pregnancy. The reason for this depression was associated with the physical fill limitation of intake (Ingvarlsen *et al.*, 1992) but also due to energy level and hormonal regulations (Forbes, 1985).

During the last trimester of pregnancy both heifers and cows may be fed large amounts of concentrates in order to prepare them for the coming lactation and this may have great effect on fibre digestion and passage kinetics that have a tremendous effect on forage intake as discussed previously. Decline of VFI during the last trimester has also been ascribed to a reduction in rumen capacity (Forbes, 1985). Decline in VFI a few days before parturition and increased VFI a few days after parturition has also been reported in dairy cows and is associated with rapid escalation of oestrogens that reduce eating activity. Effect of breed and parity were demonstrated by Foldager and Haarbo (1994) in dairy cattle who reported that the maximum intake capacity for the Danish Jersey cows was 79.4 % of the capacity for the Danish Red/Danish Friesian cows.

There is a general agreement that lactation influences VFI especially during early lactation when intake usually lags behind protein and energy requirements. Forbes (1985) reported that high mammary metabolism within the animal result in hypertrophy of the reticulo-rumen but the capacity for water increased compared to late pregnancy or non-lactating cows. As reviewed by Forbes (1985) measure of rumen volume and capacity for water showed an increased size and capacity of the reticulo-rumen in early lactation and reached plateaux after the peak of lactation. This was attributed to an increased abdominal capacity as a result of disappearance of the conceptus and involution of the

uterus to an insignificant size after three weeks. The review by Ingvarsten (1994) showed that in cows given diets of constant composition, milk yield peaks 5 to 7 weeks post-partum while maximum intake is reached between 8 and 22 weeks after calving. It was observed that there was an increase in intake from week one post partum to time of peak intake that varied between 2 and 111 %. This high variation was attributed to pre-partum feeding and low intake during early lactation and this may suggest that various factors influence intake during early lactation.

Body condition, nutritional status and disease have been reported to influence VFI. The NRC (1989) showed that lean non-lactating cows eat around 24 % more feed than fat cows. Furthermore, cows that are fat at calving tend to increase intake in early lactation at a lower rate than thinner cows (Holter *et al.* 1990). In the Cornell system for growing cattle, the degree of fatness has been included in the model and an increase in empty body fatness from 21.3 to 31.5 % is assumed to increase intake by 27 % (Rayburn and Fox, 1993). Several reviews (NRC, 1989; Ingvarsten, 1994; McDonald *et al.*, 1995; Forbes, 1995a) showed that deficiencies of energy, protein, minerals and vitamins deficiencies, absence of water, excess toxic material diseases and parasites influence the potential intake capacity of ruminants.

2.2.3 Metabolic control of VFI

There is enough evidence that VFI has a metabolic control pathway and that with high energy diets VFI approximately balances the animal's requirements for nutrients. The study of metabolic control mechanism, ranges from qualitative identification of regulative enzymes and hormonal control sites to quantitative measurement of how important each site is *in vivo*. However, although there has been much modelling of metabolism in the whole animal (Danfær, 1990) there has been little work done on the control of the pathway in ruminants, compared with non-ruminants. Crabtree (1993)

attributed this to be possibly because the newer theoretical approaches to metabolic control are themselves still in a state of flux and there is yet no general consensus. Also the entire subject is currently hampered by lack of accurate experimental data (Crabtree, 1993).

Classical theories of the control of VFI like the glucostatic, lipostatic and thermostatic theories that animals eat for amino acids are described in detail by Forbes (1995a). McDonald *et al.* (1995) cautioned that although VFI in ruminants can be controlled at the metabolic level the signals can be different from those in monogastric animals. Crabtree (1993) noted that amount of glucose absorbed from the digestive tract of ruminants is relatively small and blood glucose level show little relationship to feeding behaviour.

Specific chemicals from the endocrine and nervous system that trigger hunger and satiety have also been reported to control VFI (Poppi *et al.*, 1994). According to chemostatic theory the rise in concentration of nutrients from digestion and metabolism at sites of critical substance sends a signal to the brain to cause the animal to stop eating, and a fall in concentration causes the animal to start eating (Crabtree, 1993). Review by McDonald *et al.* (1995) showed that feedback mechanism between the gut and the brain provided by the peptide hormone, cholecystokinin (CCK) that is released into the gut when digestive products such as amino acids and fatty acids reach the duodenum and act on the hypothalamus hunger and satiety sites to regulate VFI. Other hormones like insulin, glucagon, growth hormones, oestrogen and progesterone have been reported to regulate VFI (Forbes, 1985).

The lipostatic theory has been reported to have a long-term regulation of VFI (McDonald, 1995). It has been theorised that long-term preservation of a relatively constant body weight, combined with

the animals desire to return to that body weight (if it is altered by starvation), implies that some agent associated with energy storage acts as a signal for long term regulation of VFI. This mechanism cannot be ruled out in the tropics where animals starve during the dry season and fed adequately during the rainy season. These theories were basically developed in monogastric animals therefore to what extent they can be extrapolated to the ruminants is a matter of disputes.

2.2.4 Physical and metabolic control of VFI

There is enough evidence to suggest that reticulo-ruminal mechanoreceptors stimulation of the rumen wall for a given load of digesta is responsible for physical control of VFI. Forbes (1995b) noted that not only is the reticulo-rumen elastic, but its muscular activity complicates the situation, as eating stimulates more frequent contractions. Forbes (1995b) noted further that, with high energy diets, stimulation in series of the stretch receptors by distension of the reticulo-rumen depresses VFI. It must be assumed that this increased muscular activity during feeding will act to inhibit VFI. Increased motility increases the passage rate leading to decreased distension and potential intake, a phenomenon that is too complex to include in models of control of VFI.

The rumen appears to be sensitive to the osmolality of digesta within it, especially when this is elevated by additions of salts and other osmotically active substances. Grovum (1995) observed that increasing rumen osmolality above normal range depresses intake. Anil *et al.* (1993) found that rumen distension alone (using rubber balloons) or in combination with infusion of acetate and propionate salts depressed forage intake in cattle. However, since salts were used in this study and not the real acids there is a considerable doubt as to whether their effects were due to the acids themselves or osmolality. Mbaya *et al.* (1993) showed that neither acetate, nor propionate or rumen distension significantly ($P>0.05$) depressed hay or silage intake compared with the control (water)

when given alone. However, when given in combination of either acids or rumen distension, intake was depressed significantly ($P > 0.01$). It was concluded that satiety can be induced by an additive effect of many feedback signals and that daily VFI will depend on the balance between such negative effects and the positive influences of nutrients.

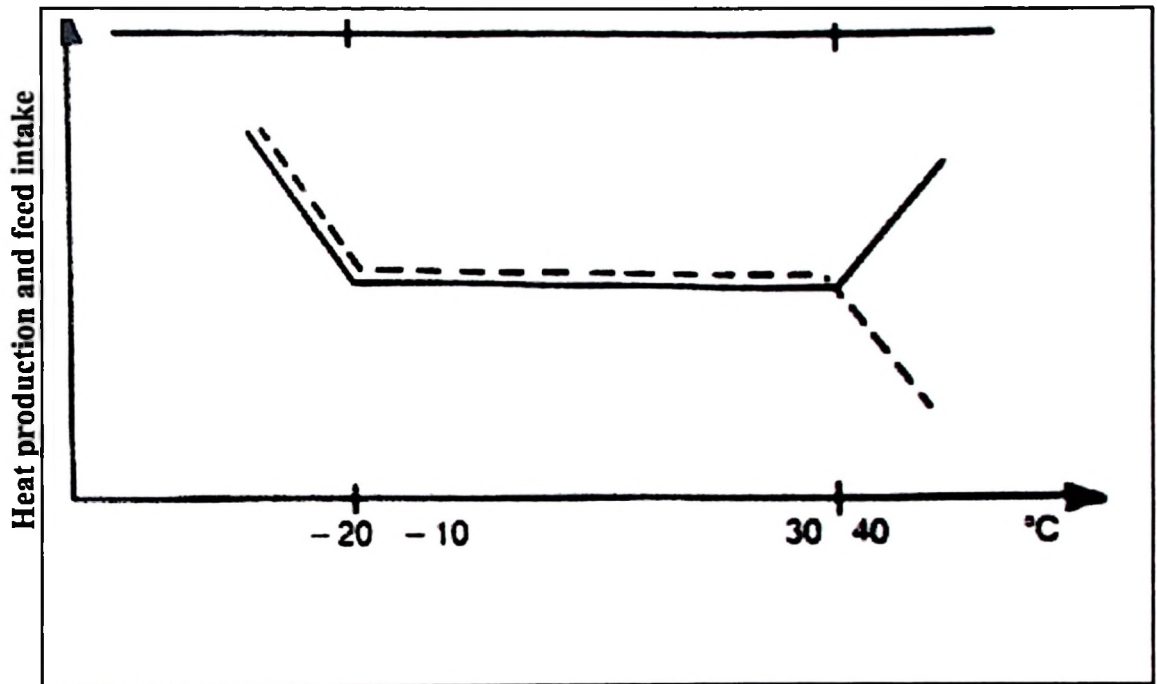
2.2.5 Environmental factors that influence VFI

Environmental factors like season, climate and management system (housing, space allowance, space at manger, time of access to the feed, frequency of feeding, temperature, humidity and photoperiod) affect VFI. Ingvarsten (1994) and Forbes (1995a) reviewed these factors in detail and suggested that these are important factors to consider in predicting VFI. Young (1987) summarised and identified the possible effects of season and climatic components on VFI and concluded that there was inadequate information that linked physiological mechanisms and climatic cues, which control VFI in ruminants.

According to the thermostatic theory an animal eats to keep warm and stops eating to prevent hyperthermia until it reaches the “comfort zone” or “thermal neutral zone” or “critical temperature”, that is the temperature below and above which it will stop eating. Madsen (1983) demonstrated that (Fig.2.1) at thermal neutral zone there is no change in feed intake or heat production due to temperatures between -20°C and 35°C . At lower critical temperature -20°C the animal will eat more and use the energy to produce more heat than is required to maintain body temperature at the expense of milk or meat production and/or growth. On the other hand at the

Heat regulation

- Increased muscle activity
- Increased feed intake
- Surface temperature
- Sweat
- Respiration
- Water intake
- Temperature will lead to stop of feed intake and death



↑
Lower critical temperature

↑
Upper critical temperature

Fig. 2.1 The relationship between the ambient temperature, heat production and feed intake in cattle (Madsen, 1983)

upper critical temperature (35°C) the animal will eat less or even stop eating (depending on the production level) but the heat production will continue to rise resulting into reduced production. This is because heat is produced during digestion and metabolism of food and it is considered that this heat increment could provide the signals used in the short-term regulation of VFI (McDonald *et al.*, 1995).

It has been established that there are thermoreceptors, sensitive to changes in heat, present in the anterior hypothalamus and also peripherally in the skin (Forbes, 1985; McDonald *et al.*, 1995). Some support for this thermostatic theory is obtained from observations, with a number of species, that food intake increases in cold climate and decreases in hot environments. Although there is not enough work done in the tropics to support this theory, Preston (1995) noted that high temperature and humidity cannot be ruled out as some of the factors limiting VFI in the tropics especially among the crossbred dairy cattle. Temperatures have also been reported to influence digestibility, microbial synthesis and passage rates. Studies by Kennedy and Milligan (1978) showed that cold exposure at lower level of intake reduced apparent digestibility of DM and OM for approximately 0.055 units, and further reduction by 0.03 at higher level of intake in cold climates. When digestibility is reduced, passage rate is also reduced resulting in reduced intake.

2.2.6 Learning, diet selection and animal's maximum comfort and appetite related to regulation of VFI

It is increasingly being realised that animals do not simply respond to immediate effects of foods, whether these be sensed by sight, smell and taste or whether these are chemical, osmotic and physical sensations generated within the visceral organs (Forbes, 1995b). It is even becoming

increasingly clear that learning when strong cues are provided plays a vital role in animal's diet selection, preference and aversion and hence influencing VFI (Nolte and Provenza, 1992). It was speculated that an animal might learn that if it continues eating it would get to a situation in which the sum of the various physical and metabolic signals emanating from its visceral organs would become unpleasant, so it stops eating before this situation arises.

Forbes (1995b) theorised that ruminants may not eat to full rumen capacity, but stop eating at a point, where they have learnt that if they stopped eating they would avoid the unpleasant feeling of fullness. Similarly, severe stimulation of chemo-osmo-, or thermo-receptors in the digestive tract wall might be avoided by appropriate conditioning (Forbes, 1995b; Provenza, 1995). Using an example of man, Forbes (1995) noted that man feels uncomfortable to have insufficient supply of nutrients and eat to reduce the discomfort of hunger. Similarly, it is uncomfortable and sometimes painful to eat too much food or poisonous food. Man, therefore, learned to avoid eating too much and eating poisonous foods. With this conceptual framework, Forbes (1995b) concluded that animals eat to "maximise comfort" by integrating positive and negative signals but then rely to a great extent on what was learned to be the consequences, in terms of comfort of eating foods on previous occasions. Given the fact that animals quickly learn to associate sensory properties of the food (Nolte and Provenza, 1992; Provenza, 1995), there is every reason to believe that ruminants control their intake of food to achieve "maximum comfort", a concept that may be difficult to test experimentally (Forbes, 1995b).

The control of VFI becomes more complicated when factors like appetite are considered. Appetite is a complex process influenced by factors both internal and external to the animal. The desire to eat and the amount consumed is determined by the animal's need for energy and protein. This is

modulated by the animal's past and present dietary as well as environmental experiences (long and short-term effects).

It is tempting to conclude that a lot of progress has been made to explain the mechanisms that control VFI. Although much work has been done to understand the mechanisms that regulate VFI in ruminants, other factors are still a mystery. In the tropics, it is generally accepted (Preston, 1995; Madsen *et al.*, 1997) that feed characteristics are dominant factors when low quality roughages are fed to the animals compared to either animal factors or the environment.

2.3 Prediction of VFI

Many attempts have been made over the last three decades to develop systems for prediction of VFI. The drive for this interest is the great impact that VFI has on the overall performance and productivity of the animal. Several reviews (Ingvarlsen, 1994; Dulphy and Demarquilly, 1994; Forbes, 1995a; McDonald *et al.*, 1995; Illius and Jessop, 1996) compared various prediction models for dairy and beef cattle and described their practical applications, weaknesses and possible modifications. In this review, those prediction models related to this study are discussed.

2.3.1 Prediction of intake from chemical composition and digestibility trials

Chemical composition and digestibility describe forage characteristics and have been used to predict intake. A review by Dulphy and Demarquilly, (1994) showed that considerable effort has been put to predict intake based on crude fibre or NDF. Using simple regression model Carro *et al.* (1991) reported a predicted voluntary DMI in 50 mature sheep of 41.2 to 69.8 g kg⁻¹ W^{0.75} per day. A high correlation ($r = -0.84$) between VFI and NDF content of 11 cultivars of alfalfa, red clover and grass legume mixture was also reported. Fonseca *et al.* (1998) reported predicted DM intake from ADF

Table 2.7 Prediction of voluntary dry matter intake (VDMI) of feeds using chemical composition, digestibility and degradability characteristics of forages

Type of forage	Animal category	X-variable	Y-variable ¹	Prediction equation	R ²	r. s. d
Straws (R1)	Steers	$a+b+c$ DM	DMI kg d ⁻¹	$-1.56 + 0.159a + 0.0658b + 56.4c$	0.88 (r)	0.38
Various forages (R2)	Steers	$a+b+c$ DM	DMI kg d ⁻¹	$-8.28+0.266a+0.102b+17.7c$	0.90 (r)	0.28
Hay (R3)	Sheep	a DM	VDMI (g kg ⁻¹ W ^{0.75})	$24.5 + 0.097$ (s.e = 0.0304) a DM	0.53*	5.61
Hay (R3)	Sheep	c DM	VDMI (g kg ⁻¹ W ^{0.75})	$38.4 + 172$ (s.e.= 45.1) c DM	0.62**	5.06
Hay (R3)	Sheep	c NDF	VDMI (g kg ⁻¹ W ^{0.75})	$36.7 + 238$ (s.e.= 62.0) c NDF	0.62**	5.13
Hay (R3)	Sheep	a DM, c DM	VDMI (g kg ⁻¹ W ^{0.75})	$21+0.0733$ (s.e.=0.01577) a DM + 138 (s.e.=26.0) c DM	0.90***	2.79
Hay (R4)	Sheep	NDF	g kg ⁻¹ LW d ⁻¹	$36.1-0.0330$ NDF	0.62**	1.64
Hay (R4)	Sheep	NDF	g kg ⁻¹ LW d ⁻¹	$32.8-0.026$ NDF (ash free)	0.52**	1.82
Hay (R4)	Sheep	ADF	g kg ⁻¹ LW d ⁻¹	$30.2- 0.036$ ADF	0.67**	1.51
Hay (R4)	Sheep	$a+bc$ DM	g kg ⁻¹ LW d ⁻¹	$9.72 + 0.301a - 8.41bc$	0.62*	1.71

*Level of significance (P<0.05), **Level of significance (P<0.01) and ***Level of significance (P<0.001).

¹The a , b and c are the degradability characteristics parameters estimated from the equation

$p = a + b(1 - e^{-ct})$ by Ørskov and McDonald (1979).

Reference 1 (R1) = Ørskov *et al.* (1988)

Reference 2 (R2) = Shem *et al.* (1995)

Reference 3 (R3) = Carro *et al.* (1991)

Reference 4 (R4) = Fonseca *et al.* (1998)

content of roughages ($R^2 = 0.67$), NDF content ($R^2 = 0.62$) and NDF (ash free) content ($R^2 = 0.52$).

The prediction equations and the standard error of the estimates are given in Table 2.7.

2.3.2 Prediction of intake from degradability characteristics

Degradation characteristics have been used to predict VFI with variable precision depending on the degradability constant used (Table 2.7). Ørskov *et al.* (1988) predicted VFI in cattle fed on a roughage-based diet from degradation characteristics either in single or in combination. Although the models could describe more than 80 % of the variation in VFI, the authors concluded that more

research was required to encompass a wide range of forages. Von Keyserlingk and Mathison (1989) predicted VFI from rate of degradation of DM and NDF and found that NDF and DM degradation accounted for 86 and 85 % respectively of the variations in VFI. Carro *et al.* (1991) obtained high correlation ($R^2 = 0.90$) between VFI of DM and the rate at which DM was degraded (Table 2.4). Unlike other authors the model was not improved by adding the rate at which NDF was degraded in the equation. It was concluded that the use of degradation constants is limited as the method may require choice of prediction constant in single or in combination that gives the best prediction of VFI. Shem *et al.* (1995) reported multiple correlation coefficients between degradation characteristics, DM and digestible DM intake and growth rate of $r = 0.90, 0.93,$ and 0.93 respectively. The authors concluded that separate use of the degradability characteristics $a, b,$ and c (Table 2.7) in multiple regressions to predict DM and digestible DM intake and growth rate gave better results than when $a+b$ or $(a+b) +c$ were used. Fonseca *et al.* (1998) reported that predicted DM intake was most accurate from 3 h DM degradation and ADF content of roughages ($R^2 = 0.68$ and 0.67 respectively). The authors concluded that the use of parameters from the equation of Ørskov and McDonald, (1979) describing DM degradation in the rumen of roughages high in NDF content did not improve the accuracy over that obtained using fibre components of feeds (NDF and ADF) or single incubation time.

2.3.3 Prediction of intake based on physical fill

Physical fill of feeds (Fill unit) has been used in various feed evaluation systems in France (Jarrige *et al.*, 1986) and in Denmark (Kristensen and Ingvarsten, 1986). Effort to improve the systems has since then provoked a lot of other experiments and feed tables that resulted in systems of predicting VFI that have practical application in France (Jarrige *et al.*, 1986; Jarrige, 1989) and in Denmark (Kristensen and Ingvarsten, 1986; Strudsholm *et al.*, 1995). To develop these systems Jarrige *et al.*

(1986) and Kristensen and Ingvarsten (1986) used a fill unit (FU) based on several feeding trials to predict VFI. The systems took into consideration the intake capacity for energy for different categories of animals and fill value (FU) ascribed to the ingestibility of each forage. The systems considered values for forage-based diets where feed intake is assumed to be limited by the reticulo-rumen capacity. Sex, body weight, growth rate, milk yield and housing conditions were also considered (Ingvarsten *et al.*, 1992; Ingvarsten and Weisbjerg, 1993). Major weaknesses of these systems were that there was no clear distinction between physical and metabolic regulations of VFI.

The method for estimating rumen fill proposed by Madsen *et al.* (1994) has shown to reflect variations in intake, which indicates that the method can predict VFI with reasonable accuracy. The method proved to be a useful tool in understanding and predicting changes in VFI associated with changes in the rates of degradation and passage assuming physical regulation of VFI. The models proposed use of physical fill (Fill) as an estimate of rumen capacity measured using rumen pool size of NDF. Stensig *et al.* (1994b) found high correlation ($R^2 = 0.82$) between the observed VFI and the predicted VFI (Fig. 2.2). The accuracy and error of prediction is given in Table 2.8.

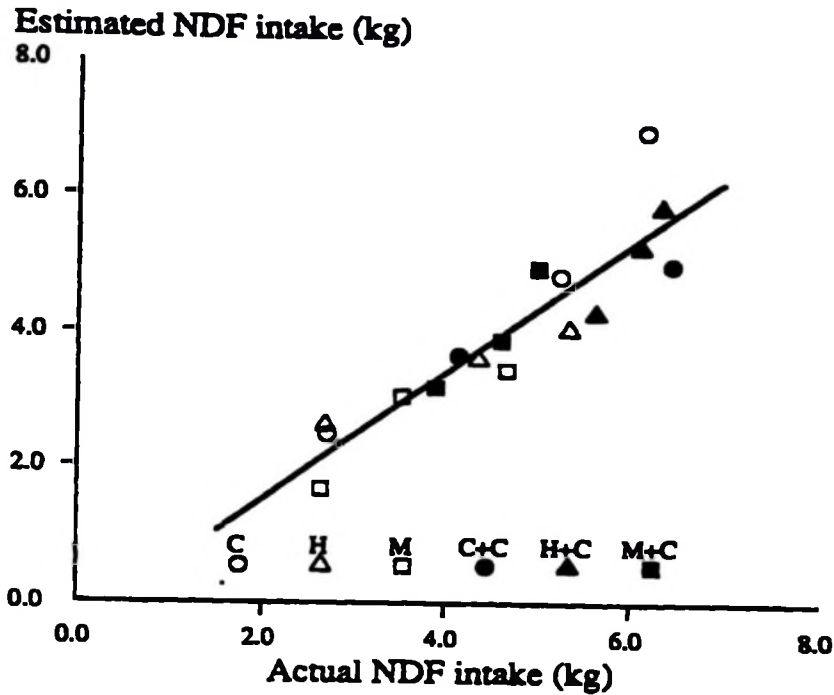


Fig. 2.2 The relationship between actual and predicted intake of NDF (Source: Stensig *et al.*, 1994b).

Table 2.8 Prediction coefficients from the general model $Y_1 = \alpha + \beta X_1$ and showing their accuracy and error of prediction from the equation $NDFI = \text{Rumen pool size/Fill and } DMI=1/\text{proportion of NDF in the feed DM multiplied by the predicted NDFI}$ (Madsen *et al.*, 1994)

Y=estimated intake (kg d ⁻¹)	X=actual intake (kg d ⁻¹)	α (SE)	β (SE)	R^2	RMSE
DM	DM	0.24 (3.60)	1.63 (0.30)	0.68	4.72
DM; cor*	DM	0.77 (1.37)	0.93 (0.11)	0.83	1.79
NDF	NDF	-0.35 (0.55)	0.94 (0.11)	0.82	0.58

Source: (Stensig *et al.*, 1994b).

*Rumen pool size corrected for microbial DM [Rumen total DM pool-((crude protein/0.5)*0.8)].

SE = standard error of estimate, R^2 = coefficient of determination, and RMSE = root mean square error.

This high relationship was attributed not only to the precision used to calculate the degradability constants by including lag time as suggested by Dhanoa (1988) and correction of the particle loss as suggested by Weisbjerg *et al.* (1990) but also because the NDF fraction is distinct from microbial and endogenous material (Stensig *et al.*, 1994b). The estimates of fill are much more robust and less dependent on an exact curve description than individual degradation curve parameters (Stensig *et al.*, 1994; Madsen *et al.*, 1994). However, the use of physical fill and rumen pool sizes to predict DMI assuming physical regulation of VFI did not take into account other factors affecting intake like metabolic regulation of VFI, palatability, different categories of animals, the interaction between feeds/diets, the animal and the environment.

While its use in practice looks promising, as it is cheap, simple and to a certain degree accurate (Table 2.8) it cannot be used as a general model to predict intake. The system can only be used where it was developed and with the animal categories developed for. The variability shown for different tropical forages for degradability characteristics (Kimambo *et al.*, 1994; Shem *et al.*, 1995; Mgheni *et al.*, 1996), rumen pool size (Kimambo *et al.*, 1996; Mgheni *et al.*, 1998) and passage rates (Shem *et al.*, 1995) and thus fill suggest that for the system to be used in practice it is necessary to have estimates of degradability characteristics, rumen pool sizes and passage rates. This may explain why the system under-estimated DMI when fill was estimated using measured degradability characteristics of forages but assumed passage rates and pool sizes (Kimambo *et al.*, 1994; Mgheni *et al.*, 1998).

2.3.4 Prediction of VFI based on models developed from regression analysis and mathematical modelling

Several attempts have been made to predict VFI using models developed from regression analysis of a range of input data (Forbes, 1977; Rook and Gill, 1990) which render them of little use in practice. The models proposed vary greatly in their design, number of factors included and parameter estimates used. Some models have been based entirely on animal characteristics (NRC, 1989; ARC, 1990), while others have placed more emphasis on feed characteristics (Kristensen and Ingvarsten, 1986; Jarrige *et al.*, 1986). The best model in terms of precision is that which is based on the most important factors that regulate VFI.

Ingvarsten (1994) suggested important factors to consider in the model of predicting VFI as shown in Table 2.9. These factors have been incorporated (Kristensen and Ingvarsten, 1986; Jarrige *et al.*, 1986; NRC, 1989; Rook and Gill, 1990) or corrected for if conditions are outside a certain range (Rayburn and Fox, 1993; Ingvarsten and Weisbjerg 1993). In addition to those given in Table 2.9, models could be corrected for mud (NRC, 1989) or corrected for silage fermentation quality (Rook *et al.*, 1990b) or corrected for the proportion of legumes in the diet (Rayburn and Fox, 1993).

Table 2.9 Important factors to consider in predicting VFI

Animal factor	Feed factor	Management, housing and environmental factors
Breed	Diet composition	Time of access to feed
Sex	Chemical composition	Frequency of feeding
Live weight	Digestibility	Separate vs complete diets
Age	Degradability profiles	Anabolic agents
Parity	Rate of passage	Food additives
Milk yield	Physical form	Minerals salts, alkaline agents
Stage of lactation	Conservation methods	Tie stalls vs loose housing
Pregnancy	Silage dry matter content	Space allowance
Previous feeding	Fermentation	Space at manger
Body condition	Palatability	Photoperiod
Fatness		Temperature

Source: Ingvarsten (1994).

This review will not attempt to give the vast amount of literature on prediction of VFI using these factors/variables, or compare their ability to predict VFI. Instead few examples will be reviewed to show how difficult and complicated prediction models can be used with accuracy under practical situations. Models of interest vary from those that use simple and multiple regressions to those employing complex systems and mathematical modelling.

2.3.4.1 Simple regression analysis models

Simple regression analysis models have been in use for many years. More complicated models were build on them as more information became available. The NRC (1989) predicted VFI in growing and finishing beef cattle as:

$$\text{DMI (kg d}^{-1}\text{)} = W^{0.75} (0.0493 \text{ NE}_M^2 - 0.0196)$$

where, DMI = dry matter intake per day, $W^{0.75}$ = metabolic body weight, NE_M = Net energy maintenance. A review by Poppi (1996) showed that intake can be predicted from digestibility and animal weight either as a constant weight ($W^{0.75}$) or individual weight ($W^{1.0}$). Although some authors (NRC, 1989) find $W^{0.75}$ to be appropriate, others argue that there is little advantage over $W^{1.0}$ and prefer to use the value ($W^{1.0}$) for simplicity. Ingvarsten (1994) noted that models assuming constant intake per kg $W^{0.75}$ may result in serious lack of fit.

2.3.4.2 Multiple regression analysis models

Prediction of VFI has also been possible through use of multiple regression analysis models. Rook and Gill (1990) used reduced ordinary least squares multiple linear regression, whereas Rook *et al.* (1990a) used principal component regression and ridge regression to described intake of grass silage in beef cattle. In an attempt to improve the models, the authors considered more variables in the model (e.g. level of concentrate allowance, silage quality and silage of good quality as a standard

forage) and produced valid prediction models of VFI but ran into problems of collinearity among the independent variables. To improve the model of Rook and Gill (1990), Rook *et al.* (1990a) used principal component and ridge regression analyses of the same data (Rook and Gill, 1990) as an alternative approach to remove the problem of collinearity. The method (principal component analyses) indicated severe collinearity among a number of variables particularly among various fermentation characteristics, between different measures of digestibility and different measures of fibre. Least squares multiple regression containing fewer variables was more effective in overcoming the problems of collinearity at the expense of maximising the R^2 . The models provided a biologically more acceptable interpretation of the independent variables than the previous models (Rook and Gill, 1990) and are likely to perform better as predictive models.

Further work to test the models of (Rook *et al.*, 1990a) using independent data (Rook *et al.*, 1990b) used stepwise least squares multiple regression analyses and reduced inputs to the model and reported a more flexible approach to prediction of VFI in practical situations. The models used feed characteristics of NDF and silage fermentation quality which made the models to have theoretical advantage but suggested further work to include animal and management factors as inputs to the model. Rook *et al.* (1990b) recommended that further work was needed to clarify the effect of factors such as breed and rearing system on intake and clarify the usefulness of various fibre measurements in intake prediction.

The new models were tested using independent data from three sites (Rook *et al.*, 1991). The models performed better than the results of (Rook *et al.*, 1990a; 1990b) but the best model obtained still gave a prediction error of proportionately 0.17 from the actual silage intake in early lactation and 0.15 in late lactation. It was concluded that there is little to be gained from further refinement of

the functional form of the model and that the construction of the number of models for specific food and management situations is preferable to the use of global models.

2.3.4.3 Mathematical modelling

The major aim of models is to give a mathematical representation of a phenomenon of interest e.g. VFI or digestibility of nutrients. In general terms, modelling addresses two broad objectives: making predictions and pursuing knowledge. Modelling also allows one to investigate mechanisms, test the consequences of assumptions and hypothesis and show where knowledge is lacking. Modelling may also be used to define hypotheses and treatments in an experimental programme and generate new data. An application of modelling is to make accurate predictions of digestion and intake for specific combinations of food and animal characteristics. Modelling the control of VFI and nutrient supply is a way of furthering our understanding of mechanisms, testing the consequences of our assumptions and of developing a mechanistic framework capable of accurate prediction of VFI.

Models can either be dynamic or static, empirical or mechanistic, stochastic or deterministic (Udén, 1998). Their basis simulates the physiological and metabolic regulation of VFI. Forbes (1977) developed empirical (input and output data), deterministic, dynamic (time dependent) models based on animal and food characteristics with promising precision. Other models developed for dairy cattle were dynamic and mechanistic (how much and how fast) and their precision was also adequate (Danfær, 1990). Their weakness is that they have only been tested on a very limited spectrum of rations and animal species and categories.

Dynamic, empirical models that take time and rates into consideration for the whole system of a dairy cow have been proposed. Forbes (1977) proposed an empirical and deterministic dynamic model in dairy cows as:

$$DMI_m = 3.55 (2.2 W)^{0.51} + DMD^{-0.46} (0.24 E_{m-p})^{0.25}$$

$$DMI_f = 10 - 5.639 (2.2 W)^{0.99} DMD^{1.53} 2.2 F^{1.01}, \text{ where,}$$

$$F = 4.0 [CW/5 - (W - CW)/3] / (CW/5)$$

DMI = the lower of DMI_m and DMI_f .

In these equations, DMI_m = dry matter (DM) intake when metabolic factors are limiting intake, DMI_f = DM intake when fill is limiting intake, W = live weight in kg, DMD = DM digestibility, E_{m-p} = chemical energy in milk and retained protein (MJ per day), F = faecal DM in kg/454 live weight, CW = post-calving weight (kg). In these models it was assumed that cows would eat to their requirements unless physical limitation intervened. The models developed here did not allow intake to change by more than 1.5 % per day. In these models an attempt to incorporate a depression in milk yield when physical limitations prevented energy requirements being met by food intake was successful only with good quality feeds and under *ad libitum* feeding. It was the opinion of the author that there is, as yet, insufficient quantitative knowledge of digestion, absorption and metabolism to construct a useful minute by minute model of events relating VFI in cattle such as those developed in rats.

A number of mathematical models describing the dynamic process in the rumen have been evaluated and proposed (Mertens, 1987; Allen and Mertens, 1988; Danfær, 1990; Huhtanen *et al.*, 1995, Danfær, 1998; Udén, 1998). Digestion is a dynamic process and is not static as most models assume. Dynamic models that simulate the physical regulation of intake and metabolic regulation are important in when dealing with a broad spectrum of rations. In feed evaluation,

mathematical models should be able to integrate scientific knowledge from different levels and disciplines of nutrition and physiology. Models that predict VFI should include chemical, digestion, and absorption of nutrients from the digestive tract accurate enough to be used the models for improvement of ration formulation in ruminants that will elicit expected production response.

It is concluded that in situations where a large body of data is available the use of regression equations and mathematical modelling is valid. However, prediction of VFI requires a more fundamental approach that involves a combination of physical, metabolic and physiological parameters in a specified environment. Thus, prediction models developed, so far, cannot be used as a general model for prediction of VFI due to lack of inclusion of all the factors that control VFI. They could, however, be adequate in the places where they were developed. It is apparent, therefore, that more input factors have to be sought and developed under specific feeding situations and defined environments.

2.4 Methods for measuring parameters used for prediction of VFI when limited by physical fill

Traditionally feed evaluation has been done based on chemical analysis and *in vivo* digestibility by sheep at maintenance level. In practice sheep digestibility is often measured by *in vitro* digestibility using rumen liquor (Tilley and Terry, 1963). These methods are suitable for estimation of potential digestibility, but pay little attention to differences in the rate of degradation (Ørskov and Ryle, 1990; Van Soest, 1994). Feed DM and N for tropical feedstuffs have been evaluated for their potential rumen digestibility and rate of degradation (Kimambo *et al.*, 1994, Shem *et al.*, 1995; Mgheni *et al.*, 1996; Tolera and Said, 1997).

Protein evaluation according to the AAT-PBV system has also been reported for tropical feeds using the nylon bag technique and the mobile bag technique (Kimambo *et al.* 1994, Mgheni *et al.*, 1994c; Mgheni *et al.*, 1996). Table 2.2 gives enough evidence to believe that tropical forages especially those from grasses and crop residues form the bulk of the forage diets and in order to be evaluated for their respective feed potential appropriate methods have to be applied. Madsen *et al.* (1997) suggested some of the methods that can be appropriate for prediction of feed intake and of energy and protein value of tropical feeds based on experience gained in Denmark. This review will focus on the methods that were used to study fibre metabolism and prediction of intake when physical fill is assumed to limit VFI of tropical forages.

2.4.1 Chemical composition

Analysis of chemical composition of feeds in terms of DM, CP and ash has been standardised by the AOAC (1990). However, for feeds with high volatile fractions (e.g. silage and fresh forages) drying in ovens at 105°C can lead to an under-estimate of DM. Even some of the NDF fractions like hemicellulose have been reported to be lost under high or low temperature treatment (Van Soest *et al.*, 1991; Van Soest, 1994). Of the chemical analyses, analysis for NDF is the most problematic. The procedure has varied markedly and the analysis is difficult to reproduce. In addition, NDF is not a nutritionally, chemically or physically uniform material (Table 2.1), which adds another dimension of complexity that makes it difficult to be standardised. Ways of improving the NDF procedure have been proposed (Van Soest *et al.*, 1991). The present and original procedures are based on extraction of a sample in neutral (pH =7) solution containing a detergent (sodium lauryl sulphate) and EDTA followed by filtration and washing with hot water and acetone. The residue recovered (NDF) is determined gravimetrically. Cellulose, hemicellulose, and cell wall bound proteins are recovered,

whereas pectins and β -glucan are dissolved although they are also CWC (Van Soest, 1994). The NDF fraction values are usually corrected for ash content.

Common problems of NDF analysis include starch and animal protein interference (Van Soest *et al.*, 1991). Using 2-ethoxyethanol facilitated removal of such interference by starch, but due to health risk 2-ethoxyethanol was replaced by triethylene-glycol. Starch removal, however, was not adequate for samples rich in starch, and hence various modifications of the original procedure have been proposed. Stensig *et al.* (1994a) used overnight incubation with a bacteria α -amylase at 38°C. In this procedure there is a risk that the bacterial amylase may be contaminated with enzymes that might degrade the fibre constituents as well. Undersander *et al.* (1993) proposed another procedure that was used by Stensig *et al.* (1998b). This procedure uses heat stable α -amylase of which one aliquot is added during refluxing and another during filtration. This method is less time consuming than overnight incubation (Stensig, 1994a). The method of overnight incubation is still used, but cannot be used for routine analysis before further evaluation.

The use of sodium sulphite to facilitate removal of contamination of proteins was proposed in NDF analysis (Van Soest *et al.*, 1991). Sulphite cleaves disulphide bonds between peptides, and thus dissolves many cross-linked proteins (Van Soest *et al.*, 1991). This is important in particular for samples that contain keratinized protein of animal origin like animal products, or hair contamination. By not including sodium sulphite in the NDF procedure can result in a markedly overestimation of the CWC of animal by-products and meat scraps (Mertens, 1995). Use of sulphite has been recommended to be optional (Van Soest *et al.*, 1991) because sulphite attacks lignin. This implies that sulphite should only be used for particular feedstuffs containing animal by-products. Mertens

(1995) showed evidence that NDF content of feeds that have been heated or cooked may be markedly over-estimated if sulphite is not used in the procedure.

2.4.2 Measurement of apparent total tract digestibility and faecal output

The digestion of feeds has either been measured by direct methods *in vivo* or *in vitro* or indirectly by use of markers (Udén *et al.*, 1980). Faecal output, however, is best measured by total collection. Weisbjerg *et al.* (1990) discussed in detail the problems associated with the use of sheep fed at maintenance level. Problems associated with *in vitro* digestibility using rumen liquor to measure digestibility were also discussed. These methods are suitable for estimating the extent to which feeds are digested but do not show the rate at which different feeds are degraded. The methods are normally measured at a restricted level of feeding while in practice the animals are fed at various levels of intended production. In contrast, Van Soest (1994) noted that balance of matter lost in the passage through the digestive tract is the most reproducible measurement for a given feedstuff. Faeces contain not only the undigested diet but also metabolic products including bacteria and endogenous wastes from animal metabolism. Consequently, apparent digestibility can be considered to be the balance of the feed less the faeces, but true digestibility is the balance between the diet escaping digestion and arriving in the faeces exclusive of metabolic products. It is evident that the coefficient of true digestibility is always higher than that of apparent digestibility if there is a metabolic loss in faeces. Van Soest (1994) noted that in total diets, protein and lipids always have a faecal metabolic loss. Fibre and carbohydrates have no metabolic faecal loss and consequently apparent digestibility is assumed equal to true digestibility.

2.4.3 *In sacco (in situ) methods*

In sacco (in situ) degradability using the nylon bag technique gives both the extent and rate of digestion. The method for estimating the degradation constants by Ørskov and McDonald (1979) is well accepted. The method can even be more accurate when different shortcomings in the procedure and the model are corrected. Weisbjerg *et al.* (1990) showed that the values of the degradation profiles are over-estimated if they are not corrected for particle losses. Dhanoa (1988) also suggested that lag time has an effect on straightening out the curvature thus under-estimating the rate of degradation and over-estimating the asymptote or even giving no estimate at all.

Rate of degradation and potential rumen digestibility can be estimated using the nylon bag technique as described by Stensig *et al.* (1994a). This is based on the mathematical description of the curves from data obtained when samples are incubated in the rumen for various time intervals. The *in sacco* method is more suitable for estimation of rate of degradation than *in vitro* methods because rumen microbes need to adapt to the new conditions (*in vitro* tube). Therefore, the *in vitro* measures tend to under-estimate microbial degradation at short incubation times (Stensig *et al.*, 1994a). Madsen *et al.* (1997) noted that interpretation of the data from *in situ* methods should, however, be made with care because parameter estimates obtained from the degradation model of Ørskov and McDonald (1979) are highly correlated. For example, the degradation rate constant gives the part of the potential degradable fraction that is degradable per unit of time. It can, therefore, not be estimated independently of the size of the potentially degradable fraction itself. When degradation data for NDF are fitted by a single exponential model (Ørskov and McDonald, 1979), the presence of a lag time at the beginning of degradation has great influence on the estimated *a*, *b* and *c* parameters. Stensig *et al.* (1994a) reported a very high lag time (14 h) in maize silage. If lag time exists and is not taken into account in the model, the asymptote is over-estimated and the rate of degradation is under-

estimated. Dhanoa (1988) for the same reasons recommended simultaneous estimation of the lag and degradation parameters in order to obtain objective and more satisfactory estimates of the parameters. Madsen *et al.* (1997) preferred the summation model (Kristensen *et al.*, 1982) which always fits the data.

2.4.4. Studies on digestion and passage kinetics of fibre

Determination of digestion and passage rates of fibre have been studied using different methods. Commonly used indirect methods are the *in situ (in sacco)* procedure (Stensig *et al.*, 1994a) for determination of ruminal digestibility and digestion rate of NDF and marker concentration sampled from the duodenum or faeces after a single dose of labelled feed particles e.g. with chromium (Udén *et al.*, 1980). The rumen evacuation technique in combination with measurements from the daily outflow from the rumen (Robinson *et al.*, 1987) is the only method by which digestion and passage rates can be measured directly *in vivo*. Although all these methods have some weaknesses, in general they give improved understanding of the digestive process and an insight of the constraints of fibre digestion.

2.4.4.1 Rumen evacuation technique

The rumen evacuation technique (RET) has been used to study rumen pool sizes of different feed constituents and microbial yield (Robinson *et al.*, 1987; Huhtanen and Jaakkola, 1993; Stensig *et al.*, 1994a; Dado and Allen, 1995; Stensig and Robinson, 1997; Stensig *et al.*, 1998b; Weisbjerg *et al.*, 1998). Data obtained from rumen evacuation methods combined with measures of outflow from the rumen have been used to describe quantitatively digestion and passage rate characteristics of NDF which is an important parameter in models of physical fill for prediction of VFI. Extrapolation of results from RET can be difficult. Robinson *et al.* (1987) using RET concluded that extrapolation

of results from RET to study kinetics of fibre digestion and passage should be done with caution because of differences in feeding level that occur during early lactation, between parity and peak intake when intake is steadily increasing. Merten (1993) suggested that RET is a useful tool to study the quantitative expression of the kinetics of digestion and passage rate of forage NDF and their response to changes in NDF composition and intake which are important parameters for prediction of VFI under different feeding situations. Values obtained from RET for the total ration can explain little about the individual feeds if the ration is a mixture of several feeds containing NDF. Therefore, to avoid confounding effects, Stensig and Robinson (1997) used fibre free concentrate to study the influence of level of feeding on fibre digestion and passage kinetics and recommended the method to be used to study fibre kinetics in high producing dairy cows.

Calculation of digestion and passage rates using the RET, however, has certain limitations:

- It is assumed that the amount of fibre digested or passed per unit time is a constant fraction of the total rumen fibre, as it assumes a simple one-compartment model (Fig.2.3) with first-order kinetics (Allen and Mertens, 1988).
- The estimated rate parameters reflect the entire dietary fraction. The method cannot be used for individual feeds in the diet with more than one fibre sources. The method requires rumen, duodenal, and ileum cannulated animals and, therefore, is restricted to a limited number of animals. In this connection, Robinson *et al.* (1987) suggested a method where the RET can only require rumen cannulated animals.

Several opinions and evaluations to overcome the above limitations have been studied. Both the size (Huhtanen *et al.*, 1995) and the specific gravity of particles (Shaver *et al.*, 1988) affect the rate of passage. Slower passage rates of digestible than indigestible fibre (Tamminga *et al.*,

1989; Huhtanen and Khalili, 1991) are also an indication of selective retention of feed particles in the rumen. Digesta kinetics parameters derived from marker studies using models with time dependency have shown two predominant compartments (Stensig *et al.*, 1998b). The first compartment probably represents the release from the non-escapable (one-compartment) to the escapable pool (two-compartments). The second represents passage from the escapable pool (Huhtanen *et al.*, 1995) to the lower gut. Selective retention of potentially digestible fibre is necessary to maximise ruminal fibre digestion. A hypothetical diagrammatic presentations of fibre kinetics assuming one-compartment model (one-pool model) and two-compartment (two-pools model) are illustrated in Fig. 2.3 and Fig. 2.4 respectively, where k_d is the digestion rate and k_p , k_{p1} and k_{p2} are passage rates.

Stensig *et al.* (1998b) demonstrated rumen digestion characteristics of NDF by fitting various one and two compartment models to the Yb concentrations in duodenal digesta. It was assumed that k_{p1} and k_{p2} were similar for indigestible and digestible fractions. Though there is some evidence that passage rates differ between both fractions, results are not consistent. Tamminga *et al.* (1989) found a higher passage rate for rumen indigestible NDF (INDF) than potentially rumen digestible NDF (DNDF) with diets of grass hay and concentrates. Studies by Stensig and Robinson (1997) found a higher passage rate for DNDF than for INDF for alfalfa silage, whereas similar passage rates of DNDF and INDF were observed for timothy silage. In practice the potentially degradable and truly undegradable fractions are not separate entities in the rumen, but are combined in particles. So it seems reasonable to assume that these fractions are reduced in size and pass to the omasum at a comparable rate. In some plants, however, INDF/DNDF ratios could differ for different fractions (Bruining *et al.*, 1998).

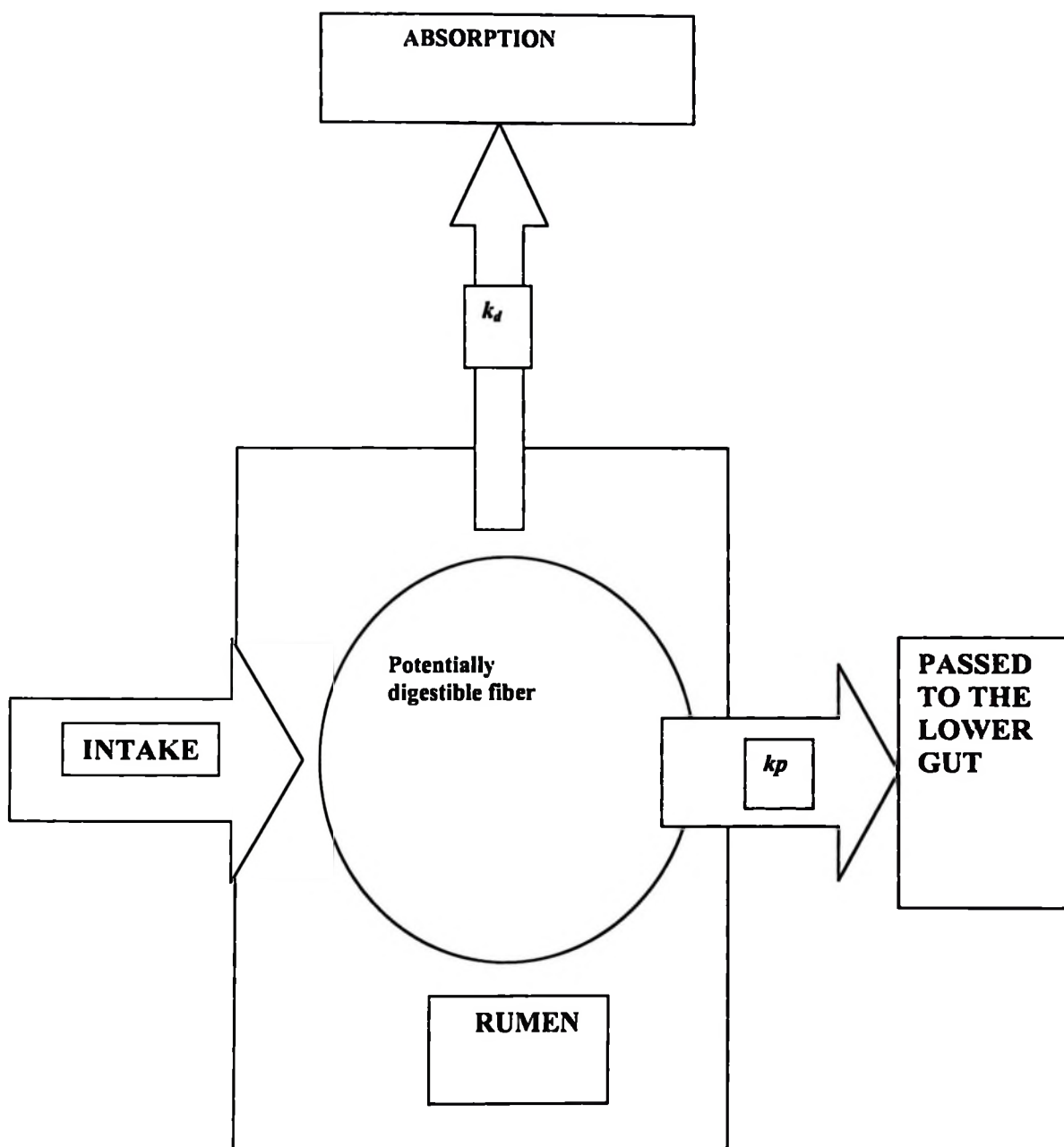


Fig.2.3 Hypothetical diagrammatic presentation of a simple model of fibre disappearance from the rumen, where k_d is the fractional rate of digestion and k_p is the fractional rate of passage

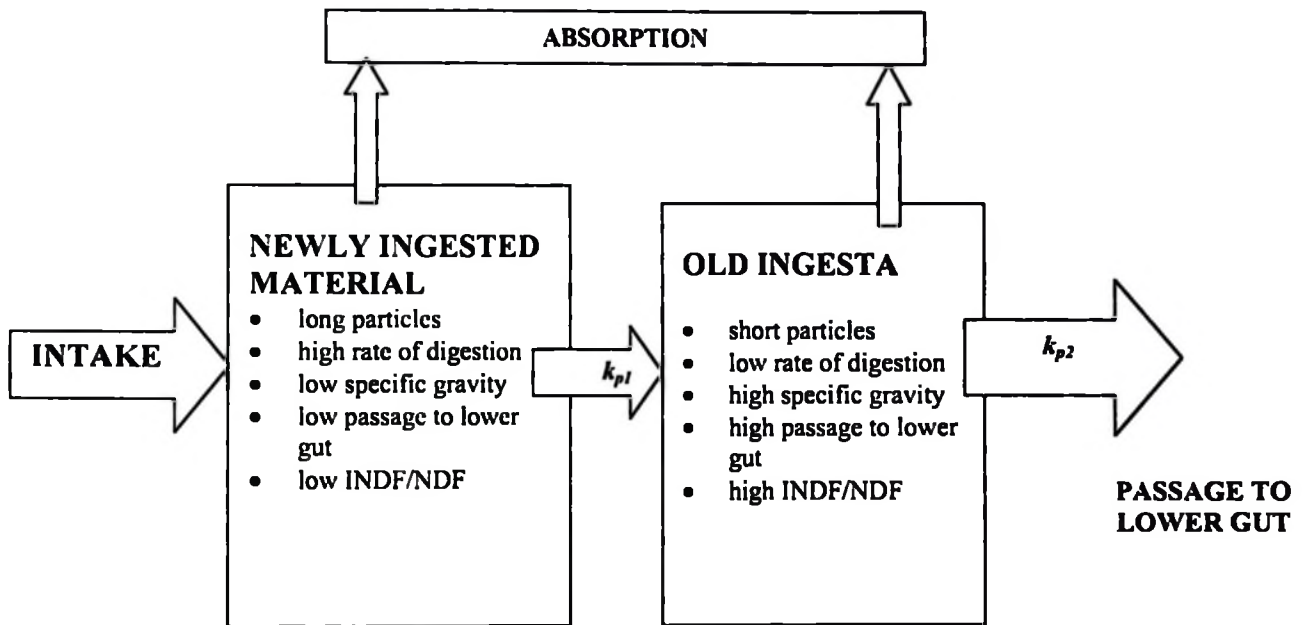


Fig. 2.4 Hypothetical diagrammatic presentation of feed intake, particle size reduction and rate of digestion and passage assuming a two pool model

Stensig *et al.* (1998b) reported that the RET is the most accurate method for estimation of mean rumen retention time (MRRT) and, therefore, can be used to calibrate more sophisticated passage models. Bruining *et al.* (1998) used a four pool model of the rumen (described as large truly undegradable, large potentially degradable, small truly undegradable and small potentially degradable particles) to account for changes in the rumen pools by differential equations and concluded that changes in the total rumen pools (as observed in reality) and simultaneous changes could not be tested. Huhtanen (1998) suggested that, although RET is very high labour intensive it is a useful tool for measuring passage rate because the problems related to microbial environment in both *in vitro* and *in situ* procedures can be avoided.

Another limitation of the RET is that rates cannot be related to individual feeds in the diets with more than one fibre source (Stensig *et al.* 1998b; Huhtanen, 1998). Measure of INDF to express the DNDF and the INDF has also been reported to be a problem when RET is used because of inaccurate recovery of the INDF postruminally (Stensig *et al.*, 1998b).

Compared to marker techniques, rate of passage of NDF calculated as rumen outflow divided by rumen pool size (Stensig *et al.*, 1994a) has the advantage of being well defined in terms of the digestion as a dynamic process (Huhtanen, 1998). Stensig *et al.* (1994a) suggested that before RET is used as a routine analysis, it is important to evaluate and reduce the potential source of errors like sampling of the rumen content, evacuation procedure and optimal evacuation time to reduce diurnal variation in the pool size.

2.4.4.2 Markers technique

Several internal and external markers have been used to estimate digestibility and passage rates (Udén *et al.*, 1980; Stensig *et al.*, 1994a; Huhtanen and Kukkonen, 1995). Markers have also been used to measure digestion where direct measurements are inconvenient or difficult. However, the requirements for the type of marker used to measure passage rate in gastrointestinal tracts are more critical than for balanced trials. There are several criteria for an ideal marker, but no single marker fulfils all of them. Udén *et al.* (1980) noted that in measuring passage rate of particles and liquid, the marker should not separate from the respective labelled fractions. This is assuming that the marker is in equilibrium with the pool of the fraction that it is intended to label. While no individual marker satisfies these conditions, particulate markers are generally less satisfactory than liquid ones (Udén *et al.*, 1980; Ramanzin *et al.*, 1991; Stensig *et al.*, 1994a). The authors further noted that particulate markers may have the added problem of migrating to the particles not originally labelled.

The digestibility of feed particles mordanted with chromium is markedly reduced and specific gravity is increased depending on the quantity of chromium attached (Ramanzin *et al.*, 1991). Labelling with ytterbium affect digestion less than chromium (Stensig *et al.*, 1994a), but on the other hand it has been criticised for the potential risk of migration and for uneven distribution between particle size in forage cell walls (Ramanzin *et al.*, 1991). Despite these pitfalls, Udén *et al.* (1980) showed that chromium-mordanted fibre is more stable as particulate marker than cerium-mordanted fibre dosed in the rumen and recovered in faeces. Similar findings have also been reported (Huhtanen *et al.*, 1994; Stensig *et al.*, 1994a; Huhtanen and Kukkonen, 1995).

Alternative to external markers are the internal markers contained in feeds. Recoverable indigestible feed fractions can be used as internal markers. The use of rumen pool sizes and faecal

output of total-NDF; digestible NDF (DNDF) and indigestible NDF (INDF) have been used to derive digestion and passage rates (Allen and Mertens, 1988; Robinson *et al.*, 1987; Dado and Allen, 1995; Stensig and Robinson, 1997; Stensig *et al.*, 1998b). Although there has been no standard days used for *in sacco* long incubation to fractionate the CWC into total NDF, DNDF and INDF, Stensig *et al.* (1998b) used 10 days, whereas, Robinson *et al.* (1987) used 30 days. The INDF obtained from the feed, rumen contents and faeces have been used to calculate the DNDF that describe biological availability of fibre fractions. The fibre fractions have been used to derive the rate of intake, passage rate and rate of digestion (Robinson *et al.* 1987; Stensig *et al.*, 1998b, Weisbjerg *et al.*, 1998) with satisfactory estimates of passage rates (Huhtanen and Kukkonen, 1995). This is because the principles and methods used have been derived from intake and flow data, whereas use of heavy metals like chromium change the chemical and physical properties of the particles with which it is mordanted.

2.4.4.3 Use of mathematical models

Generally, ruminal NDF digestibility is determined as the ratio: [(intake-duodenal flow)/intake]. It can also be calculated from the kinetics parameters using mathematical models (Huhtanen *et al.*, 1995). Ruminal digestibility of fibre estimated from digestion and passage kinetics utilising mathematical models have been proposed using similar assumptions of simple one-compartment models (Allen and Mertens, 1988; Stensig *et al.*, 1994a; Huhtanen *et al.*, 1995). Allen and Mertens (1988) derived ruminal NDF digestibility (RNDFD) assuming that mass digested or passed per unit of time is proportional to the mass in the rumen (first order kinetics) and that inflow and pool sizes of fibre are constant (steady state) is then derived using the equation:

$$RNDFD = \frac{k_d}{k_d + k_p}$$

where, k_d is the digestion rate and k_p is the passage rate. Thus ruminal digestibility can be determined as the fractional rate constant (k_d) divided by total fractional rate constant of disappearance from the rumen ($k_d + k_p$). Using degradation parameters Stensig *et al.* (1994a) incorporated a discrete lag time (t_0), a water soluble fraction (a), which is near zero because NDF is not water soluble and the water insoluble but potentially digestible NDF fraction (b) and estimated the ruminal NDF digestibility (RNDFD) as follows:

$$RNDFD = a + \frac{bk_d}{k_d + k_p} e^{-k_p t_0}$$

The two equations above assumed one-compartment models with age-independency using marker technique, and age-dependency using rumen evacuation technique (Allen and Mertens, 1988; Huhtanen *et al.*, 1995; Stensig *et al.*, 1998b). This approach has some limitation as discussed previously, but on the other hand it is simple and, therefore, easy to understand but results can be difficult to interpret.

Stensig *et al.* (1994a) using the two models (Allen and Mertens, 1988) reported that values of RNDFD calculated were almost equal (grass cubes 0.66 vs 0.656; hay 0.653 vs 0.639 and maize silage 0.380 vs 0.384) using passage rates estimated in the same experiment. At low rates of passage (long mean rumen retention time) differences in RNDFD are mainly caused by the tendency of the model of Ørskov and McDonald (1979) to over-estimate the asymptote when lag time is present (Stensig *et al.*, 1994a). On a study to test how RNDFD was related to *in vivo*.

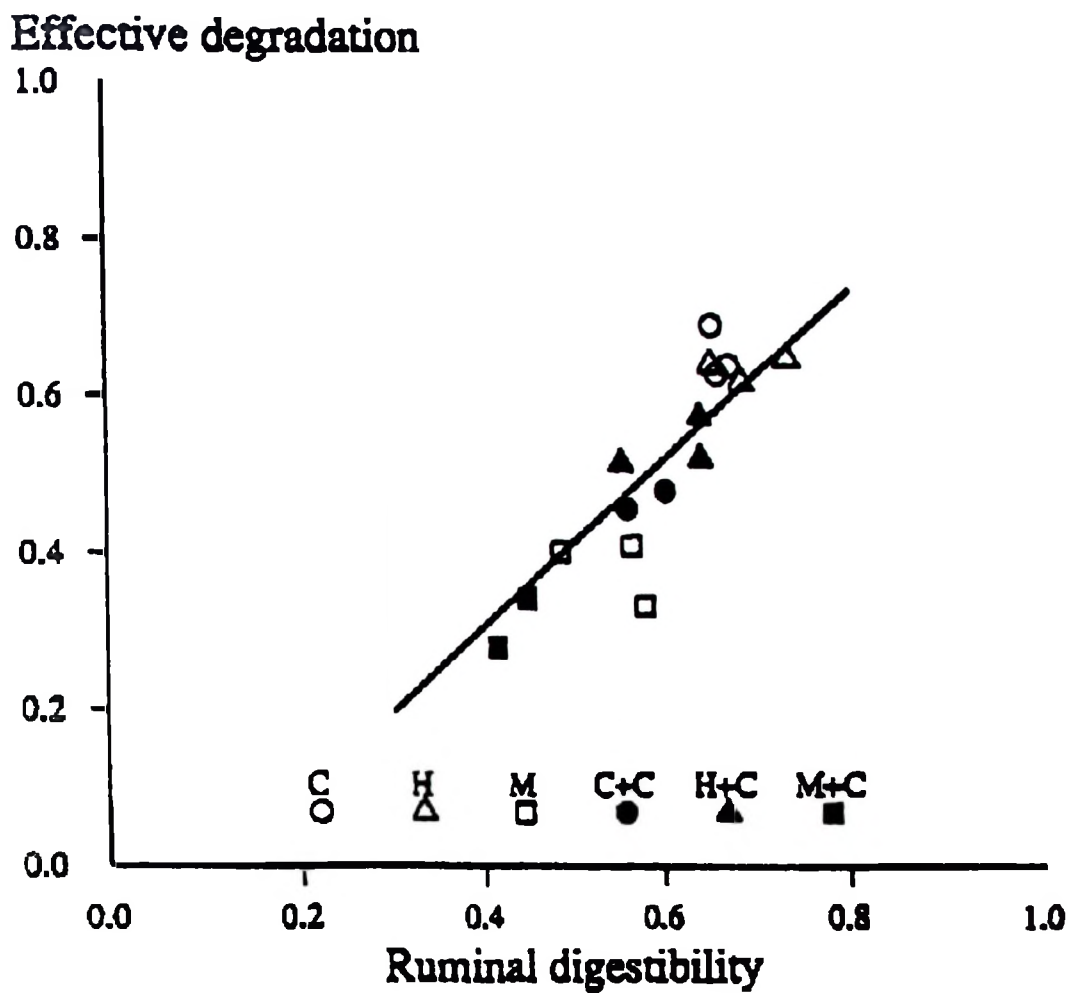


Fig. 2.5 Relationship between ruminal digestibility (feed-ileum and effective degradability (ED) of NDF (Source: Stensig *et al.*, 1994a)

digestibility of NDF Stensig *et al.* (1994a) observed a linear relationship (Fig.2.5) across feedstuffs which were highly significant ($R^2 = 0.77$) but regression within roughages indicated some discrepancy.

Digestion is a time-dependent process. Mathematical models that include digestible and indigestible fibre fractions assuming one-compartment models are limited by the assumption that the probability of particles escaping from the rumen is independent of their age and size as discussed previously. Such discrepancies provoked a lot of experiments and mathematical models to improve the prediction in terms that can explain better the digestion process of NDF under different feeding level and allowed prediction of nutritive values of forages in diets with different supplements.

Based on data obtained from markers and RET, models that assumed two-compartments (Allen and Mertens, 1988; Huhtanen *et al.*, 1995) and where discrete lag time was incorporated (Stensig *et al.*, 1998b) were developed to predict ruminal digestibility of NDF (RNDFD) as:

$$RNDFD = a + \frac{bk_d}{k_{p2} - k_{p1}} \left(\frac{k_{p2}}{k_{p1} + k_d} e^{-k_{p1}t_0} - \frac{k_{p1}}{k_{p2} + k_d} e^{-k_{p2}t_0} \right)$$

..... For $k_{p1} \neq k_{p2}$

In this model it is assumed that k_{p1} is the passage rate from the rumen non-escapable (first compartment) to the escapable pool (second compartment) and k_{p2} is the age-independent passage rate from the second compartment. The results obtained from the derived passage and digestion kinetics improved the fit for marker excretion curves (Stensig *et al.*, 1998b) and gave ruminal digestibility of NDF that were close and more comparable to total tract *in vivo*

digestibility. Similar findings were derived when hind gut digestion was taken into account (Huhtanen *et al.*, 1995).

2.5 General conclusion from the literature reviewed

- The most important factor limiting feed intake in ruminants is the physical fill of indigestible feed residue in the rumen and the hypothesis holds true in tropical forages where the fibre fraction is more than 70 % (Table 2.2).
- Evidence to support this hypothesis has been tested experimentally elsewhere and resulted in feed evaluation systems describing the physical fill of feeds viz: Danish Fill System (Kristensen and Ingvarsen, 1986) and the French Fill System (Jarrige *et al.*, 1986).
- Parameters mostly accounted for include description of feeds in terms of physical fill (degradability characteristics and passage rate), digestibility coefficients, energy concentration, physical form and other quality indicators in specific forages like silage (DM and fermentation quality).
- Animal factors influencing VFI have been used to describe differences obtained in intake in terms of body weight, sex, breed, milk yield, growth rate, gestation, parity and stage of lactation and fatness (Jarrige, 1989; Ingvarsen and Weisbjerg, 1993; Rayburn and Fox, 1993) and corrections made to improve the feeding systems in France, Denmark and United States of America (The Cornell System).
- In some studies metabolic and physical regulations of VFI were included in the models of prediction of intake as described by Forbes (1977) and were found to describe the response in feed intake with more biological explanation. This set the basis for mechanistic and dynamic models. More complex models that described feed characteristics were developed in beef cattle (Rook *et al.*, 1990b) based on silage quality. In addition to level of concentrate inclusion in the diet, Rook *et al.* (1991) developed

models in dairy cattle with prediction error of ± 0.17 in early lactation and $0.15 \pm$ in late lactation. The models form the basis for ARC Feed Evaluation System.

- In many studies VFI has been measured and predicted using only a few types of feeds and few animals. Small numbers of animals are the source of error in models for estimating intake.
- Models developed are difficult to extrapolate outside the conditions in which measurements were made because interactions between the environment, feeds and animals should be expected and have not been taken into account in most models.
- Some models proposed for prediction of VFI are too complex to be used in practice. It is, therefore, important to choose the most important factor to include in the model taking into account the accuracy of individual feed analysis and their costs.
- The review showed inadequate research and understanding of the physiological mechanisms involved in regulation of VFI.
- It was also a general agreement that analytical methods and procedures used to derive the variables for prediction of intake should be accurate enough to give a reasonable relationship when challenged to *in vivo* data.
- Flexible models that allow incorporation of new variables found to be necessary to include in models of prediction of intake are preferred.
- Despite the great amount of work done on developing models for prediction of intake the greatest problem to overcome is and will be to find a sufficient general model or system of predicting intake.

This work was, therefore, undertaken to develop a cheap and practical system of predicting how much forage the animal can consume when fed tropical forages *ad libitum* and describe its limitations in feed evaluation.

3 MATERIALS AND METHODS

3.1 Objectives of the study and experimental design

Two experiments were conducted simultaneously to estimate the maximum intake capacity and physical fill when tropical forages were fed to mature non pregnant cross-bred heifers kept under zero-grazing systems. The objectives were to describe tropical feeds in terms of their rumen degradable characteristics, rumen pool size and passage rate in order to estimate the physical fill of tropical forages. The study was to test the hypothesis that in the tropics, where ruminants are fed forages of high fibre content and low digestibility, the physical fill must be important in regulation of feed intake. The parameters were used to predict voluntary intake and describe the variations and possible sources of error for each forage. To achieve these objectives five forages were studied by feeding them either as a sole diet with only mineral and vitamin supplementation (Experiment 1) or the forages were supplemented with fishmeal (FM) and urea (Experiment 2). This was to ensure that nitrogen (N) was not limiting maximum intake capacity as may be the case in experiment 1.

The forage diets in experiment 1 were:

Diet 1 = *Brachiaria brizantha* hay (BH) + minerals and vitamins (BH)

Diet 2 = Maize silage (MS) + minerals and vitamins (MS)

Diet 3 = Lucerne hay (LH) + minerals and vitamins (LH)

Diet 4 = Lucerne (20%) and grass mixture hay (LGH) + minerals and vitamins (LGH)

Diet 5 = Urea-treated rice straw (UTRS) + minerals and vitamins (UTRS)

In experiment 2 the forage diets were:

Diet 1 = *Brachiaria brizantha* hay + minerals and vitamins (UNBH)

Diet 2 = *Brachiaria brizantha* hay + minerals and vitamins + urea + FM (SBH)

Diet 3 = Maize silage + minerals and vitamins + urea + FM (SMS)

Diet 4 = Lucerne hay + minerals and vitamins + urea + FM (SLH)

Diet 5 = Urea-treated rice straw + minerals and vitamins + urea + FM (SUTRS)

The experimental design was a 5 x 5 Latin Square in both experiments. The standard method was randomly re-arranged (Table 3.1) to reduce carry-over effect of any forage into the succeeding period.

Table 3.1 Arrangement of the two 5 x 5 Latin Squares in experiment 1 and 2

Period	<i>Animal</i>					<i>Animal</i>				
	1	2	3	4	5	6	7	8	9	10
1	UTRS	BH	LH	MS	LGH	SUTRS	UNBH	SBH	SLH	SMS
2	MS	LGH	UTRS	BH	LH	SLH	SMS	SUTRS	UNBH	SBH
3	LH	MS	LGH	UTRS	BH	SBH	SLH	SMS	SUTRS	UNBH
4	LHG	UTRS	BH	LH	MS	SMS	SUTRS	UNBH	SBH	SLH
5	BH	LH	MS	LGH	UTRS	UNBH	SBH	SLH	SMS	SUTRS

Experiment 1 *Experiment 2*

3.2 Materials

3.2.1 Animals and their management

Ten (10) mature non-pregnant dairy heifers about 3 years old were rumen fistulated by a veterinary surgeon, from the Department of Veterinary Surgery, Obstetrics and Reproduction, Faculty of Veterinary Medicine, Sokoine University of Agriculture (SUA). After 10 days the animals were fitted with large, 10 cm internal diameter, flexible rumen cannula (Bar Diamond Inc, Idaho, USA) in the dorsal rumen sac. The animals were used for the experiments one year after they were fistulated. They were randomly allocated into two experiments of five animals each. The animals were kept in individual feeding stalls fitted with water measuring devices and automatic drinkers.

3.2.2 Forage: Processing, physical form, chemical and agronomic description

Five (5) forages [*Brachiaria brizantha* hay (BH), Maize (*Zea mays*) silage (MS), Lucerne (*Medicago sativa*) hay (LH), Lucerne and grass hay (LGH) and urea-treated (50 g kg⁻¹) rice straw (UTRS)] were used. To avoid the confounding of the results, all forages were used in a preserved form. Their preservation methods, processing, physical form, chemical and agronomic description is given below.

***Brachiaria brizantha* hay (BH):**

Brachiaria brizantha, also known as signal grass is a coarse, broad-leaved rhizomatous perennial grass widely grown naturally in most soils in the tropics and requires moderate rainfall. The grass was cut from an established pasture at Magadu Dairy Farm (DASP-SUA), Morogoro Region. Weeding was done once and N fertiliser (250 kg ha⁻¹) was applied during the vegetative stage. Although N fertiliser was applied, the grasses appeared a little stunted, with some yellow patches and not uniform in growth due to inadequate rainfall during that year (1996). The forage was harvested at blooming stage using a reciprocating mower. The grass was

left to dry for 5 days and turning was done on the 4th and 5th day then baled. The bales were stored in a roofed but open and raised wooden floor. Hay was used after one year. Prior to the commencement of the experiments random samples of bales was taken by taking at random one bale out of ten bales and proceeded until all bales stored were sampled. The bales were opened and random samples were collected, oven dried (at 60°C) to constant weight and processed for subsequent analyses. Analysis of CP was 60.2 g kg⁻¹ DM. During feeding the hay was chopped 10-15 cm by a big knife as the animals were found to select for the leaves since feeding was *ad libitum*.

Maize (*Zea mays*) silage (MS)

Maize (var. STAHA) was cultivated at Magadu Dairy Farm (DASP-SUA) Morogoro Region. The crop was spaced at 75 x 30 cm, weeded once and N fertiliser (250 kg ha⁻¹) was applied when maize had grown about knee height. Whole maize crop was cut about 10-15 cm above the ground at the milk stage. The sampling of maize for separation of different plant fractions was done during harvesting for evaluation of the silage quality. Sampling was done by taking randomly 10 plants from each trailer load harvested as brought from the field and weighed. The maize plant botanical fractions were separated into stem + leafsheath + panicles (SLSP), cobs, green and dead leaves and weighed. The proportion of the maize plant botanical fractions (% of the total plant by weight) was 55, 32, 12, and 1 % for SLSP, cobs and green and dead leaves respectively. The whole maize plant materials were chopped about 2-4 cm length and put direct into a concrete square silo. The material was compacted manually. The silo was covered with polythene sheet (gauge 500) on top of which soft boards and concrete blocks were randomly placed for safe coverage. When opened (after one year) random samples were collected using an auger, room dried (in a wire mesh trays of 1.0 x 1.5 m). The pH of the maize silage was 4.26, whilst volatile fatty acids (VFA) and lactic acid concentrations (g kg⁻¹ DM) were 0.72, 0, 0.36 and 8.76 for acetate, propionate, butyrate and lactate respectively. The NH₃-N of the maize

silage (% of the total N) was 0.4 % and CP was 61.2 g kg⁻¹ DM and water-soluble carbohydrates were 26.1 g kg⁻¹ DM making the overall quality of the MS to be moderate (medium). The MS was made at the end of June 1996 and opened for use at the beginning of June 1997. During opening, mouldy and slightly burnt MS was observed on the sides of the silo. Hence during feeding the MS was collected straight from the silo (every feeding time) selectively, avoiding the spoiled portions on the sides and fed in the same physical form. The rest of the silage remained covered throughout the experimental periods.

Lucerne (*Medicago sativa*) hay (LH)

It is a deep-rooted perennial herb with a thick trunk root system grown in both temperate and tropical environments. Lucerne also known as alfalfa was grown at Kahe NAFCO Farm–Moshi, Kilimanjaro Region. The hay was made from a re-growth during the dry season under irrigation and, therefore, was easy to control the stage of cut. It was weeded several times to obtain pure LH. It was cut using a reciprocating mower, when 50 % of Lucerne had flowered, and left in the field to dry for 4 days then baled. Storage was similar to that of BH. The CP content analysed from samples collected from bales taken at random as in BH gave a CP of 177.9 g kg⁻¹ DM. During feeding the hay was chopped to about 10-15 cm by a big knife as the animals were found to select for the leaves since feeding was ad libitum. However, it was difficult to control losses of leaves in LH during handling.

Lucerne and grass hay (LGH)

This was grown and cut under similar conditions as Lucerne on the same Farm but not weeded. The forage was cut when 50 % of the proportion of the Lucerne has flowered. Cutting, baling, storage and sampling were done in a similar way as for LH and BH. The CP content of the LGH was 150.5 g kg⁻¹ DM. The proportion of Lucerne in the LGH was 20 %, whereas 50 %

composed of different grasses, predominantly *Digitaria* sp. and the rest were weeds. Feeding was done without chopping, as the animals did not show any tendency for selective feeding.

Urea-treated rice straw (UTRS)

Rice straw (var. SUPA) was collected from Dakawa Rice (NAFCO) Farm situated 40 km north-west of Morogoro town (Morogoro Region). The paddy was harvested by a combine harvester and the straw was baled immediately after the grain harvest. Storage was similar to that of BH, LH and LGH. Prior to the beginning of each experimental period the straw was treated with 50 g kg⁻¹ DM of urea in 600 ml of water kg⁻¹ DM straw. The UTRS material was covered with polythene sheet (gauge 500) and stored in a concrete silo for three weeks. Urea-treatment and feeding was without chopping.

3.3 Methods

Two experiments were carried out simultaneously to measure voluntary feed intake (VFI) and rumen fibre metabolism with or without fishmeal (FM) and urea supplementation.

3.3.1 Measure of VFI (Experiments 1 and 2)

In experiment 1 (expt.1), five rumen fistulated animals were fed five forage-based diets with only mineral and vitamin supplementation for five periods. The experimental periods lasted for 30 days including 14 days preliminary periods. The animals were weighed at the beginning of the experiment (ILBW) and at the end of each period (FLBW). Chopping of the feeds was carried out to some forages as described before to minimise selection but not too fine to affect its physical form. The animals were fed individually *ad libitum*. Feeding was adjusted everyday to be 10-15 % in excess of the *ad libitum* intake using the previous day level of intake. Fresh feeds were provided twice per day at 0900 and 1500 h. All feeds and orts were weighed daily,

sampled, and prepared for subsequent analyses. The dry matter (DM) was determined everyday in both feeds and orts.

In experiment 2 (expt.2) forages were supplemented with 200 g of FM, a true protein, and urea 20 g/100 kg live body weight as a non protein N. This was to be sure that N was not limiting VFI as would have been the case in expt.1. In this experiment, one forage (LGH) was omitted and instead BH was fed without supplementation to form a standard forage that was used to adjust animal differences that would be expected in expts.1 and 2. This made it possible to compare expts.1 and 2 to study the effect of FM and urea supplementation on major variables measured. All the procedures and parameters measured in expt.2 were exactly similar to expt.1.

In expts.1 and 2 minerals and vitamins (See their composition in Table 3.2) were provided at 20 g d⁻¹ of minerals (MACLIK SUPER) plus 20 g d⁻¹ of a mineral and vitamin premix (MINOVIT SUPER) for optimum microbial activity (ARC, 1990). Fresh and clean water was provided from the automatic drinkers all the time and water intake was recorded using water measuring devices (water meters). The ambient temperature and humidity were recorded daily from the Meteorological Station at SUA campus situated near and opposite the experimental site to the North and the values are shown in Appendix.1 and 2.

3.3.2 Faecal output

Faecal output was measured for seven days in both experiments. The faeces were collected by standing behind the animal all day (24 h) and faeces collected immediately when or after the animal is or has defecated. This was assuming that the faeces were reasonably dry and urine will drain through the slope and disappeared as soon as the animal has urinated. Voided faeces were collected in a bucket of known weight and thoroughly mixed from time to time and covered to prevent any losses. Each morning all the faeces voided were weighed and recorded. The faeces

Table 3.2 Composition of the vitamins and minerals (MINOVIT SUPER, PHARMVITA and MACLIK SUPER)

Ingredient	Composition per 1000 g ¹		MACLIK SUPER	
	MINOVIT SUPER	PHARMVITA ²	Element	Elemental %
Vitamin A (IU)	7 500 000	5 000 000	NaCl	27.00
Vitamin D3 (IU)	1 500 000	1 000 000	Ca	18.51
Vitamin B1 (mg)	1 000	600	P	11.00
Vitamin B2 (mg)	2 750	2 500	Mg	3.00
Vitamin B12 (mg)	5	7.5	Fe	0.50
Vitamin C	-	1 250	Cu	0.16
D-Calcium pantothenate (mg)	5 000	5 000	Mn	0.40
Vitamin E (mg)/(IU)	2 500	1 500	Zn	0.50
Vitamin K/(Vitamin k3) (mg)	1 500	1 250	S	0.40
Niacine /(Nicotinic acid) (mg)	12 500	5 500	Co	0.02
Choline chloride/(Choline) (mg)	60 000	(65)	I	0.02
Ethoxyquin (mg)	5 000	-	Se	0.0015
Manganese oxide/(sulphate) (mg)	16 130	(90)	Mo	0.0002
Potassiumiodide (mg)	353	-	Ca: P	1.68: 1
Cobaltsulphate (mg)	286	-		
Zincoxide	2 500	70		
Copperoxide/(copper sulphate)	1 283	(1.5)		
Ferrocabonate (mg)	20 323	-		
Carrier to 1000g	-	-		
Lysine	-	50		
Methionine	-	50		
Manganese iodine (mg)	-	300		
Content (g)	-	500		

¹Composition is as per manufacturer's information.

²PHARMVITA was used when indigestible NDF (INDF) was determined by *in situ* long time (30 days) incubation.

were emptied on to a plain polythene sheet, mixed thoroughly and 5% by weight was sub-sampled in duplicate, weighed and stored in a cold room (-10°C) everyday. These samples were later thawed in a tray of known weight and DM determined in an oven at 80°C in Day 1 and 60°C in subsequent days to constant weights. The dried sub-samples for seven days were mixed again within animal and period and ground to pass through a 2.5 mm screen. An aliquot sample was taken from a composite sample for subsequent analyses.

3.3.3 *In sacco* degradability

In sacco degradability was carried out using standard procedures in three rumen fistulated mature non-pregnant heifers fed BH (80 % of the ad libitum feeding) and supplemented with 2 kg d⁻¹ concentrate mixture as shown in Table 3.3. *In sacco* degradability was also carried out simultaneously with intake and *in vivo* digestibility trials in all animals using forage samples as sampled from the forages described in section 3.2.2. The feed samples were incubated on Day 16 and taken out before rumen evacuations started. Feeding regime and water supply were therefore similar to expts.1 and 2.

Table 3.3 Composition of the concentrate fed to rumen fistulated heifers in the standard nylon bag technique

Ingredient	CP content (%)	Proportion (% of DM)	Calculated CP (%) contribution in diet
Maize meal	9.35	25	2.34
Maize bran	10.54	35	3.69
Cotton seed cake	35.89	35	12.56
Fish meal	63.21	5	3.16
Total		100	21.75*

* Laboratory analysis for the concentrate mixture had CP of 22.93 %

Forage samples were air dried and milled to pass through a 2.5 mm screen. Rumen incubation times were 0, 2, 4, 8, 16, 24, 48, 96, 144 and 192 h. Approx. 1 g of sample was incubated in nylon bags (measuring 7.5 x 10 cm and pore size 36 x 36 μm) in duplicate for each incubation time for DM, N, and NDF degradation. All bags were inserted at the same time during morning feeding and taken out as scheduled, rinsed and frozen to arrest microbial activity. After the longest incubation time (192h) all samples were machine washed in cold water for 20 min. The samples (except those used to analyse NDF) were treated in a stomacher (Model 400 Lab Blender) before analysis to remove microbial contamination. Samples for DM and N were filtered through N-free filter paper (No. AGF (607) 90mm) of known weight. The residue was dried in an oven at 100°C for 20 h. Residues for NDF degradability were not dried but transferred directly to glass filter crucibles of known weight for NDF analyses. Particle loss determination was carried out according to the procedures described by Weisbjerg *et al.* (1990).

3.3.4. Measure of rumen pool size of DM and NDF

Rumen pool sizes were measured by rumen evacuation method as described by Stensig *et al.* (1994a) during the last seven days of the experiments. Evacuation was done in three days as follows: at 1700 h (evening) on Day 24, at 0700 h (morning) on Day 27 and at 1300 h (mid-day) on Day 29. Evacuation protocols were such that a minimum time interval of 48h between two evacuations was allowed to avoid any effect that might occur on subsequent measurements. The rumen mat was removed from the rumen manually by hand and the material not removable by hand was removed by scooping with a cup that was small enough to pass through the rumen cannula. The mat fraction was separated from the bailable liquid and both fractions were weighed. About 1/ of the liquid was sampled and the rest was immediately returned to the rumen to avoid nutrient losses that may affect microbial activity. The mat was weighed and thoroughly mixed by hand in a big pot to

avoid mechanical mixing that might cause physical breakdown of the digesta and unnecessary oxygenation. About 5% by weight was sampled, and the rest returned into the rumen immediately. That means attempts were made to minimise microbiological changes by working fast. Even when the animals were at the highest level of intake the entire procedure seldom exceeded 15-20 min per animal. Finally the two samples were composted into their proportional weights to form two samples of 500 g each of the rumen digesta and the left overs were returned to their respective animals. The samples were oven dried at 80°C (Day 1) and 60°C (Day 2) to constant weight to determine DM. The samples were ground through 2.5mm sieve for subsequent analysis.

3.3.5. Determination of indigestible NDF (INDF)

In sacco long incubation was used to determine the INDF as described by Robinson *et al.* (1987). After termination of the two experiments, three (3) of the largest animals (selected for uniformity to reduce animal variation) used in expts.1 and 2 were fed BH (80 % of the ad libitum feeding) supplemented with FM (200 g d⁻¹) and urea (20 g/100 kg live body weight d⁻¹). In addition minerals (MACLIK SUPER: 20 g d⁻¹) and vitamins (PHARMVITA: 20 g d⁻¹) were provided (See Table 3.2 for their composition). After 14 days of preliminary period, determination of INDF in the feeds, rumen contents (obtained during rumen evacuation procedures) and faeces (obtained during *in vivo* digestibility trials) was estimated using long time (30 days) incubation procedure.

Approximately 3 g of feed, rumen digesta and faecal samples ground to pass through 2.5 mm sieve were weighed into nylon bags measuring 10 x 20cm and with a pore size of 36 x 36 µm. The bags were protected for possible losses from the rumen by tying a fishing nylon net around them. The bags were incubated in three rumen fistulated animals for 30 days. After 30 days incubation, all samples were washed in tap water to remove feed particles and then machine-washed in cold water

for 20 min. The residues were transferred into a beaker and boiled in 100 ml of NDF solution to remove microbial contamination and obtain the INDF residue. The residue was ashed to obtain ash free INDF that was also used to calculate the DNDF parameter used to derive NDF, DNDF and INDF intake, digestion and passage rates.

3.3.6 Determination of passage rate of chromium mordanted fibre (CR-MF)

Passage rate of NDF through the whole tract was also estimated using chromium mordanted fibre (CR-MF) as described by Udén *et al.* (1980). Chromium mordanted fibre was prepared using a modified method as described by Udén *et al.* (1980). Samples of each forage were ground to pass through a 5 mm screen. Air equilibrated samples of 0.5 kg each were weighed into two approximately 10 l stainless steel pots and soaked using distilled water. Immediately the fibre in the two pots was boiled gently while stirring using wooden spoons. The water was drained and distilled water re-filled again until all the fibre in the two pots were well covered and boiled steadily. The procedures were repeated 6-7 times until the water drained was clear. The fibre was soaked overnight and water drained off 6-7 times using cold distilled water until the water drained was colourless again.

Sodium dichromate (355 g) was dissolved in a bucket using distilled hot water. Hot water was added to cover the fibre then sodium dichromate solution was added to the fibre while stirring vigorously. The material was then returned into stainless steel pots in three equal portions. The fibre was covered with distilled hot water to 15 - 20 cm below the top of each pot and covered with aluminium foil. The pots were placed (on top of foil to catch overflow if it occurs) in an oven at 105°C for 24 h. Carefully, the pots were removed from the oven and the covers removed. After cooling the solution was drained, the pots filled with distilled cold water and repeated rising 6-7

times. Ascorbic acid (500 g) was dissolved in distilled cold water. All the CR-MF was poured into a 20 l bucket and filled about half way with cold distilled water. Ascorbic acid solution was added and then the bucket filled to 10 - 15 cm below the top. The material was stirred vigorously on and off for 1 h. The solution was drained and 6-7 rinses were applied with 2 h interval between each rinse. The CR-MF was spread on top of trays covered with aluminium foil and dried in an oven at 60°C to constant weight.

The animals were dosed with 120 g of air equilibrated CR-MF on day 16 of both expts.1 and 2. Two equal portions of CR-MF were wrapped into newspaper for each animal. The animals were dosed by placing the fibre on the cranial sac of the rumen where the food enters the rumen from the oesophagus. Faecal samples were collected 24 h after rumen dose of CR-MF followed by sampling after every 12 h up to 96 h after CR-MF dose.

3.3.7 Collection of rumen fluid for pH and NH₃ measurements

Rumen fluid was sampled by squeezing the rumen fluid through a fine tea sieve. Sampling was done on day 19, 20 and 21 of expts.1 and 2. The sampling of rumen fluid was carried out every 2 h over a 24 h period. Rumen pH was measured immediately using a portable pH meter.

3.3.8 Chemical analysis

Dry matter, ash and nitrogen (Macro-Kjeldahl) analyses were carried out using the procedures as outlined by the AOAC (1990). Rumen NH₃ was measured using a modified (without digestion) macro-Kjeldahl procedure described by AOAC (1990). All the samples analysed for NDF were done according to the methods described by Van Soest *et al.* (1991). In all analyses, however, sodium sulphite and α -amylase were omitted. Chromium concentration in faeces was extracted

according to a modified procedure as described by Jeng and Bergeseth (1992). Collected faecal samples were dried at 80°C to facilitate grinding. The samples were ground to pass through a sieve size of 1.0 mm. Extraction of the chromium from faecal samples was done by weighing 3 g of the sample into a large crucible and ashing at 450°C for 12 h. The ash was left to cool and 5 ml of concentrated nitric acid (conc. HNO₃) was added and left to soak for 4 - 6 h while covered. Carefully, the residue was transferred into 50 ml volumetric flask and diluted with distilled water up to the 50 ml meniscus mark. The material was then filtered into 50 ml or 100 ml bottles through filter paper (medium speed and average pore size of 1.4 - 2.9 µm). Chromium concentration in the filtrate was determined using Atomic Absorption Spectrophotometer (UNICAM 919).

3.3.9 Calculations

Calculation of DM, N and NDF degradation

Degradation data from individual animals for DM, N and NDF were calculated from disappearance of DM, N or NDF from the nylon bags after washing for zero hour or after rumen incubation in the equation:

$$DF = WI - WR/WI \dots \dots \dots (Model 3.1)$$

where, **DF** = degradation fraction from nylon bags

WI = weight of the fraction incubated

WR = weight of the fraction in the residue

Correction for particle loss in NDF

Correction of NDF for particle loss from the nylon bags was done on individual degradation data according to Weisbjerg *et al.* (1990):

$$C(t_i) = M(t_i) - P \left[1 - \left(\frac{M(t_i) - (P + W)}{1 - (P + W)} \right) \right] \dots\dots\dots(\text{Model 3.2})$$

- where, $C(t_i)$ = Corrected degradability at time t_i
- $M(t_i)$ = Measured degradation at time t_i
- W = Water soluble fraction determined using N free filter paper (not measured but assumed to be equal to zero as NDF is not water soluble).
- P = Particle loss (washing loss from the nylon bags minus W).

In theory, the washing loss for NDF from the nylon bags (0 h) should be considered as particle loss (P) because this fraction is not water- soluble. Correction was also made on the assumption that the particles were degraded at the same rate as the fraction remaining in the nylon bag.

Estimation of the degradability characteristics

Rumen degradability characteristics of DM, N and NDF of the forage samples were calculated using the exponential equation by Ørskov and McDonald (1979) with lag time as suggested by Dhanoa (1988):

$$Y(t) = a \quad \text{for } t \leq t_0$$

$$Y(t) = a + b (1 - e^{-c(t-t_0)}) \quad \text{for } t > t_0 \dots\dots\dots(\text{Model 3.3})$$

- where, $Y(t)$ = the degraded feed fraction at time t .
- a = soluble feed fraction (the intercept) for DM and N. For NDF it will be near zero, as NDF is not soluble in water.
- b = insoluble but potentially degradable fraction.
- c = rate constant (h^{-1}).
- t = incubation time (h).
- t_0 = lag time (h).

The parameters were estimated by PROC NLIN (SAS, 1996). Parameters of all the models where lag time was included were bound only to accept $t_0 \geq 0$.

Calculation of passage rate using CR-MF

Assuming a one compartment model with first order kinetics, chromium concentration can be described using a single exponential equation:

$$Cr_t = Cr_0 e^{-kt} + \epsilon_t \dots\dots\dots(\text{Model 3.4})$$

- where, Cr_t = [Cr] of faeces measured at time t_t
- Cr_0 = [Cr] at time t_0
- k = rate constant for [Cr] decline (h^{-1})
- t_t = time of sample collection (h)
- ϵ_t = random error term

Model 3.4 was transformed to a linear relationship by the natural logarithm (\ln) in the model:

$$\ln[Cr_t] = \ln[Cr_0] - kt_t + \epsilon_t \dots\dots\dots(\text{Model 3.5})$$

where, k = passage rate (h^{-1}) and the rest are as in Model 3.4.

Passage rate was estimated as the regression coefficient using PROC REG (SAS, 1996).

Calculation of intake, digestion and passage rates from rumen pool sizes of NDF and faecal output.

In theory, digestion is a time dependent process (dynamic process). However, the concepts of fibre kinetics assume first order kinetics. The derived intake, digestion and passage rates assume that rumen pool sizes and fluxes are at equilibrium (steady state), that the passage rate of DNDF and IDNF are equal and that the rumen incubation of 30 days is an accurate measure of INDF *in vivo*. In theory, faecal output of INDF should be equal to INDF intake.

In this study because measured INDF intake was too different from INDF output the values for INDF intake were omitted and INDF intake assumed to be equal to INDF faecal output. The kinetics of NDF intake, passage and digestion were calculated using the model presented by Robinson et al. (1987). Rates of intake (k_i), passage (k_p) and digestion (k_d) were calculated as:

Rates of intake (k_i):

$$k_i (\text{h}^{-1}) = \frac{\text{NDF intake (kg /24 h)}}{\text{rumen pool size of NDF(kg)}} \dots\dots\dots(\text{Model 3.6})$$

Rate of passage (k_p):

$$k_p (\text{h}^{-1}) = \frac{\text{NDF faecal output (g /24 h)}}{\text{rumen pool size of NDF(kg)}} \dots\dots\dots(\text{Model 3.7})$$

Rate of digestion (k_d):

$$k_d (\text{h}^{-1}) = k_i - k_p \dots\dots\dots(\text{Model 3.8})$$

Rate constants for DNDF and INDF were calculated in similar ways (Model 3.6, 3.7 and 3.8).

Calculation of effective degradability (ED)

a) Calculation of effective degradability (ED) assuming one-compartment (pool) model

The rumen degradability constants were weighted with passage rate to calculate the rumen effective degradability (ED) which simulate what really happens in the rumen. In the nylon bag technique, the feed particles are not allowed to pass out of the nylon bag even when they are indigestible. The ED was, therefore, calculated according to the equation given by Ørskov and McDonald (1979):

$$ED = a + \frac{bc}{c + k_p}$$

.....(Model 3.9)

where, **a**, **b**, and **c** are parameters obtained from Model 3.3 and **k_p** is the passage rate (h⁻¹).

When lag time is included ED can be calculated using the following model:

$$ED = a + \frac{bc}{c + k_p} \times e^{-kt_0}$$

.....(Model 3.10)

where, **a**, **b**, **c** and **t₀** are parameters estimated by Model 3.3 and **k** is the passage rate (h⁻¹).

Passage rates used to calculate ED are those estimated from chromium mordanted fibre (CR-MF) and rumen evacuation technique (RET) and they are described in tables of results. A constant passage rate of 2 % h⁻¹ was also used to calculate physical fill as a standard for comparison and to test if passage rate can be a constant value to estimate ruminal digestibility.

Calculation of passage rate based on in vivo digestibility and in sacco rumen potential digestibility of NDF

If the NDF is assumed to be all potentially digestible in the rumen, then ED should be equal to or close to *in vivo* digestibility. And if in theory ED is equal to *in vivo* digestibility, then passage rate can be calculated from *in vivo* digestibility and potential degradability estimated from *in sacco* digestibility. Based on Model 3.9 the passage rate (k_p) can be calculated as:

$$k_p = \frac{c \times b}{ED} - c \quad \dots\dots\dots(\text{Model 3.11})$$

where, k_p is the rate of passage and b and c are constants derived from Model 3.3.

Using Model 3.11 and substituting ED for *in vivo* digestibility of NDF (IVDNDF) passage rate of NDF can be calculated as:

$$k_p = \frac{b \times c}{IVDNDF} - c \quad \dots\dots\dots(\text{Model 3.12})$$

where k_p is the passage rate (h^{-1}), b and c are parameters obtained from Model 3.3 and *IVDNDF* is the observed *in vivo* digestibility of NDF.

b) Calculation of effective degradability (ED) assuming a two-compartment (pool) model

Using passage rate estimated from CR-MF and RET methods mean rumen retention time (MRRT) were calculated as reciprocals of passage rate. With the one-pool model MRRT was calculated as $1/k_p$, whereas with the two-pool model MRRT was calculated as $1/k_{p1} + 1/k_{p2}$.

Passage rate measured in total tract using CR-MF and that measured in the rumen using RET were used to derive k_{p1} and k_{p2} with several assumptions as follows:

$$\begin{aligned}
 \text{MRRT-2} &= 1/k_p \text{ (CR-MF)} \\
 \text{Total MRRT} &= 1/k_p \text{ (RET-total NDF)} \\
 \text{MRRT-1} &= \text{Total MRRT} - \text{MRRT-2} \\
 k_{p1} &= 1/\text{MRRT-1} \\
 k_{p2} &= k_p \text{ (CR-MF)}
 \end{aligned}$$

The ED of NDF (EDNDF) assuming a two-pool model was then calculated as:

$$EDNDF = a + \frac{bc}{k_{p2} - k_{p1}} \left(\frac{k_{p2}}{k_{p1} + c} e^{-k_{p1}t_0} - \frac{k_{p1}}{k_{p2} + c} e^{-k_{p2}t_0} \right)$$

for $k_{p1} \neq k_{p2}$ (Model 3.13)

Parameters in the model where ED was calculated assuming a two-compartment (pool) model were bound only to accept $k_{p1} \geq 0$.

c) Calculation of hind gut fermentation.

To be able to compare the above ruminal digestibility calculated assuming a one-pool model (ED) and that calculated assuming a two-pool model (EDNDF) with the *in vivo* data, the total tract digestibility of NDF (*in vivo*) was corrected for hind gut fermentation. The hind gut fermentation (HGF) was calculated by assuming that 10 % of duodenal flow will be digested in the hind gut (Robinson *et al.*, 1987). It follows that faecal output (FOP) in kg d⁻¹ is 90 % of the ileum flow. Then HGF can be calculated as given in Model 3.14, where, NDFI = NDF intake in kg d⁻¹.

$$HGF = \left(\frac{FOP}{90} \times 10 \right) \div NDFI$$

.....(Model 3.14)

Calculation of the physical fill

The feedstuff will remain in the rumen until it has either been degraded and utilized or passed out of the rumen undegraded. The physical fill of a given feedstuff fraction in the rumen can then be calculated based on the equation of physical fill suggested by Madsen *et al.* (1994). With lag time included, the Fill (day) was calculated as:

$$Fill = \frac{1-a}{k_p} \times (1 - e^{-kt_0}) + \frac{1-a-b}{k_p} \times e^{-kt_0} + \frac{b}{c+k_p} \times e^{-kt_0}$$

.....(Model 3.15)

where, Fill divided by 24 is the physical fill with the unit (day), a, b, c and t₀ are parameters from Model 3.3 and k is the passage rate (h⁻¹).

Passage rates used to calculate Fill (day) are those estimated from chromium mordanted fibre (CR-MF) and rumen evacuation technique (RET) and they are described in tables of results. A constant passage rate of 2 % h⁻¹ was also used to calculate Fill (day) as a standard for comparison and to test if passage rate can be a constant value in the fill system.

Prediction of intake

Predicted NDF intake (PNDFI) of feedstuff ascribed to a limitation of the physical capacity of the reticulo-rumen was calculated as:

$$\text{PNDFI (kg d}^{-1}\text{)} = \frac{\text{Rumen pool size of NDF (kg)}}{\text{Fill (day)}} \dots\dots\dots(\text{Model 3.16})$$

Finally the potential DM intake (PDMI) of the forages assuming physical limitation was predicted as:

$$\text{PDMI (kg d}^{-1}\text{)} = \frac{1}{\text{NDF in forage DM}} * \text{PNDFI} \dots\dots\dots (\text{Model 3.17})$$

where, PNDFI = predicted NDF intake by Model 3.16 and the NDF in the forage DM= the proportion of NDF in the forage DM.

3.2.10 Statistical analysis

Statistical analysis was executed by the General Linear Model (GLM) of SAS (1990) to test the differences between the forages on the parameters measured within and between experiments 1 and 2. Thus, it was assumed that the main effects were normally distributed with standard deviation of $\delta_A [N (0, \delta_A)]$. The main effects and the error term (ϵ_{ijk}) are assumed independent. The GLM model used was:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \epsilon_{ijk} \dots\dots\dots(\text{Model 3.18})$$

where, Y_{ijk} = the observation of the i th forage on the j th cow during the k th period

μ = overall mean

α_i = forage effect

β_j = cow effect

γ_k = period effect

ϵ_{ijk} = random error

The effect of supplementation was tested using GLM where the experiments were linked by the unsupplemented BH a forage diet which was similar for the two experiments. The GLM model was:

$$Y_{ijk\ell} = \mu + \alpha_i + \beta_j + \gamma_k + \delta_\ell + S \times F + \epsilon_{ijk\ell} \dots\dots\dots(\text{Model 3.19})$$

where, $Y_{ijk\ell}$ = the observation effect of supplementation on the i th forage on the j th cow during the k th period

μ = overall mean

α_i = forage effect

β_j = cow effect

γ_k = period effect

δ_t = supplementation effect

S x F = supplementation and forage interaction

ε_{ijkl} = random error

The difference between treatment means was compared by GLM PDIFF in expts.1 and 2. However, since data from two animals from expt.2, period 2 were omitted in experiment 2, the standard error of the LSM means was different between treatment means, but the ratio between the two standard errors was constant for all parameters where the values of the two animals were removed and the lowest value was used. The relationship between the measured and the predicted parameters within and between forages was tested using a simple linear regression model:

$$Y_i = \alpha + \beta X_i + \varepsilon_i \dots\dots\dots(\text{Model 3.20})$$

where, Y_i = the dependent parameter

X_i = the independent parameter

α = the intercept

β = the regression coefficient

4 RESULTS

4.1 Health of the animals

The animals remained generally in good health throughout the experimental periods. In period 2, experiment 2, (first day of the collection period) the animals were accidentally given double the level of urea supplementation in the morning and evening feeding time. Two among the four animals fed urea showed serious signs of urea toxicity. The observed symptoms were excessive salivation, indigestion, no rumination, muscular twitching and the animals were completely off feed. The other two animals had less signs observed but had excessive drinking of water but eating normally. No medication was applied apart from manipulation of the rumen environment by addition of concentrate to decrease the pH and flushing water in the rumen. There was no marked response to this but finally all the rumen content were evacuated (which had high proportion of undigested material) and rumen digesta from rumen fistulated steers was poured to the rumen (to about half the rumen fill). After a few hours the animals started eating and drinking gradually until they fully recovered, returning to normal *ad libitum* intake. Data from the two animals in period 2 for all parameters measured were omitted from the analysis.

4.2 Chemical composition

Chemical composition of all the forages and supplements used in experiment 1 (Expt.1) and 2 (Expt.2) is given in Table 4.1. Feed DM as fed varied substantially among the forages ranging from 222- 819 g kg⁻¹DM. During feeding MS had the lowest DM (222 g kg⁻¹ DM) compared to other forages. Fishmeal was relatively dry with 883 g kg⁻¹ DM and urea was assumed to be 100% DM. The crude protein (CP) content was quite variable among the forages, ranging from 63-151g kg⁻¹ DM.

Table 4.1 Chemical composition of tropical forages and nitrogen supplements (fishmeal and urea) used in experiments 1 and 2*

Type of feedstuff	Feed as fed (g kg ⁻¹)	DM (g kg ⁻¹ DM)		
		Ash	CP	NDF
Nitrogen supplements:				
Fishmeal (FM)	883	184	633	NA ²
Urea**	NA	NA	NA	NA
Forages:				
<i>Brachiaria brizantha</i> hay (BH)	819	93	64	748
Maize (<i>Zea mays</i>) silage (MS)	222	101	63	737
Lucerne (<i>Medicago sativa</i>) hay (LH)	815	110	151	615
Lucerne /grass hay (LGH)	817	116	111	750
Urea-treated rice (<i>Oryza sativa</i>) straw (UTRS)	784	180	74	770

*In this and subsequent tables, figures and appendices the following abbreviations will be used: DM = Dry matter, CP= Crude protein, NDF= Neutral detergent fibre and N = Nitrogen, FM = Fishmeal, NA = not analysed, BH =*Brachiaria brizantha* hay, MS = Maize silage, LH = Lucerne hay, LGH = Lucerne grass mixture hay, and UTRS = Urea-treated rice straw. In experiment 2, the forage diets are preceded by an S to read SBH, SMS, SLH, and SUTRS to indicate supplemented forages except unsupplemented BH = UNBH.

**Urea used was a commercial fertiliser grade 46% N (manufacturer's information).

The NDF (ash free) fraction ranged from 615 - 770 g kg⁻¹ DM. The UTRS had the highest ash content (180 g kg⁻¹ DM) and this could be attributed to high silica content in rice straws. The ash contents in LH, LGH and MS were generally high at 110, 116 and 101g kg⁻¹ DM respectively compared to BH which was 93 g kg⁻¹ DM.

4.3 *In sacco (in situ)* rumen degradability

Values given in Table 4.2 and subsequent tables are Least Squares Means. Tables 4.2 and 4.3 give forage rumen degradability characteristic (RDC) values derived by fitting the values obtained in different incubation times (Appendix 3 - 6) in a non-linear exponential equation (Model 3.3). The results are from studies carried out by a standard procedure (Table 4.2) and by incubating the forages in the rumen of animals fed their respective diets in expts.1 and 2 (Table 4.3). There was no marked difference in the extent and rate at which these forages were degraded in the standard procedure and in expts.1 and 2 except for the rate at which the **b** fraction for N was degraded. Although the difference was not tested statistically, the rate of degradation of the **b** fraction for N was higher in the standard procedure (4.9-33.1% DM h⁻¹) than in expts.1 (3.4-24.2 % DM h⁻¹) and expt.2 (2.7- 25.0 % DM h⁻¹). There was, however, a marked difference ($P < 0.0001$) in the rate and extent at which these forages were degraded in the standard procedure and in expts.1 and 2. The lag time for DM, N and the NDF fractions within forages incubated in the standard procedure and those incubated in the forage diets in expts.1 and 2 were not different ($P > 0.05$).

Table 4.2 Degradability constants of dry matter (DM), nitrogen (N) and neutral detergent fibre (NDF) for tropical forages and FM conducted in a standard procedure

Type of feed	Degradability constants (% DM)										Lag time (h)			
	a					b					c (% h ⁻¹)		DM	N
	DM	N	DM	N	NDF	DM	N	NDF	DM	N	NDF	DM		
Forages:														
BH	22.7 ^a	29.7 ^a	52.3 ^a	61.2 ^a	69.5 ^a	2.9 ^a	7.2 ^a	2.9 ^a	0.37	0.02	0.88			
MS	37.6 ^b	69.2 ^b	47.3 ^b	28.7 ^b	76.3 ^b	2.9 ^a	4.9 ^a	3.7 ^a	1.13	0.95	1.92			
LH	34.6 ^c	58.6 ^c	34.3 ^c	30.9 ^b	47.2 ^c	29.8 ^b	33.1 ^b	8.8 ^b	0.00	1.16	0.00			
LGH	22.3 ^a	59.0 ^c	44.9 ^b	28.7 ^b	58.3 ^d	4.3 ^a	7.2 ^a	3.6 ^a	0.00	0.00	0.00			
UTRS	16.9 ^d	43.7 ^d	54.9 ^d	45.5 ^c	71.8 ^a	3.2 ^a	6.8 ^a	2.9 ^a	0.11	0.00	0.33			
SEM	0.6	1.9	0.8	1.7	1.3	3.9	1.8	0.4	0.55	0.70	0.92			
P-value	0.0001	0.0001	0.0001	0.0001	0.0001	0.0043	0.0001	0.0001	0.58	0.61	0.62			
forage														
Fish meal (FM)¹:														
FM	35.8	43.4	51.5	38.1	NA ¹	4.4	2.7	NA	0.00	0.00	NA			

^{abcd}Means within columns with different superscript are significantly different (P<0.05).
¹NA= means not analysed and urca was assumed to be 100% degradable in the rumen.

Table 4.3 Degradability constants of dry matter (DM), nitrogen (N) and neutral detergent fibre (NDF) for tropical forages incubated during experiments 1 and 2

Diet	Degradability constants (% DM)											Lag time (h)		
	a			b			c (% h ⁻¹)			DM	N	NDF		
	TOFI ¹	DM	N	DM	N	NDF	DM	N	NDF					
Experiment 1:														
BH	23.3 ^a	38.7 ^a	51.3 ^a	47.5 ^a	69.9 ^a	2.9 ^a	2.9 ^a	3.4 ^a	3.8 ^{bc}	3.84	0.49	2.39		
MS	34.8 ^b	65.1 ^b	51.9 ^a	31.3 ^b	76.1 ^b	2.7 ^a	2.7 ^a	3.9 ^a	2.0 ^a	2.72	0.00	3.26		
LH	29.9 ^c	40.8 ^a	39.8 ^b	47.1 ^a	49.9 ^c	16.9 ^b	16.9 ^b	24.2 ^b	6.9 ^a	0.19	0.45	0.00		
LGH	21.6 ^{ad}	30.5 ^c	45.6 ^c	53.7 ^a	61.7 ^a	5.9 ^a	5.9 ^a	6.9 ^a	5.0 ^{ab}	1.21	0.08	1.25		
UTRS	17.7 ^d	47.4 ^d	54.1 ^a	40.3 ^a	70.3 ^a	3.3 ^a	3.3 ^a	4.3 ^a	3.2 ^{bc}	1.01	0.40	2.70		
SEM	1.3	1.9	1.2	2.1	2.8	1.3	1.3	0.9	0.7	1.33	0.35	0.82		
P-value	0.0001	0.0001	0.0001	0.0001	0.0004	0.0001	0.0001	0.0001	0.0051	0.35	0.80	0.11		
diet														
Experiment 2:														
UNBH	21.0 ^a	38.4 ^a	55.5 ^a	49.1 ^a	64.4 ^{ab}	2.2 ^a	2.2 ^a	2.7 ^a	3.0 ^a	1.05	0.11	2.06		
SBH	21.0 ^a	37.7 ^a	53.5 ^a	45.1 ^{ab}	60.5 ^b	3.1 ^a	3.1 ^a	3.8 ^a	2.9 ^a	1.37	0.23	1.00		
SMS	32.6 ^b	63.5 ^b	48.8 ^b	27.2 ^c	75.2 ^a	4.7 ^a	4.7 ^a	10.1 ^a	2.6 ^a	0.59	0.28	0.50		
SLH	31.3 ^b	44.3 ^a	33.2 ^c	40.9 ^b	53.6 ^b	30.2 ^b	30.2 ^b	25.0 ^b	9.1 ^b	0.14	0.27	0.00		
SUTRS	18.3 ^a	38.4 ^a	52.0 ^a	41.6 ^b	74.8 ^a	4.5 ^a	4.5 ^a	3.2 ^a	3.6 ^a	2.35	0.08	3.01		
SEM	1.1	1.2	1.2	0.2	3.0	1.7	1.7	0.3	0.3	0.62	0.15	0.67		
P-value	0.0001	0.0001	0.0001	0.0003	0.0075	0.0001	0.0001	0.0006	0.0001	0.27	0.87	0.14		
diet														

^{ab}Means within columns with different superscript are significantly different (P<0.05). ¹TOFI means type of forage incubated

Fig 4.1, 4.2 and 4.3 shows the degradation profiles for DM, CP and NDF from the standard procedure, expt.1 and expt.2 respectively obtained from individual degradations at different incubation time (Appendices 3 – 6). The degradation profiles followed different courses for DM, N and NDF and for different forages. There were, however, no marked differences in degradation when forages were incubated in either the standard diet or in expts.1 and 2. Although the forages were degraded at different rates and extent for DM, N and NDF all forages showed high rates at the beginning up to 48h, then increased at a decreasing rate up to 96 h, then formed a plateau an indication that the asymptotes have been achieved. A different degradation curve was, however, observed in LH for DM and N and to lesser extent in NDF. The degradation curve showed an extremely high rate of degradation at the beginning up to 48 h, then decreased in all subsequent incubation times. Due to this behaviour values of LH after 48 h for DM and N were omitted but resulted in a high standard error of the estimate by Model 3.3 (Table 4.2). The NDF fraction in LH did not show a noticeable decrease after 48 h. More or less similar behaviour after 48 h was observed in LGH for DM, N and NDF as this forage had about 20 % of LH. There was a very small and almost undetectable lag time in all forages when incubated in forage diets in expts.1 and 2 including the standard procedure, which is also illustrated in Fig. 4.1, 4.2 and 4.3.

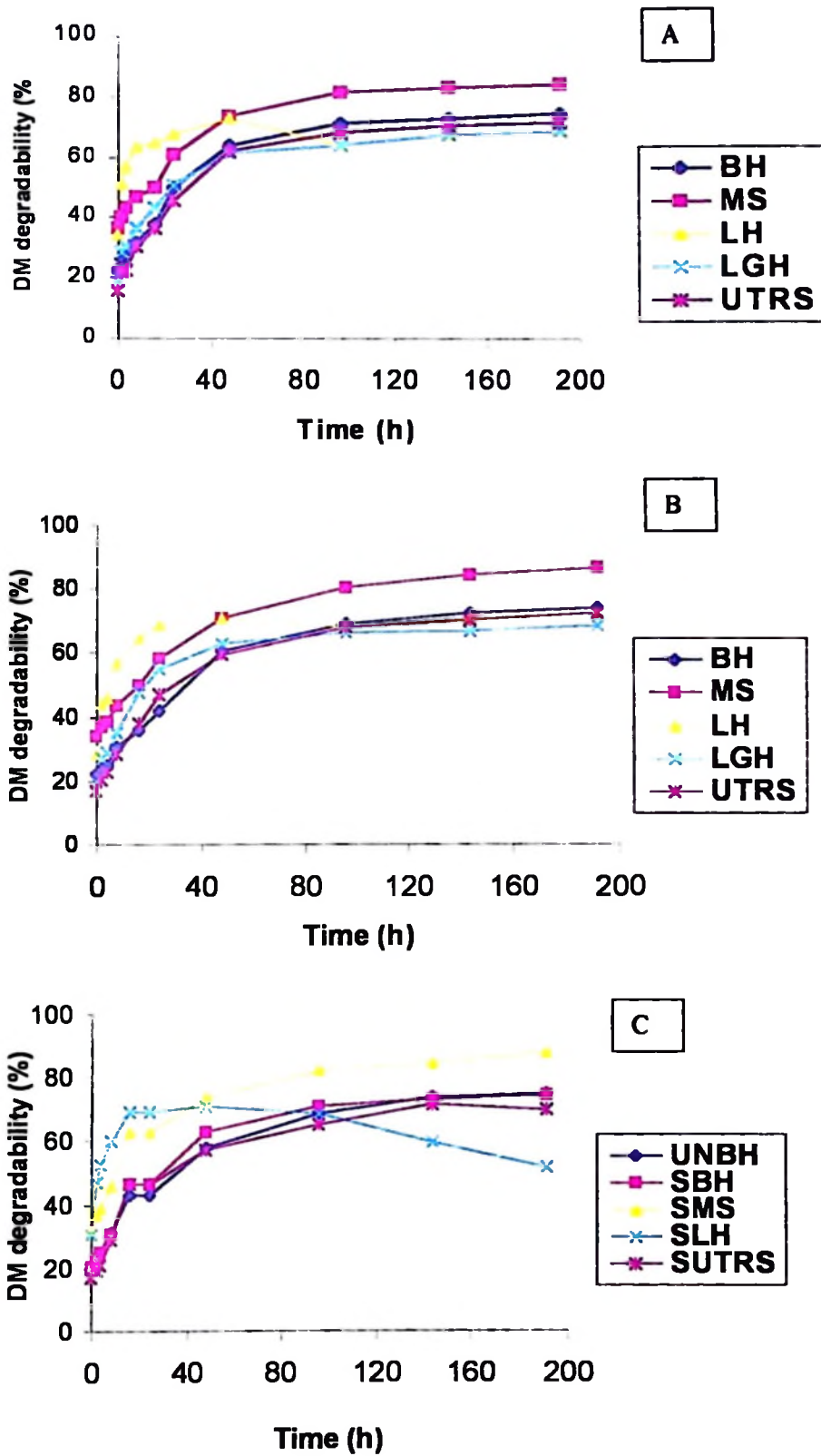


Fig: 4.1 Degradation of DM for the forages incubated according to the standard procedure (A), or in different forage diets in experiments 1 (B) and 2 (C)

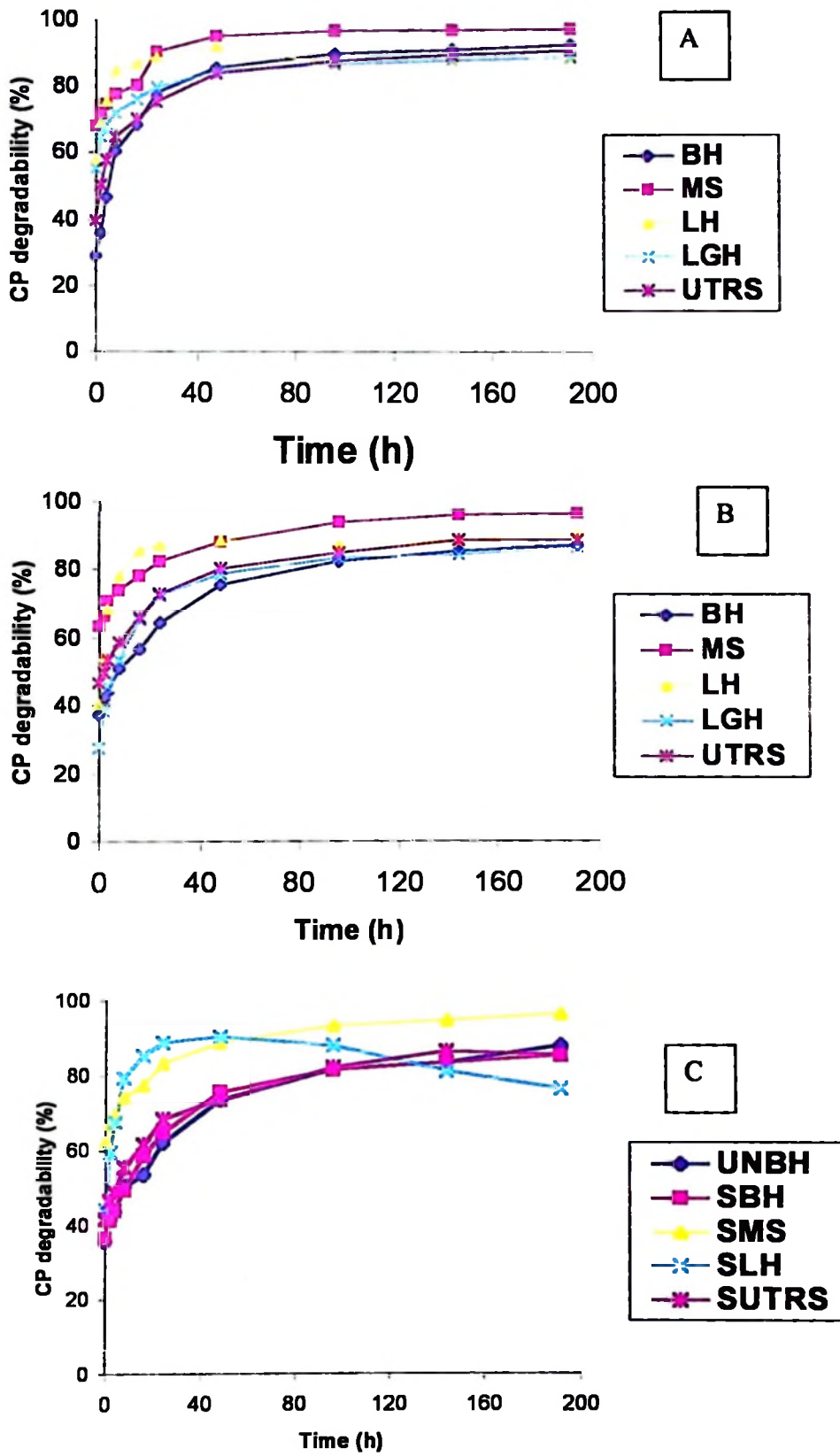


Fig:4.2 Degradation of CP for the forages incubated according to the standard procedure (A), or in different forage diets in experiments 1 (B) and 2 (C)

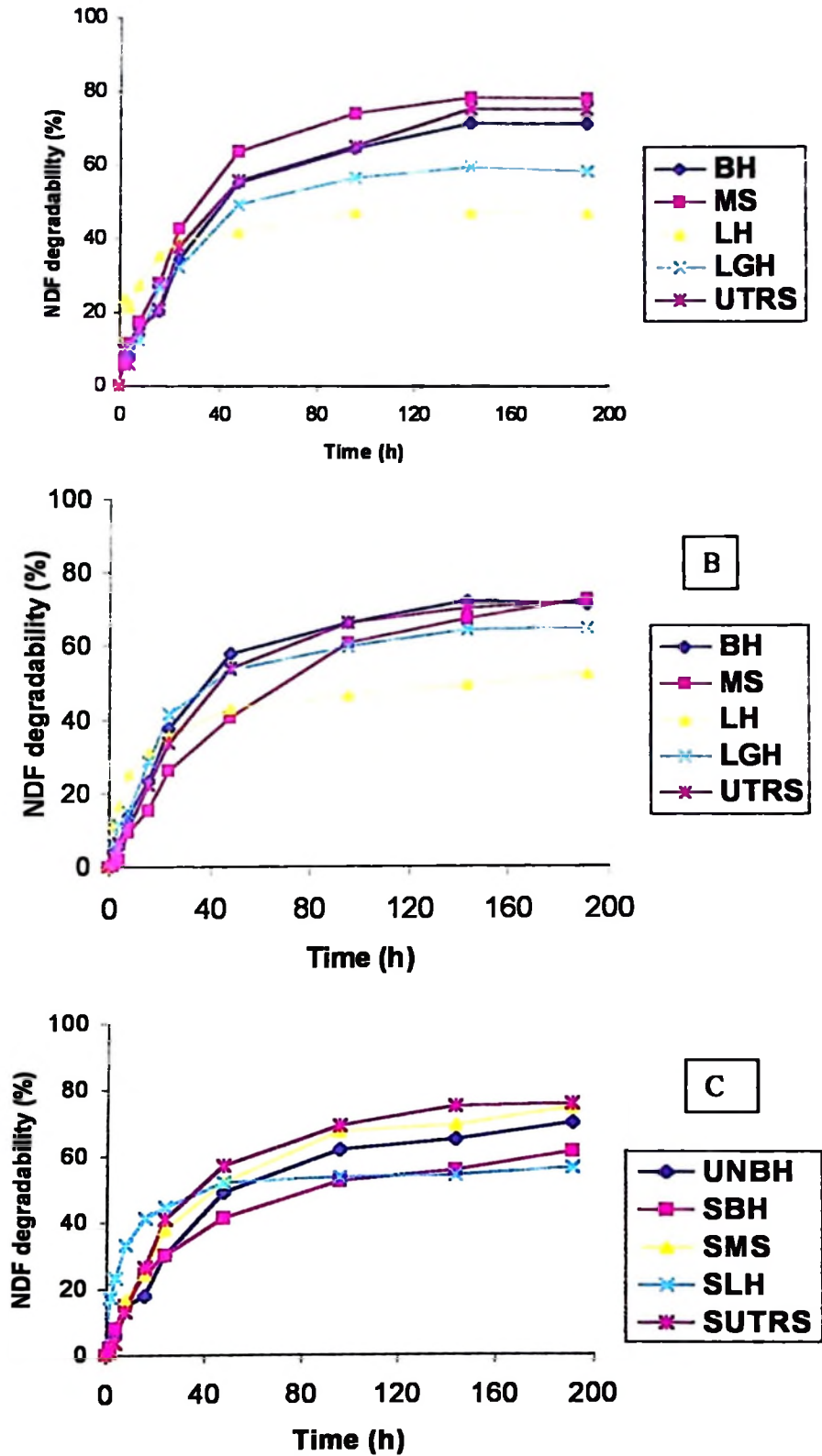


Fig:4.3 Degradation of NDF for the forages incubated according to the standard procedure (A), or in different forage diets in experiments 1 (B) and 2 (C)

4.4 Intake of DM, OM, NDF, CP and water

Total and forage daily intake for DM, OM, NDF, protein and water in experiments 1 and 2 are given in Table 4.4. There were highly significant differences ($P < 0.01$) for total DM intake (TDMI) and forage DM intake (FDMI) between forages in the sole forage diets (Expt.1). The MS was consumed the least (4.2 kg d^{-1}), whereas LGH was consumed the highest (6.7 kg d^{-1}). The total OM intake (TOMI), the forage OM intake (FOMI) and NDF fraction intake were highly significantly ($P < 0.01$) different between the forage diets. The crude protein (CP) intake and water intake were very highly significant ($P < 0.0001$) different between the forage diets. Intake of supplemented forage diets in expt.2 (TDMI, FDMI, TOMI, FOMI and NDF) was not different ($P > 0.05$). However, as expected, there was a very highly significant difference ($P < 0.0003$) in the total CP intake between the four supplemented forages and the unsupplemented forage diets due to FM and urea supplementation in Expt.2. A significant difference ($P < 0.004$) in CP intake was also observed in forage CP intake in Expt.2. Water intake was also significantly different ($P < 0.044$) between the forage diets in Expt.2.

4.5 Body weight of the animals

The body weights of the animals at the beginning (ILBW) and at the end (FLBW) of each period in experiments 1 and 2 are given in Table 4.5. Body weights corrected for rumen contents are also given in Table 4.5. Appendices 7 and 8 give the body weights of the animals as weighed at the beginning of the experiments and at the end of each period 1-5 regardless of their forage diets. Generally all animals gained weights during the experiment periods.

Table 4.4 Measured intake (kg d⁻¹) of total and forage DM, OM, N, NDF and water (l d⁻¹) in experiments 1 and 2

Total and forage intake	Diet					SEM	P-value forage
	BH	MS	LH	LGH	UTRS		
Experiment 1:							
Total DM ¹ (kg d ⁻¹)	5.10 ^b	4.20 ^c	6.52 ^a	6.70 ^a	6.34 ^{ab}	0.46	0.0093
Total OM ¹ (kg d ⁻¹)	4.60 ^{bc}	3.75 ^c	5.79 ^{ab}	5.91 ^a	5.17 ^{ab}	0.40	0.0143
Forage DM (kg d ⁻¹)	5.06 ^b	4.16 ^c	6.48 ^a	6.66 ^a	6.31 ^{ab}	0.46	0.0093
Forage OM (kg d ⁻¹)	4.59 ^{bc}	3.73 ^c	5.77 ^{ab}	5.89 ^a	5.16 ^{ab}	0.40	0.0143
Forage NDF (kg d ⁻¹)	3.79 ^b	3.06 ^b	4.02 ^a	5.00 ^a	4.86 ^a	0.35	0.0106
Forage CP (kg d ⁻¹)	0.32 ^{cd}	0.26 ^d	0.98 ^a	0.74 ^b	0.47 ^c	0.06	0.0001
Water intake (l d ⁻¹)	21.7 ^b	10.1 ^c	29.9 ^a	30.5 ^a	22.6 ^b	1.7	0.0001
Experiment 2:							
	UNBH	SBH	SMS	SLH	SUTRS		
Total DM ¹ (kg d ⁻¹)	4.86	5.03	4.57	6.12	6.57	0.43	0.0578
Forage DM (kg d ⁻¹)	4.82	4.82	4.36	5.91	6.36	0.43	0.0688
Forage OM (kg d ⁻¹)	4.38	4.37	3.90	5.26	5.13	0.39	0.1928
Total OM ¹ (kg d ⁻¹)	4.40	4.53	4.05	5.42	5.29	0.39	0.1688
Forage NDF (kg d ⁻¹)	3.64	3.67	3.13	3.68	4.84	0.31	0.0640
Urea DM (g d ⁻¹)	0.0 ^b	53.78 ^a	54.04 ^a	50.52 ^a	53.70 ^a	1.95	0.0001
Forage CP (kg d ⁻¹)	0.32 ^b	0.32 ^b	0.35 ^b	0.76 ^a	0.64 ^a	0.07	0.0035
Urea CP (kg d ⁻¹)	0.0 ^b	0.155 ^a	0.155 ^a	0.145 ^a	0.154 ^a	0.006	0.0001
Total CP (kg d ⁻¹)	0.32 ^c	0.59 ^b	0.61 ^b	1.01 ^a	0.91 ^a	0.07	0.0003
Water intake (l d ⁻¹)	21.4 ^b	23.4 ^{ab}	14.0 ^c	30.0 ^a	25.7 ^{ab}	2.8	0.0436

^{abc}Means within rows with different superscript are significantly different (P<0.05).

¹FM DM, OM and CP intake were 0.1766, 0.1441 and 0.1118 kg d⁻¹ respectively and constant in all diets in experiment 2 except in UNBH diet. Similarly minerals and vitamins DM intake were 0.0368 kg d⁻¹ for all diets in both experiments 1 and 2. See the minerals and vitamins composition in Table 3.1

The initial live body weights of the animals were not different in expt.1 ($P>0.9$) and expt.2 ($P>0.3$). The final body weights were different ($P<0.01$) in expt.1 and not ($P>0.10$) in expt.2. A similar trend was observed in the ILBW after correction for rumen contents using the wet digesta obtained by rumen evacuation in expts.1 and 2. There were significant weight changes in expt.1 ($P<0.002$) and not in expt.2 ($P>0.5$). In expt.1 animals fed MS forage diet lost weight (6.6 kg), those fed BH diet lost less weight (0.8 kg), whereas those fed LGH, LH and UTRS gained weights (27.0, 21.4 and 18.4 kg respectively) in 30 days. In expt.2 all animals gained weight by 3, 4, 18, 24 and 28 kg for UNBH, SBH, SUTRS, SMS, and SLH forage diets respectively in 30 days. Body weights corrected for possible variations due to rumen fill showed similar trends. Correction for possible variation due to rumen contents for body weight changes remained numerically the same. Intake expressed as percentage of livebody weight and intake in g per kg metabolic body weight ($\text{g kg}^{-1} \text{W}^{0.75}$) are given in Table 4.5 for TDMI and FDMI. Significant differences ($P<0.0001$) were observed between forages in both expts.1 and 2 for TDMI and FDMI when expressed as percentage of body weight or $\text{g kg}^{-1} \text{W}^{0.75}$.

4.6 *In vivo* digestibility coefficients

Apparent digestibility coefficients of the forage diets (Expt.1) and the supplemented forage diets (Expt.2) are shown in Table 4.6. The extent to which the forages were digested in the sole forage diets (Expt.1) was highly significantly different for DM ($P<0.004$), ash ($P<0.01$) and OM (0.03) and very highly significantly different between forages ($P<0.0001$) for CP. There was a highly significant difference ($P<0.02$) for DM and ($P<0.04$) for CP digestibility between the supplemented forage diets (Expt.2), whereas ash digestibility in these diets showed a very highly significant difference ($P<0.0002$) among the forage diets.

Table 4.5 Initial (ILBW) and final (FLBW) live and corrected body weights (kg) and body weight changes (LBWC), total (TDMI) and forage (FDMI) dry matter intake expressed as a percentage or 0.75 exponent of FLBW (Experiments 1 and 2)

Intake and livebody weight parameters	Diet					SEM	P-value forage
	BH	MS	LH	LGH	UTRS		
Experiment 1:							
ILBW (kg)	265	268	264	261	262	6	0.9229
FLBW (kg)	264 ^b	261 ^b	286 ^a	288 ^a	281 ^a	5	0.0060
LBWC (kg)	-0.8 ^b	-6.6 ^b	+22.4 ^a	+27.0 ^a	+18.4 ^a	5.0	0.0017
CILBW (kg)*	221	228	216	210	214	6	0.2639
CFLBW (kg)*	221 ^b	221 ^b	237 ^a	238 ^a	232 ^a	4	0.0178
CLBWC (kg)*	-0.8 ^b	-6.6 ^b	+21.4 ^a	+27.0 ^a	+18.4 ^a	5.0	0.0017
Intake (as percentage FLBW):							
TDMI	1.91 ^b	1.61 ^c	2.14 ^a	2.24 ^a	2.37 ^a	0.07	0.0001
Forage DM	1.90 ^b	1.59 ^c	2.13 ^a	2.23 ^a	2.36 ^a	0.07	0.0001
Intake (g kg⁻¹ W^{0.75}):							
TDMI	77.7 ^c	64.8 ^d	88.3 ^b	93.2 ^{ab}	97.7 ^a	3.0	0.0001
Forage DMI	77.2 ^c	64.3 ^c	87.8 ^b	92.7 ^{ab}	97.2 ^a	3.0	0.0001
Experiment 2:							
	UNBH	SBH	SMS	SLH	SUTRS		
ILBW (kg)	254	269	239	253	265	9	0.3090
FLBW (kg)	257	273	263	281	283	6	0.0962
LBWC (kg)	+3.20	+ 3.80	+24.24	+28.20	+ 17.78	11.41	0.4699
CILBW (kg)*	221	229	196	215	221	12	0.5998
CFLBW (kg)*	221	231	224	241	235	6	0.2160
CLBWC (kg)*	3.20	3.80	24.24	28.20	17.78	11.41	0.4699
Intake (as percentage FLBW):							
TDMI	2.04 ^c	1.82 ^d	1.71 ^d	2.36 ^a	2.20 ^b	0.05	0.0001
Forage DM	2.02 ^c	1.75 ^d	1.63 ^d	2.29 ^a	2.13 ^b	0.05	0.0001
Intake (g kg⁻¹ W^{0.75}):							
TDMI	81.6 ^c	74.1 ^d	69.3 ^d	97.3 ^a	90.6 ^b	2.0	0.0001
Forage DM	81.0 ^c	70.9 ^d	66.0 ^d	94.2 ^a	87.6 ^b	2.0	0.0001

^{abcd}Means within rows with different superscript are significantly different (P<0.05).

*Corrected for rumen digesta using wet digesta obtained from rumen evacuation.

Table 4.6 *In vivo* apparent digestibility coefficients (ADC) of DM, OM, NDF, N and ash for the tropical forage based diets without or with FM and urea supplementation and potential rumen (PRD) and maximum rumen (MRD) digestibility in experiments 1 and 2

Parameter measured	Diet					SEM	P-value diet
	BH	MS	LH	LGH	UTRS		
Experiment 1:							
Apparent digestibility coefficients (%):							
DM	53.5 ^{bc}	58.2 ^{ab}	61.7 ^a	53.1 ^{bc}	50.7 ^c	1.7	0.0043
OM	56.3 ^{bc}	60.6 ^{ab}	62.9 ^a	55.7 ^c	60.2 ^{abc}	1.5	0.0260
NDF	54.6	61.2	57.7	59.4	60.6	2.3	0.3181
N	38.9 ^{bc}	32.8 ^c	67.0 ^a	49.8 ^b	6.5 ^d	5.1	0.0001
Ash	27.2 ^b	37.2 ^{ab}	52.5 ^a	33.9 ^{ab}	5.5 ^c	6.8	0.0056
Potential (PRD) and maximum rumen (MRD) digestibilities of NDF (%):							
PRD*	84.9 ^b	86.5 ^b	73.1 ^d	77.8 ^c	95.2 ^a	1.3	0.0001
PRD (<i>in sacco</i>)**	69.9 ^b	76.1 ^a	49.9 ^c	61.7 ^b	70.3 ^b	2.8	0.0004
MRD (192h)***	71.8 ^b	73.0 ^a	52.5 ^c	65.3 ^b	72.6 ^b	0.3	0.0037
Experiment 2:							
	UNBH	SBH	SMS	SLH	SUTRS		
Apparent digestibility coefficients (%):							
DM	55.2 ^{ab}	52.3 ^b	63.1 ^a	62.7 ^a	49.0 ^b	2.6	0.0168
OM	57.9	54.9	65.1	64.4	60.5	2.5	0.0983
NDF	60.3	56.4	64.7	59.4	56.6	2.4	0.2554
N	44.7 ^c	66.2 ^{ab}	69.8 ^a	69.2 ^a	45.8 ^{bc}	6.3	0.0444
Ash	29.4 ^b	28.5 ^b	45.3 ^a	49.7 ^a	0.2 ^c	4.3	0.0002
Potential (PRD) and maximum rumen (MRD) digestibilities of NDF (%):							
PRD*	87.1 ^b	83.8 ^b	87.3 ^b	75.3 ^c	94.8 ^a	1.3	0.0001
PRD (<i>in sacco</i>)**	64.4 ^{ab}	60.5 ^b	75.2 ^a	53.6 ^b	74.8 ^a	3.0	0.0075
MRD (192h)***	69.6 ^{ab}	61.1 ^b	74.3 ^a	56.1 ^b	75.3 ^a	0.3	0.0296

^{abcd}Means within rows with different superscript are significantly different ($P < 0.05$).

*PRD were determined by long time (30 days) nylon bag incubation.

**PRD (*in sacco*) was the b value as NDF is insoluble

***MRD is the degradability at 192 h *in sacco*

There was no significant difference in expt.1 ($P>0.32$) and expt.2 ($P>0.26$) for the NDF fraction digestibility between the forage diets. The CP digestibility for the UTRS forage diet was extremely low, a phenomenon that might be difficult to explain conclusively.

4.7 Rumen fermentation

The mean, minimum and maximum rumen pH and NH_3 as measured in the animals fed on the forage diets in expts.1 and 2 are given in Table 4.7. Diurnal variations in pH and NH_3 concentration are given in Appendix Table 6 (Expt.1) and 7 (Expt.2).

4.7.1 Rumen pH

Absolute differences were small between forage diets and not significantly different in expt.1 ($P>0.2$) and expt.2 ($P>0.7$). In expt.1 the minimum pH among the diets ranged between 6.3- 6.8, whereas maximum ranged between 6.9-7.2. In expt.2 minimum pH among the diets ranged between 6.5-6.7, whereas maximum pH ranged between 6.8-7.0. Rumen pH diurnal fluctuations are illustrated in Fig.4.4. The pH diurnal fluctuations showed minor peaks during the day and marked peaks before feeding and slight drops thereafter in experiments 1 and 2 within forage diets.

4.7.2 Rumen NH_3 concentration

Rumen NH_3 concentrations were very highly different in expt.1 ($P<0.0003$) and expt.2 ($P<0.0002$) between the forage diets. In expt.1, LH and LGH had the highest NH_3 concentration in the rumen compared to the UTRS, BH and MS. In expt.2 the SLH and the SUTRS forage diets gave the highest NH_3 concentration in the rumen relative to SMS and SBH. As expected the UNBH had the lowest NH_3 concentration in the rumen. Rumen NH_3 diurnal fluctuations are

demonstrated in Fig. 4.5. Diurnal fluctuations were observed in almost all forage diets in expt.2 except UNBH. Diurnal fluctuations were more clearly demonstrated in LH, LGH and to a lesser extent in UTRS compared to BH and MS forage diets. To the forages, which showed clear diurnal NH_3 fluctuations there were high peaks few hours after feeding especially in expt.2 except for UNBH.

Table 4.7 Effect of feeding tropical forage based diets without or with FM and urea supplementation on pH and NH_3 concentration in ruminal fluid (Experiment 1 and 2)

Parameter measured	Diet					SEM	P-value diet
	BH	MS	LH	LGH	UTRS		
Experiment 1:							
pH:							
Minimum	6.4	6.8	6.7	6.3	6.3	NA ¹	NA
Maximum	7.1	7.2	6.9	6.9	7.0	NA	NA
Mean	6.8	6.9	6.9	6.7	6.7	0.07	0.2167
NH_3 (mg l⁻¹):							
Minimum	46.4	23.2	85.1	65.2	50.4	NA	NA
Maximum	81.4	97.8	232.2	137.1	177.7	NA	NA
Mean	63.8 ^{cd}	58.7 ^d	189.0 ^a	105.3 ^b	95.4 ^{bc}	12.6	0.0003
Experiment 2:							
	UNBH	SBH	SMS	SLH	SUTRS		
pH:							
Minimum	6.5	6.7	6.7	6.5	6.5	NA	NA
Maximum	7.0	6.9	7.0	7.0	6.8	NA	NA
Mean	6.8	6.8	6.8	6.7	6.7	0.05	0.7193
NH_3 (mg l⁻¹):							
Minimum	43.5	56.9	52.5	151.0	49.6	NA	NA
Maximum	56.9	108.0	132.3	245.4	205.4	NA	NA
Mean	50.9 ^b	79.0 ^b	96.6 ^b	196.3 ^a	157.9 ^a	14.0	0.0002

^{abc}Means within rows with different superscript are significantly different (P<0.05).

¹NA means not analysed.

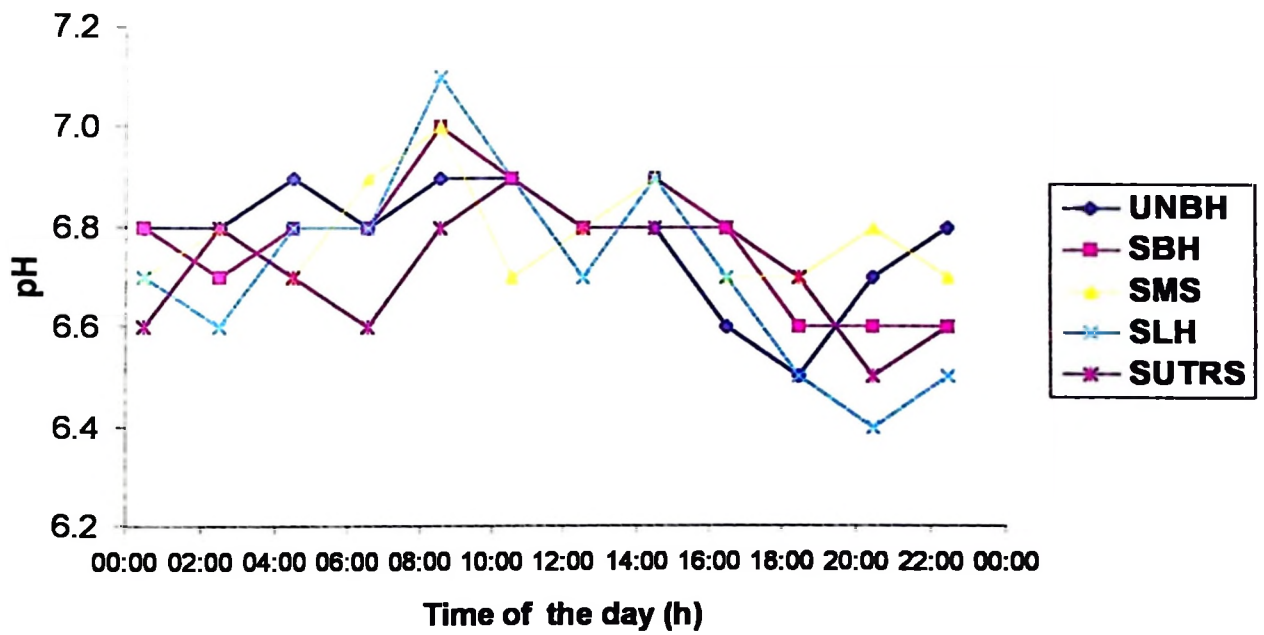
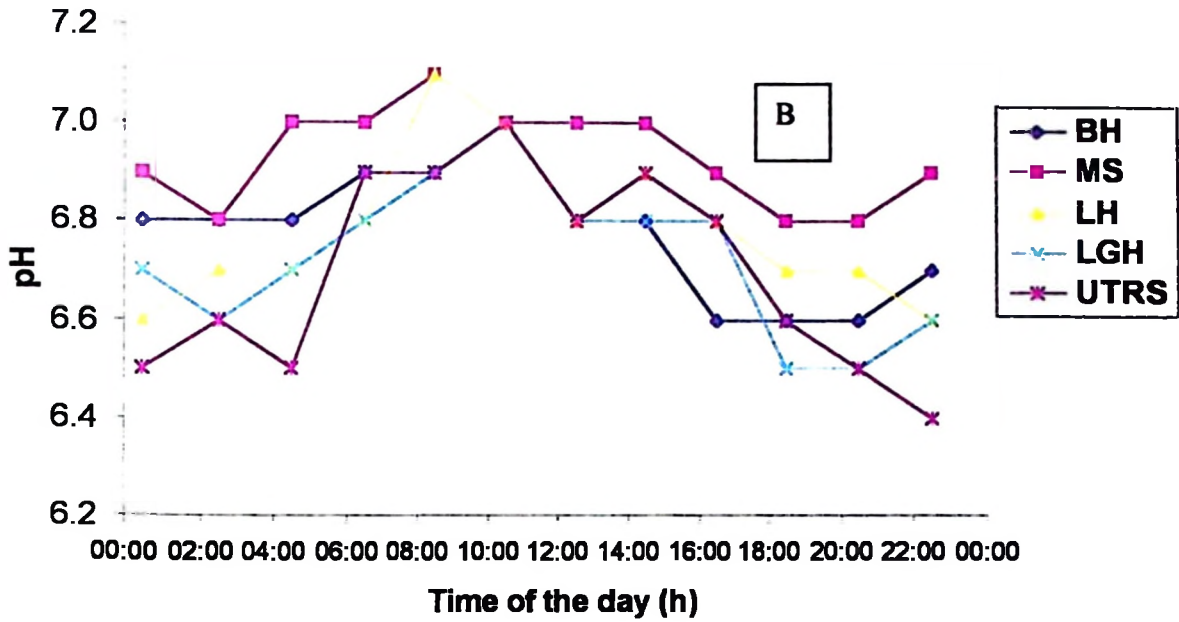


Fig: 4.4 Diurnal pH fluctuations in the rumen of animals fed forage diets in experiments 1 (A) and 2 (B)

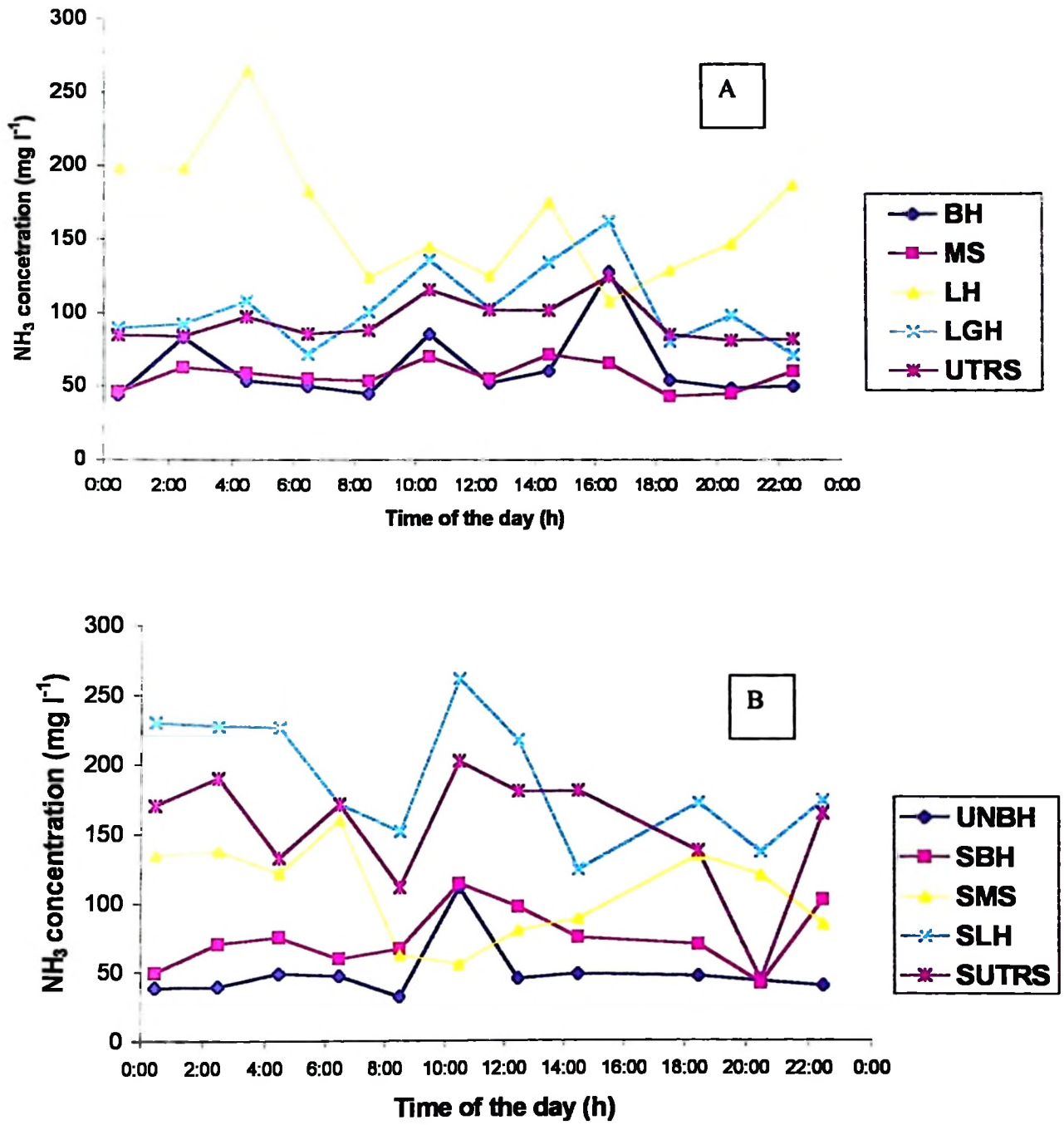


Fig: 4.5 Diurnal NH₃ fluctuations in the rumen of animals fed forage diets in experiments 1 (A) and 2 (B)

4.8 Rumen pool sizes

Rumen pool sizes of total wet digesta and its DM content, rumen pool size of DM, NDF, DNDF and INDF at different times of evacuations and as a mean of the three evacuations are shown in Table 4.8 (Expt.1) and Table 4.9 (Expt.2). In general the rumen pool sizes of the different fractions were higher in the evening evacuation than in the mid-day and especially the morning evacuations which had the lowest pool sizes. In expt.1 there was a significant difference between the forage diets in pool size of total wet digesta ($P<0.002$), DM content ($P<0.004$), dry digesta (% DM) ($P<0.001$), NDF ($P<0.012$), DNDF ($P<0.0001$) and INDF ($P<0.0001$). The pool sizes of wet digesta, DM, NDF were higher in animals fed LGH and UTRS and lowest in MS than in LH and BH forage diets. Animals fed on LH had the highest (2.7 kg) INDF pool, whereas MS fed animals had the lowest (0.6 kg) compared to those fed UTRS (0.8 kg), BH (1.0 kg) and LGH (2.3 kg). Animals fed LGH had the highest (5.2 kg) NDF pool, whereas those fed MS had the lowest (3.8 kg) compared to animals fed BH (4.8 kg), LH (4.7 kg) and UTRS (4.5 kg). There was no significant difference in NDF pool for the animals fed LGH, BH, LH and UTRS. The difference observed was only between the pool size for animals fed MS compared to animals fed other forage diets. As for DNDF, animals fed LH had the least DNDF pool (2.0 kg), and BH had the highest pool (3.9 kg), whereas LGH was close to LH (2.9), MS (3.2 kg) and UTRS (3.6 kg). In expt.2 the above pool sizes were also different in wet digesta ($P<0.003$), DM content ($P<0.02$), DM ($P<0.001$), NDF ($P<0.002$), DNDF ($P<0.0001$) and INDF ($P<0.0001$). Highest pool sizes of total wet digesta, DM, and NDF were found in animals fed SUTRS and SLH compared to those fed SBH and UNBH and least in SMS. High INDF pool was found in animals fed SLH (2.9 kg) and least in SUTRS (0.8 kg) and UNBH (0.8 kg). Animals fed SBH had the highest (4.9 kg) NDF pool, whereas SMS fed animals had the lowest (3.3 kg) compared to those fed UNBH (4.0 kg). Animals fed SLH and SUTRS had similar NDF pool (4.3 kg).

Table 4.8 Rumen pool sizes (kg) of wet digesta DM, NDF, DNDF and INDF evacuated at three different times and as an average of the three rumen evacuations (Experiment 1)

Rumen pool sizes	Type of forage					SEM	P-value diet
	BH	MS	LH	LGH	UTRS		
Morning evacuation (07:00h):							
Wet digesta	43.7	40.0	48.4	49.8	48.7	2.5	0.0737
DM (%)	12.7	12.2	11.2	11.6	12.5	0.6	0.3724
Dry digesta	5.6	4.9	5.4	5.9	6.1	0.4	0.3843
NDF	4.4	3.8	4.1	4.4	3.8	0.3	0.6113
DNDF*	3.5 ^a	3.2 ^{ab}	1.5 ^c	2.4 ^b	3.1 ^{ab}	0.3	0.0016
INDF**	0.9 ^b	0.6 ^b	2.6 ^a	2.0 ^a	0.7 ^b	0.2	0.0001
Mid-day evacuation (13:00h):							
Wet digesta	48.4 ^a	43.1 ^b	46.1 ^{ab}	57.7 ^a	53.8 ^a	2.3	0.0045
DM (%)	12.9 ^{ab}	10.8 ^c	12.1 ^{bc}	11.7 ^{bc}	13.8 ^a	0.4	0.0029
Dry digesta	6.1 ^a	4.7 ^b	5.6 ^a	6.7 ^a	7.4 ^a	0.3	0.0004
NDF	4.5 ^a	3.6 ^b	4.3 ^a	4.9 ^a	4.8 ^a	0.2	0.0089
DNDF	3.6 ^{ab}	3.0 ^{bc}	1.7 ^d	3.0 ^{bc}	3.9 ^a	0.3	0.0023
INDF	0.9 ^c	0.6 ^c	2.6 ^a	1.9 ^b	0.9 ^c	0.2	0.0001
Evening evacuation (17:00h):							
Wet digesta	54.1 ^c	46.9 ^d	60.9 ^b	70.9 ^a	56.6 ^{bc}	3.0	0.0013
DM (%)	13.9 ^a	10.8 ^b	12.5 ^c	12.0 ^c	13.6 ^a	0.3	0.0003
Dry digesta	7.5 ^a	5.1 ^b	7.6 ^a	8.6 ^a	7.7 ^a	0.4	0.0005
NDF	5.6 ^a	3.9 ^b	5.6 ^a	6.2 ^a	4.7 ^{ab}	0.4	0.0056
DNDF	4.5 ^a	3.3 ^{ab}	2.8 ^b	3.3 ^{ab}	3.8 ^a	0.3	0.0216
INDF	1.2 ^b	0.6 ^c	2.8 ^a	2.9 ^a	1.0 ^{bc}	0.3	0.0001
Mean:							
Wet digesta	48.7 ^{bc}	43.3 ^c	51.8 ^{bc}	59.5 ^a	53.0 ^b	2.1	0.0022
DM (%)	13.1 ^a	11.3 ^b	11.9 ^b	11.8 ^b	13.3 ^a	0.3	0.0038
Dry digesta	6.3 ^a	4.9 ^b	6.2 ^a	7.1 ^a	7.1 ^a	0.3	0.0011
NDF	4.8 ^a	3.8 ^b	4.7 ^a	5.2 ^a	4.5 ^{ab}	0.2	0.0123
DNDF	3.9 ^a	3.2 ^{bc}	2.0 ^d	2.9 ^c	3.6 ^{bc}	0.2	0.0001
INDF	1.0 ^c	0.6 ^c	2.7 ^a	2.3 ^b	0.8 ^c	0.1	0.0001

^{abcd}Means within rows with different superscript are significantly different ($P < 0.05$).

*DNDF = Digestible NDF.

**INDF = Indigestible NDF.

Table 4.9 Rumen pool sizes (kg) of wet digesta DM, NDF, DNDF and INDF evacuated at three different times and as an average of the three rumen evacuations (Experiment 2)

Rumen pool sizes	Type of forage					SEM	P-value diet
	UNBH	SBH	SMS	SLH	SUTRS		
Morning evacuation (07:00h):							
Wet digesta	36.3 ^c	41.6 ^b	38.6 ^{bc}	40.2 ^b	48.3 ^a	1.4	0.0040
DM (%)	12.0	13.1	11.5	11.5	12.0	0.6	0.4272
Dry digesta	4.4	5.4	4.4	4.6	5.7	0.3	0.0643
NDF	3.4	4.2	3.2	3.4	3.5	0.2	0.0726
DNDF*	2.7 ^a	3.0 ^a	2.6 ^a	0.9 ^b	2.8 ^a	0.2	0.0007
INDF**	0.7 ^b	1.2 ^b	0.7 ^b	2.4 ^a	0.7 ^b	0.2	0.0004
Mid-day evacuation (13:00h):							
Wet digesta	42.0 ^{bc}	45.9 ^b	35.6 ^c	47.3 ^{ab}	54.5 ^a	2.2	0.0043
DM (%)	12.3	13.3	11.1	11.7	13.4	0.6	0.1093
Dry digesta	5.0 ^{bc}	6.1 ^b	3.9 ^c	5.5 ^b	7.2 ^a	0.2	0.0014
NDF	3.8 ^b	4.8 ^a	2.9 ^c	4.2 ^{ab}	4.3 ^{ab}	0.2	0.0051
DNDF	2.9 ^c	3.8 ^a	2.4 ^c	1.7 ^d	3.5 ^b	0.2	0.0001
INDF	0.9 ^b	1.0 ^b	0.5 ^b	2.5 ^a	0.8 ^b	0.2	0.0001
Evening evacuation (17:00h):							
Wet digesta	49.8 ^b	55.9 ^{ab}	46.3 ^b	56.9 ^{ab}	62.7 ^a	2.7	0.0267
DM (%)	12.7 ^a	13.3 ^a	10.4 ^b	12.7 ^a	13.9 ^a	0.4	0.0027
Dry digesta	6.4 ^b	7.5 ^{ab}	4.9 ^c	7.3 ^b	8.7 ^a	0.4	0.0015
NDF	4.8 ^a	5.6 ^a	3.8 ^b	5.4 ^a	5.2 ^a	0.3	0.0113
DNDF	4.0 ^a	4.2 ^a	3.1 ^b	2.1 ^c	4.2 ^a	0.2	0.0005
INDF	0.9 ^b	1.5 ^b	0.6 ^b	3.3 ^a	1.0 ^b	0.3	0.0002
Mean:							
Wet digesta	42.7 ^{cd}	47.8 ^{bc}	40.2 ^d	48.2 ^b	55.2 ^a	1.7	0.0028
DM (%)	12.4 ^{ab}	13.2 ^a	11.0 ^c	11.9 ^{bc}	13.1 ^{ab}	0.4	0.0181
Dry digesta	5.3 ^c	6.3 ^{ab}	4.4 ^d	5.8 ^{bc}	7.2 ^a	0.3	0.0008
NDF	4.0 ^b	4.9 ^a	3.3 ^c	4.3 ^b	4.3 ^b	0.2	0.0020
DNDF	3.2 ^{bc}	3.7 ^a	2.7 ^c	1.6 ^d	3.5 ^{ab}	0.2	0.0001
INDF	0.8 ^b	1.2 ^b	0.6 ^b	2.7 ^a	0.8 ^b	0.2	0.0001

^{abcd}Means within rows with different superscript are significantly different ($P < 0.05$).

*DNDF = Digestible NDF.

**INDF = Indigestible NDF.

As for DNDF, animals fed SLH had the least DNDF pool (1.6 kg), and SBH had the highest DNDF pool (3.7 kg) followed by animals fed SUTRS (3.5 kg), UNBH (3.2 kg) and SMS (2.7 kg). Approximately more than 50 % (Expt.1) and more than 60 % (Expt.2) of the rumen pool sizes of NDF were indigestible in animals fed LH and SLH respectively.

4.9 Rate of digestion and passage

When passage rate was estimated as the decline in faecal chromium concentration, the 24 h and 36 h faecal samples were omitted. Chromium had not yet started to decline probably because the samples were taken too early. The passage rates (k_p) measured using the chromium mordanted fibre (CR-MF) and by using the rumen evacuation technique (RET) and that estimated from the relationship between *in vivo* digestibility and *in sacco* rumen degradability constants (RDC) are shown in Table 4.10 (Expt.1) and Table 4.11 (Expt.2). The passage rates were affected by diets (Table 4.10 and Table 4.11) for all methods used except in expt.1 using CR-MF. There was no agreement between the three methods. The k_p measured by using CR-MF method was higher than k_p calculated from rumen evacuation procedures (RET) in expts.1 and 2. In addition the k_p based on CR-MF and the RET methods did not show any marked pattern or trend in relationship to the level of NDF intake for different forages in expts.1 and 2. The passage rates estimated from the relationship between the *in vivo* digestibility of NDF and the RDC were very low in expts.1 and 2 and negative for LH (Expt.1) and SLH (Expt.2). Despite these negligible k_p values, their estimates fit with *in vivo* data but cannot be used for any further calculations. The rate of digestion k_d of NDF and DNDF derived from NDF kinetics in expt.1 (Table 4.10) and expt.2 (Table 4.11) are lower than those obtained from the *in sacco* indirect method (Table 4.3) but very close both in expts.1 and 2.

Table 4.10 NDF fractions intake, mean rumen pool sizes, faecal output, rate of passage measured using chromium mordanted fibre (CR-MF), derived kinetics for NDF, DNDF and INDF* and passage rate calculated from *in vivo* digestibility (ADC) and rumen degradability characteristics (RDC) of NDF (Experiment 1)

Parameter Estimated	Diet					SEM	P-value diet
	BH	MS	LH	LGH	UTRS		
Intake (kg d⁻¹):							
NDF	3.79 ^b	3.06 ^b	4.02 ^{ab}	5.00 ^a	4.86 ^a	0.35	0.0106
DNDF	3.22 ^a	2.63 ^b	2.95 ^a	3.90 ^a	4.62 ^a	0.30	0.0043
INDF**	0.58 ^b	0.43 ^{bc}	1.06 ^a	1.10 ^a	0.24 ^c	0.07	0.0001
Mean rumen pool sizes (kg) of:							
NDF	4.8 ^a	3.8 ^b	4.7 ^a	5.2 ^a	4.5 ^{ab}	0.2	0.0123
DNDF	3.9 ^a	3.2 ^{bc}	2.0 ^d	2.9 ^c	3.6 ^{bc}	0.2	0.0001
INDF	1.0 ^c	0.6 ^c	2.7 ^a	2.3 ^b	0.8 ^c	0.1	0.0001
Faecal output (kg d⁻¹):							
NDF	1.73 ^a	1.20 ^b	1.67 ^a	2.01 ^a	1.88 ^a	0.12	0.0019
DNDF	1.16 ^b	0.77 ^c	0.61 ^d	0.91 ^{bc}	1.65 ^a	0.10	0.0001
INDF	0.58 ^b	0.43 ^{bc}	1.06 ^a	1.10 ^a	0.24 ^c	0.07	0.0001
Passage rates (% h⁻¹):							
CR-MF ¹	2.26	3.24	2.98	2.56	2.79	0.37	0.4201
ADC and RDC ²	0.95 ^a	0.45 ^a	-0.92 ^b	0.23 ^a	0.51 ^a	0.28	0.0053
Derived NDF kinetics (% h⁻¹):							
Rate of intake (k_i):							
NDF	3.47	3.65	3.69	4.11	4.58	0.34	0.2024
DNDF	3.66 ^b	3.77 ^b	6.87 ^a	5.77 ^a	5.38 ^{ab}	0.66	0.0220
INDF**	2.70 ^b	3.48 ^a	1.64 ^c	2.06 ^{bc}	1.17 ^c	0.23	0.0001
Rate of passage (k_p):							
NDF	1.54 ^{ab}	1.36 ^b	1.53 ^b	1.63 ^{ab}	1.78 ^a	0.08	0.0323
DNDF	1.28 ^b	1.04 ^b	1.41 ^b	1.30 ^b	1.93 ^a	0.13	0.0058
INDF	2.70 ^b	3.48 ^a	1.64 ^c	2.06 ^{bc}	1.17 ^c	0.23	0.0001
Rate of digestion (k_d):							
NDF (k_d)	1.93	2.29	2.16	2.16	2.80	0.29	0.3143
DNDF (k_d)	2.37 ^c	2.74 ^b	5.46 ^a	4.46 ^{ab}	3.46 ^b	0.60	0.0192
c NDF (<i>in sacco</i>)	3.8 ^{bc}	2.0 ^c	6.9 ^a	5.0 ^{ab}	3.2 ^{bc}	0.7	0.0051

^{ab}Means within rows with different superscript are significantly different (P<0.05).

*INDF was determined by long time (30 days) nylon bag incubation.

** Assumed that INDF intake is equal to faecal output INDF as INDF is not digestible and rate of digestion is therefore zero.

¹Passage rate estimated using chromium mordanted fibre (CR-MF)

²Passage rate calculated using *in vivo* apparent digestibility coefficients (ADC) and rumen degradability characteristics (RDC) of NDF (Model 3.12).

Table 4.11 NDF fractions intake, mean rumen pool sizes, faecal output, rate of passage measured using chromium mordanted fibre (CR-MF), derived kinetics for NDF, DNDF and INDF* and passage rate calculated from *in vivo* digestibility (ADC) and rumen degradability characteristics (RDC) of NDF (Experiment 2)

Parameter estimated	Diet					SEM	P-value diet
	UNBH	SBH	SMS	SLH	SUTRS		
Intake (kg d⁻¹):							
NDF	3.64	3.66	3.13	3.68	4.84	0.31	0.0640
DNDF	3.18 ^b	3.08 ^b	2.73 ^b	2.75 ^b	4.61 ^a	0.26	0.0071
INDF**	0.47 ^b	0.5 ^b	0.40 ^{bc}	0.92 ^a	0.23 ^c	0.07	0.0018
Mean rumen pool size (kg) of:							
NDF	4.0 ^b	4.9 ^a	3.3 ^c	4.3 ^b	4.3 ^b	0.2	0.0020
DNDF	3.2 ^{bc}	3.7 ^a	2.7 ^c	1.6 ^d	3.5 ^{ab}	0.2	0.0001
INDF	0.8 ^b	1.2 ^b	0.6 ^b	2.7 ^a	0.8 ^b	0.2	0.0001
Faecal output (kg d⁻¹):							
NDF	1.43 ^b	1.56 ^b	1.05 ^b	1.47 ^b	2.11 ^a	0.15	0.0203
DNDF	0.96 ^b	0.98 ^b	0.65 ^c	0.60 ^c	1.88 ^a	0.09	0.0001
INDF**	0.47 ^b	0.5 ^b	0.40 ^{bc}	0.92 ^a	0.23 ^c	0.07	0.0018
Passage rates (% h⁻¹):							
CR-MF ¹	2.61 ^b	2.92 ^b	3.86 ^a	3.66 ^a	2.22 ^b	0.21	0.0030
ADC and RDC ²	0.20 ^b	0.38 ^{ab}	0.48 ^{ab}	-0.84 ^c	1.13 ^a	0.21	0.0032
Derived NDF kinetics (% h⁻¹):							
Rate of intake (k_i):							
NDF	3.82 ^{ab}	3.09 ^c	4.17 ^{ab}	3.54 ^{bc}	4.67 ^a	0.27	0.0360
DNDF	4.23 ^{bc}	3.43 ^c	4.45 ^{bc}	7.29 ^a	5.39 ^b	0.56	0.0058
INDF	2.39 ^{bc}	2.14 ^{bc}	3.46 ^a	1.41 ^c	1.54 ^{bc}	0.26	0.0039
Rate of passage (k_p):							
NDF	1.50 ^b	1.32 ^b	1.38 ^b	1.41 ^b	2.02 ^a	0.13	0.0498
DNDF	1.28 ^c	1.10 ^c	1.07 ^c	1.59 ^b	2.19 ^a	0.17	0.0122
INDF	2.39 ^{bc}	2.14 ^{bc}	3.46 ^a	1.41 ^c	1.54 ^{bc}	0.26	0.0039
Rate of digestion (k_d):							
NDF (k_d)	2.32	1.77	2.79	2.09	2.65	0.21	0.0641
DNDF (k_d)	2.95 ^b	2.32 ^b	3.37 ^b	5.70 ^a	3.19 ^b	0.42	0.0020
c NDF (in sacco)	3.0 ^b	2.9 ^b	2.6 ^b	9.1 ^a	3.6 ^b	0.3	0.0001

^{abc}Means within rows with different superscript are significantly different ($P < 0.05$).

*INDF was determined by long time (30 days) nylon bag incubation.

**Assumed that INDF intake is equal to faecal output INDF as INDF is not digestible and rate of digestion is therefore zero.

¹Passage rate estimated using chromium mordanted fibre (CR-MF)

²Passage rate calculated using *in vivo* apparent digestibility coefficients (ADC) and rumen degradability characteristics (RDC) of NDF.

4.10 Rumen physical fill, mean rumen retention time (MRRT) and effective degradability (ED) calculated using four different passage rates in expts. 1 and 2

4.10.1 Rumen physical fill-{Fill (day)}

Fill was calculated using RDC obtained from the nylon bag technique and passage rate (Model 3.15). Fill of NDF in the rumen for the forage diets in expts.1 and 2 are given in Table 4.12. The results showed a significant difference ($P<0.05$) in fill for the forage when calculated using passage rate obtained from RET-total NDF in expts.1 and 2, whereas there were no differences ($P>0.05$) when other methods were used.

There were differences between forages in fill when calculated using k_p obtained from rumen evacuations for total NDF in expt.1 ($P<0.045$) and expt.2 ($P<0.046$). Fill values were not different ($P>0.7$) between forages when calculated using k_p from CR-MF in expt.1. Fill values calculated using an assumed passage rate of 2 % h^{-1} as a constant value was also not different between forages ($P>0.34$) in expts.1 and expt.2 ($P>0.09$). There was no agreement between the four approaches except when fill was calculated using k_p obtained from NDF, DNDF and INDF and assumed constant passage rate (2 % h^{-1}) for BH forage diet in expt.1 and for UNBH and SMS in expt.2.

4.10.2 Mean rumen retention time (MRRT)

The time in which the forages ingested spent in the rumen is given in Table 4.13 for expts.1 and 2. The MRRT was calculated as the reciprocal of passage rate, therefore, similar variations as those demonstrated by passage rates were observed.

Table 4.12 Physical fill (Fill) of NDF in the rumen as estimated using degradation characteristics (RDC) and passage rates (k_p) estimated from chromium mordanted fibre (CR-MF), rumen evacuation technique (RET) or assumed passage rate of 2% h⁻¹ in experiments 1 and 2

Diet	Fill (day) calculated using four different passage rates			
	Fill-1	Fill-2	Fill-3	Fill-4
Experiment 1:				
BH	1.19	1.55 ^{ab}	1.25	1.25
MS	0.99	1.84 ^a	1.50	1.38
LH	0.98	1.77 ^a	1.64	1.35
LGH	1.00	1.41 ^b	1.24	1.20
UTRS	1.08	1.35 ^b	1.74	1.23
SEM	0.12	0.12	0.14	0.07
<i>P</i> -value diet	0.6839	0.0447	0.0992	0.3364
Experiment 2:				
UNBH	1.33	1.65 ^a	1.32	1.32
SBH	1.03	1.91 ^a	1.54	1.37
SMS	0.69	1.55 ^a	1.21	1.21
SLH	0.73	1.64 ^{ab}	1.66	1.17
SUTRS	1.19	1.09 ^b	1.27	1.13
SEM	0.15	0.12	0.13	0.05
<i>P</i> -value diet	0.0746	0.0459	0.2426	0.0886

^bMeans within columns with different superscript are significantly different ($P < 0.05$).

Fill - 1 = Fill (day) calculated from k_p estimated from chromium mordanted fibre (CR-MF).

Fill - 2 = Fill (day) calculated from k_p estimated from rumen evacuation technique (RET) using derived k_p for NDF.

Fill - 3 = Fill (day) calculated from k estimated from rumen evacuation technique (RET)- using derived k_p for NDF, DNDF and INDF (Model 3.15).

Fill - 4 = Fill (day) calculated using an assumed passage rate (k_p) of 2 % h⁻¹.

Table 4.13 Mean rumen retention time (MRRT) of NDF as estimated from passage rates (k_p) estimated from chromium mordanted fibre (CR-MF) and rumen evacuation technique (RET) in experiments 1 and 2

Diet	MRRT (h) calculated using different passage rates			
	MRRT-1	MRRT-2	MRRT-3	MRRT-4
Experiment 1:				
BH	46	66 ^{abc}	81 ^a	38 ^b
MS	32	75 ^a	99 ^a	30 ^b
LH	35	69 ^{ab}	81 ^a	62 ^b
LGH	39	61 ^{abc}	77 ^{ab}	49 ^b
UTRS	42	57 ^c	53 ^b	90 ^a
SEM	5	4	8	5
<i>P</i> -value diet	0.3340	0.0396	0.0163	0.0001
Experiment 2:				
UNBH	49	67	79	42 ^b
SBH	35	79	95	50 ^{ab}
SMS	24	76	99	31 ^b
SLH	28	73	73	75 ^a
SUTRS	44	51	48	74 ^a
SEM	7	7	11	7
<i>P</i> -value diet	0.1639	0.2266	0.0870	0.0075

^{ab}Means within columns with different superscript are significantly different ($P < 0.05$).

MRRT-1 = Calculated from reciprocal of passage rate (k_p) estimated from chromium mordanted fibre (CR-MF).

MRRT-2 = Calculated from reciprocal of passage rate (k_p) estimated from rumen evacuation technique (RET) using derived k_p for total NDF.

MRRT-3 = Calculated from reciprocal of passage rate (k_p) estimated from rumen evacuation technique (RET)- using derived k_p for DNDF.

MRRT-4 = Calculated from reciprocal of passage rate (k_p) estimated from rumen evacuation technique (RET)- derived k_p for INDF.

4.10.3 Effective degradability of forage NDF

Effective degradability (ED) of forages calculated using passage rate measured from CR-MF, total NDF or DNDF obtained from RET is given in Table 4.14 for expts.1 and 2. Differences in ED for individual forage were consistent with their respective passage rates and decreased with increasing passage. The ED were not different in both experiments except in expt.1 when ED was calculated from passage rate obtained from CR-MF ($P < 0.04$).

4.10.4 The relationship between *in vivo* and ruminal digestibility (ED)

The relationship between NDF *in vivo* digestibility and ED was tested using simple regression analysis (Model 3.20) and the results are given in Table 4.17 for expts.1 and 2. The main idea here was to test how ED corresponds to *in vivo* digestibility. In expt.1 the relationship between ED and *in vivo* digestibility was zero across forages. In expt.2 the relationship improved ($P < 0.002$) when ED was calculated using passage rate obtained from RET-DNDF ($R^2 = 0.40$), RET-total NDF ($R^2 = 0.34$) and CR-MF had poor relationship ($R^2 = 0.11$).

4.11 Effect of FM and urea supplementation

The effects of supplementation of selected major variables considered to have effect on intake are given in Table 4.18. The results showed that there was no interaction (supplementation x forage) since supplementation gave similar effect in all forage diets.

Table 4.14 Effective degradability (ED) of NDF calculated using degradation characteristics (RDC) and passage rates (k_p) estimated from chromium mordanted fibre (CR-MF), rumen evacuation technique (RET) or assumed passage rate of 2% h⁻¹ in experiments 1 and 2

Diet	Effective degradability (ED) calculated using different passage rates (k_p) in (%)							
	ED-1	ED-2	ED-3	ED-4	ED-5	HGF	RNDFD	ADC
Experiment 1:								
BH	38.0 ^a	44.5	47.5	39.8	50.2	4.8	51.9	54.6
MS	25.4 ^b	41.3	46.0	34.0	46.2	4.3	56.9	61.2
LH	31.9 ^{ab}	37.7	38.4	35.4	39.0	4.5	53.0	57.7
LGH	38.8 ^a	44.9	47.5	42.2	46.8	4.7	54.9	59.4
UTRS	36.0 ^a	42.9	41.6	40.8	49.5	4.2	58.1	60.6
SEM	3.0	3.1	3.3	3.2	3.6	0.3	2.5	2.3
<i>P</i> -value diet	0.04	0.50	0.26	0.34	0.34	0.06	0.60	0.32
Experiment 2:								
UNBH	32.6	41.2	43.7	36.7	46.4	4.3	56.8	60.3
SBH	29.4	40.2	42.5	34.1	45.0	4.8	52.5	56.4
SMS	29.3	49.0	53.5	41.7	54.7	4.1	59.4	64.7
SLH	38.2	46.2	45.6	43.9	50.1	4.6	54.4	59.4
SUTRS	45.6	45.1	43.9	45.7	50.4	4.4	56.5	56.6
SEM	3.2	3.6	3.8	2.6	4.2	0.2	2.7	2.4
<i>P</i> -value diet	0.08	0.53	0.45	0.09	0.68	0.26	0.26	0.26

^{ab}Means within columns with different superscript are significantly different ($P < 0.05$).

ED - 1 = ED calculated from k_p estimated from chromium mordanted fibre (CR-MF).

ED - 2 = ED calculated from k_p estimated from rumen evacuation technique (RET) -total NDF.

ED - 3 = ED calculated from k_p estimated from rumen evacuation technique (RET)- DNDF.

ED - 4 = ED calculated using an assumed passage rate (k_p) of 2 % h⁻¹.

ED - 5 = ED calculated using Model 3.13 that assumes two-compartment model.

HGF = Hind gut fermentation calculated by assuming that 10 % of duodenal flow will be digested in the hind gut (Robinson *et al.*, 1987).

RNDFD = The total tract NDF digestibility (ADC) corrected for hind gut fermentation

4.12 Predicted intake

The predicted NDF intake (PNDFI) using rumen pool size of NDF (kg) and Fill (day) calculated using passage rate estimated using either RET or CR-MF method is given in Table 4.15 for expts.1 and 2. Measured NDF intakes for different forages are also given in Table 4.15 for easy comparison. The PNDFI for the forage-based diets were over-estimated when Fill calculated from passage rate estimated from CR-MF were used except in expt.1 for UTRS. In expt.2, PNDFI was over-estimated for SBH, SLH and SMS, whereas, UNBH and SUTRS were under-estimated. The PNDFI was under-estimated when passage rate obtained from RET was used to calculate Fill for all forage diets in experiments 1 and 2.

Table 4.16 gives the potential DM intake (PDMI) of the forages estimated from the PNDFI (Model 3.16). A similar trend to that obtained for PNDFI was observed for PDMI for forages in expts.1 and 2. The accuracy of predicting DM intake (Model 3.17) from PNDFI from NDF parameters and measured passage rates tested by simple regression analysis and their linear relationships are given in Table 4.17.

In expt.1 the best relationship ($R^2 = 0.70$) was obtained when DM intake was predicted using pool size of NDF and Fill calculated from RET-total NDF ($P < 0.0001$). Lowest $R^2 = 0.31$ was obtained when passage rate estimated from RET-DNDF plus INDF ($P < 0.004$) were used. Medium $R^2 = 0.47$ was obtained when passage rates estimated from CR-MF ($P < 0.0002$). In expt.2 the relationship was highest ($R^2 = 0.75$) for RET-total NDF ($P < 0.0001$) and followed by $R^2 = 0.46$ for RET-DNDF plus INDF ($P < 0.0005$) and lowest ($R^2 = 0.10$) for CR-MF ($P > 0.16$).

Table 4.15 Predicted NDF intake (PNDFI) estimated from rumen pool sizes of NDF and Fill calculated from passage rates (k) measured using chromium mordanted fibre (CR-MF), rumen evacuation technique (RET), derived passage rates of NDF, DNDF and INDF or assumed passage rate of 2 % h^{-1} (Experiments 1 and 2)

PNDFI (kg d^{-1})	Diet					SEM	R ²	P-value diet
	BH	MS	LH	LGH	UTRS			
Experiment 1:								
MNDFI*	3.79 ^b	3.06 ^b	4.02 ^a	5.00 ^a	4.86 ^a	0.35	0.75	0.011
PNDFI ¹ CR-MF	4.04	3.79	5.01	5.14	4.76	0.58	0.73	0.398
PNDFI ² (RET) Total-NDF	3.12 ^{ab}	2.09 ^c	2.75 ^b	3.65 ^a	3.32 ^{ab}	0.22	0.83	0.005
PNDFI ³ (RET) All NDF fractions	3.88 ^a	2.57 ^b	2.98 ^b	4.16 ^a	2.62 ^b	0.25	0.84	0.085
PNDFI ⁴ $k = 2\% h^{-1}$	3.81 ^{ab}	2.78 ^c	3.57 ^b	4.29 ^a	3.63 ^b	0.21	0.89	0.111
Experiment 2:								
	UNBH	SBH	SMS	SLH	SUTRS			
MNDFI*	3.64	3.67	3.13	3.68	4.84	0.31	0.82	0.064
PNDFI ¹ CR-MF	3.35 ^b	4.74 ^{ab}	4.38 ^{ab}	6.10 ^a	3.74 ^b	0.45	0.77	0.020
PNDFI ² (RET) Total-NDF	2.41 ^b	2.61 ^b	2.12 ^b	2.84 ^{ab}	3.63 ^a	0.22	0.82	0.038
PNDFI ³ (RET) All NDF fractions	2.99	3.33	2.64	2.73	3.17	0.29	0.63	0.540
PNDFI ⁴ $k = 2\% h^{-1}$	3.00 ^b	3.58 ^a	2.79 ^b	3.74 ^a	3.65 ^a	0.17	0.91	0.013

^{ab}Means within rows with different superscript are significantly different ($P < 0.05$).

¹Predicted NDF intake using Fill calculated from k_p estimated from chromium mordanted fibre (CR-MF).

²Predicted NDF intake using Fill calculated from k_p estimated from rumen evacuation technique (RET)-total NDF.

³Predicted NDF intake using Fill calculated from k_p estimated from rumen evacuation technique (RET)- NDF, INDF and DNDF.

⁴Predicted NDF intake using Fill calculated from assumed k_p of 2 % h^{-1} .

*Measured NDFI as given in Table 4.4.

Table 4.16 Predicted DM intake (PDMI)* estimated from predicted NDF intake (PNDFI) in Table 12 and the proportion of NDF in the forage DM (Experiments 1 and 2)

PNDFI (kg d ⁻¹)	Diet					SEM	R ²	P-value diet	
	BH	MS	LH	LGH	UTRS				
Experiment 1:									
MDMI**	5.06 ^b	4.16 ^c	6.48 ^a	6.66 ^a	6.31 ^{ab}	0.46	0.76	0.009	
PDMI ¹									
CR-MF	5.38 ^b	5.16 ^b	8.09 ^a	6.85 ^{ab}	6.22 ^{ab}	0.63	0.79	0.040	
PDMI ² (RET)									
Total-NDF	4.16 ^a	2.85 ^b	4.44 ^a	4.86 ^a	4.32 ^a	0.28	0.84	0.003	
PDMI ³ (RET)	All	5.18 ^a	3.52 ^b	4.80 ^a	5.54 ^a	3.42 ^b	0.33	0.85	0.002
NDF fractions		5.07 ^{ab}	3.79 ^c	5.78 ^a	5.72 ^a	4.73 ^b	0.25	0.92	0.001
PDMI ⁴ k = 2% h ⁻¹									
Experiment 2:									
PDMI ¹									
MDMI**	UNBH	SBH	SMS	SLH	SUTRS				
	4.82	4.82	4.36	5.91	6.36	0.43	0.79	0.069	
PDMI ¹									
CR-MF	4.47 ^b	6.32 ^b	6.06 ^b	9.79 ^a	5.09 ^b	0.64	0.85	0.003	
PDMI ² (RET)									
Total-NDF	3.21 ^b	3.48 ^b	2.95 ^b	4.56 ^a	4.80 ^a	0.34	0.79	0.030	
PNDFI ³ (RET) ALL									
NDF fractions	3.98	4.45	3.67	4.39	4.21	0.47	0.50	0.807	
PDMI ⁴									
k = 2% h ⁻¹	4.00 ^b	4.77 ^b	3.90 ^b	6.02 ^a	4.89 ^b	0.25	0.92	0.002	

^{ab}Means within rows with different superscript are significantly different ($P < 0.05$).

¹Calculated DMI from predicted NDF intake using Fill calculated from k estimated from chromium mordanted fibre (CR-MF).

²Calculated DMI from predicted NDF intake using Fill calculated from k estimated from rumen evacuation technique (RET) -total NDF.

³Calculated DMI from predicted NDF intake using Fill calculated from k estimated from rumen evacuation technique (RET) - total NDF, DNDF and INDF.

⁴Calculated DMI from predicted NDF intake using Fill calculated from assumed k of 2 % h⁻¹.

*PDMI = 1/(proportion of NDF in the forage DM x PNDFI (Model 3.17).

**Measured DMI as given in Table 4.4

Table 4. 17 The accuracy of predicting forage DM intake (FDMI) using rumen pool size of NDF and Fill and that of NDF digestibility (NDFD) using effective digestibility (ED) of NDF calculated from passage rates estimated from different methods in experiments 1 and 2

PFDMI from:	Equation	R ²	RMSE	SE of estimate ¹		P>value	
				β	α	β	α
Experiment 1:							
Fill-1	DMI (kg d ⁻¹) = 2.81 + 0.46X	0.47	1.10	0.10	0.68	0.0002	0.004
Fill-2	DMI (kg d ⁻¹) = 1.19 + 1.10X	0.70	0.83	0.15	0.64	0.0001	0.079
Fill-3	DMI (kg d ⁻¹) = 3.04 + 0.60X	0.28	1.26	0.19	0.88	0.0002	0.004
Fill-4	DMI (kg d ⁻¹) = 2.59 + 0.63X	0.36	1.21	0.17	0.91	0.002	0.009
ED-1	NDFD (g kg ⁻¹) = 0.61 - 0.08X	0.01	0.06	0.13	0.04	0.563	0.0001
ED-2	NDFD (g kg ⁻¹) = 0.58 + 0.02X	0.00	0.06	0.17	0.07	0.918	0.0001
ED-3	NDFD (g kg ⁻¹) = 0.57 + 0.05X	0.00	0.06	0.16	0.07	0.775	0.0001
ED-4	NDFD (g kg ⁻¹) = 0.55 + 0.10X	0.02	0.06	0.16	0.06	0.535	0.0001
ED-5	NDFD (g kg ⁻¹) = 0.57 + 0.05X	0.01	0.06	0.15	0.07	0.743	0.0001
RNDFD	NDFD (g kg ⁻¹) = 0.52 + 0.05X	0.01	0.06	0.16	0.08	0.743	0.0001
Experiment 2:							
Fill-1	DMI (kg d ⁻¹) = 4.16 + 0.18X	0.10	1.36	0.12	0.82	0.0002	0.004
Fill-2	DMI (kg d ⁻¹) = 0.98 + 1.16X	0.75	0.71	0.15	0.57	0.0001	0.101
Fill-3	DMI (kg d ⁻¹) = 1.02 + 1.04X	0.46	1.05	0.25	1.06	0.001	0.345
Fill-4	DMI (kg d ⁻¹) = 1.99 + 0.70X	0.45	1.06	0.17	0.84	0.001	0.029
ED-1	NDFD (g kg ⁻¹) = 0.53 + 0.24X	0.11	0.07	0.15	0.05	0.139	0.0001
ED-2	NDFD (g kg ⁻¹) = 0.44 + 0.38X	0.34	0.06	0.12	0.05	0.004	0.0001
ED-3	NDFD (g kg ⁻¹) = 0.44 + 0.05X	0.40	0.05	0.10	0.05	0.001	0.0001
ED-4	NDFD (g kg ⁻¹) = 0.47 + 0.35X	0.23	0.06	0.14	0.06	0.022	0.0001
ED-5	NDFD (g kg ⁻¹) = 0.44 + 0.33X	0.30	0.06	0.12	0.06	0.016	0.0001
RNDFD	NDFD (g kg ⁻¹) = 0.38 + 0.37X	0.30	0.06	0.14	0.07	0.016	0.0001

Fill - 1 = Fill (day) calculated from k_p estimated from chromium mordanted fibre (CR-MF).

Fill - 2 = Fill (day) calculated from k_p estimated from rumen evacuation technique (RET) - total NDF.

Fill - 3 = Fill (day) calculated from k_p estimated from rumen evacuation technique (RET) - total NDF digestible NDF (DNDF) and indigestible NDF (INDF).

Fill - 4 = Fill (day) calculated using an assumed passage rate (k_p) of 2 % h⁻¹.

ED - 1 = ED calculated from k_p estimated from chromium mordanted fibre (CR-MF).

ED - 2 = ED calculated from k_p estimated from rumen evacuation technique (RET) - total NDF.

ED - 3 = ED calculated from k_p estimated from rumen evacuation technique (RET) - digestible NDF.

ED - 4 = ED calculated using an assumed passage rate (k_p) of 2 % h⁻¹.

ED - 5 = ED calculated using Model 3.13 that assumes two-compartment model.

RNDFD = Ruminal NDF digestibility (RNDFD) where hind gut fermentation calculated by assuming that 10 % of duodenal flow will be digested in the hind gut (Robinson *et al.*, 1987) was corrected from total tract NDF digestibility.

¹ The symbols β and α are the coefficient of regression and the intercept respectively, whereas X is the predicted values.

Table 4.18 Effect of supplementation on some major variables¹

Variable	Level of significant	
	Supplementation	Supplementation x Forage type
Intake:		
Forage DMI	0.0001	0.8375
Nitrogen intake	0.0001	0.0602
NDF intake	0.0001	0.9128
Water intake	0.0001	0.8823
Rumen pool sizes of :		
Wet digesta	0.0001	0.3859
Dry digesta	0.0001	0.6442
NDF	0.0001	0.6097
DNDF	0.0001	0.6813
INDF	0.0001	0.7177
In vivo digestibility of :		
DM	0.0001	0.4673
OM	0.0019	0.5545
NDF	0.0771	0.4546
N	0.0001	0.0148
Ash	0.0001	0.7186
Rumen fermentation		
PH	0.1018	0.4583
NH ₃	0.0001	0.4047
Passage rates:		
CR-MF*	0.0137	0.1764
RET* * Total NDF	0.0062	0.4089
DNDF	0.0002	0.7584
INDF	0.0001	0.2645
Fill (day):		
Fill- value (CR-MF)***	0.2368	0.7064
Fill-value (RET)****	0.0882	0.0942
Rate of digestion:		
Rate of digestion (in sacco)	0.0001	0.1519

¹Comparison based on unsupplemented BH that was fed in both experiments.

*Passage rate estimated from CR-MF.

**Passage rate estimated from RET.

***Fill calculated from passage rate obtained from CR-MF.

****Fill calculated from passage rate obtained from RET-total NDF

Table 4.19 gives R^2 values obtained from simple regression analysis of measured and predicted LSMeans intake (Table 4.16) and where passage rate from RET-total NDF were used to estimate fill values. The precision improved from $R^2 = 0.70$ to $R^2 = 0.84$ in expt. 1 and from $R^2 = 0.75$ to $R^2 = 0.97$ in expt. 2; and from both expts. $R^2 = 0.88$.

Table 4.19 Calculated R^2 obtained from simple regression analysis of the measured and predicted LSMeans (Table 4.16) dry matter intake instead of individual observations.

GROUP	Method	R^2 obtained from individual observations	R^2 obtained from LSMeans
Expt.1	Fill-1*	0.70	0.84
	Fill-2**	0.36	0.70
Expt.2	Fill-1	0.75	0.97
	Fill-2	0.45	0.51
Expt.1 and 2	Fill-1	NA***	0.88
	Fill-2	NA	0.62

*Fill-1 = Fill calculated from passage rate estimated from rumen evacuation technique (RET) method total NDF (RET-total NDF).

**Fill-2 = Fill calculated from a constant passage rate of 2 % h⁻¹

*** NA = Not analysed.

5 DISCUSSION

5.1 Description of forage characteristics

The chemical composition values of the forages in the present study (Table 4.1) were close to values reported for tropical grass and legume forages (Kimambo *et al.*, 1994; Shem *et al.*, 1995; Mgheni *et al.*, 1996; Mero and Udén, 1998) and urea-treated rice straws (Tuen *et al.*, 1991; Mgheni *et al.*, 1993). Variation in chemical composition in these forages was expected because these forages were of different species, cut at different physiological maturity stages, grown from different localities and the rice straw used was treated with urea. Apart from species, stage of cut and ecological variations other differences can be attributed to physical forms, preservation methods and severity of losses of leaves that normally occur in lucerne hays.

Lucerne hay had lower CP content ($151 \text{ g kg}^{-1} \text{ DM}$) than values reported elsewhere of $222 \text{ g kg}^{-1} \text{ DM}$ (Weiss and Shockey, 1991), $180 \text{ g kg}^{-1} \text{ DM}$ (Holden *et al.*, 1994) and $204 \text{ g kg}^{-1} \text{ DM}$ (Stensig and Robinson, 1997). Higher CP and lower NDF observed in Lucerne hay (LH) and Lucerne grass hay (LGH) compared to the other forages viz: Maize silage (MS), *Brachiaria* hay (BH) and Urea-treated rice straw (UTRS) were because legumes, in general, have lower NDF and higher CP and mineral contents than grasses. Similar trends have been reported for temperate grasses and legumes (Weiss and Shockey, 1991) and for tropical grass and legumes forages (Kimambo *et al.*, 1994; Mgheni *et al.*, 1996).

Increased CP content in UTRS even up to double folds relative to ordinary rice straws have also been demonstrated elsewhere in rice straw based diets (Djajanegara and Doyle, 1989; Tuen *et al.*, 1991; Mgheni *et al.*, 1993). Low CP content found in MS was due to low CP of the maize crop ensiled and losses that might have occurred during ensiling. Sarwatt *et al.* (1989) reported

similar CP (6.0 % DM) in tropical maize silage cut at post-anthesis but higher CP (6.7 and 11.1 % DM) when cut at anthesis and pre-anthesis respectively. In this study, MS was prepared from a maize crop cut post anthesis and the soil N content (although not measured) might have been low, a situation that can contribute to low N in MS compared to the literature values (Stensig *et al.*, 1994a; Bal *et al.*, 1997). The results suggest that stage of cut was critical for production of maize silage of good quality.

The BH also had relatively low CP compared to samples from same field cut at about the same stage of growth (Kimambo *et al.*, 1994; Mgheni *et al.*, 1996). This may suggest that, season and year have a profound effect on the CP content in forages. Differences in CP and other nutrients like NDF content attributed to season and year of harvest have been reported in Tanzania at similar and different stages of cut in *Chloris gayana* grass (Mbwile and Udén, 1997).

The NDF values obtained in BH and UTRS were comparable to those reported by other workers in tropical forages (Kimambo *et al.*, 1994; Shem *et al.*, 1995) but higher than that reported by Djajanegara and Doyle (1989) for urea-treated rice straw. In contrast, higher NDF values (Tuen *et al.*, 1991; Mgheni *et al.*, 1993) than what has been obtained in this study have been reported in urea- treated rice straws. This implies that although urea-treatment increased the nutrient availability (Djajanegara and Doyle, 1989; Tuen *et al.*, 1991) it also lead to losses of soluble nutrients and increased NDF fraction (Tuen *et al.*, 1991; Mgheni *et al.*, 1993). The NDF value for MS (737 g kg⁻¹ DM) was much higher than those reported elsewhere (Stensig *et al.*, 1994a; De Boever *et al.*, 1997; Bal *et al.*, 1997). This was because MS used in this study was tropical forage (C⁴ plants) which physiologically should have higher NDF content than temperate forages (C³ plants). Similar arguments can explain higher NDF values found in LH (615 g kg⁻¹ DM)

compared to alfalfa silage (469 g kg⁻¹DM) reported elsewhere (Weiss and Shockey, 1991; Stensig and Robinson, 1997).

Other possible explanation of silage of lower quality than that reported in the literature (Bal *et al.*, 1997) was the use of square concrete silo which gave poor compaction that resulted into burned and browning (Maillard reactions) or mouldy silage. In such silage NDF fractions have been reported to be high due to reduce soluble fractions. High losses due to effluent from wet ensilaged material (<30% DM) have been reported (Gasa *et al.*, 1991; Van Soest, 1994). The silage produced had 22 % DM (Table 4.1). It is obvious that the material ensiled was of low DM and losses of high magnitude may have occurred. Silage usually stabilises two months after it has been ensiled (Van Soest, 1994; Bal *et al.*, 1997) and can stay for a long time if the silage is well preserved. However, since the preservation methods in this study were not optimal, long time ensiling (one year) might have contributed to further losses of the soluble fractions in MS and resulted in low CP and higher NDF compared to what has been reported in the literature (Stensig *et al.*, 1994a; Bal *et al.*, 1997).

Variability in chemical composition of feeds can sometimes be caused by analytical procedures used. The analysis of DM, ash and CP can easily be reproduced using the AOAC (1990) standardised procedure. The analysis of NDF has not been standardised and the procedures vary considerably and so are the results. Although starch was not measured in this study, the presence of neutral detergent insoluble and resistant starch in tropical maize silage can not be ruled out since the use of α -amylase as suggested by Van Soest *et al.* (1991) was omitted.

The apparent digestibility coefficients showed high variations (Table 4.6) for DM digestibility (DMD) of about 11 %, OM digestibility (OMD) of 7 %, NDF digestibility (NDFD) of 6 %, N digestibility (ND) of 60 % and ash digestibility (AD) of 50 % units between the forages measured. Such results suggest that if the energy value of tropical forages is to be estimated correctly then it is necessary to estimate each forage separately as routine analysis to be included in the feed tables or feeding systems. Van Soest (1994) noted that the balance of matter lost in the passage through the digestive tract is the most reproducible measurement of a given feedstuff. It is evident therefore, that the variations observed in this study are characteristic of a given forage. For this reason each forage digestibility will be discussed separately and possible source of variation explained.

The DMD and OMD for BH (Expt.1) and UNBH and SBH (Expt.2) forage diets are comparable to those reported for tropical forages in the literature (Göhl, 1981). Differences in digestibility coefficients among these forage diets made of the same forage (BH) can be ascribed to animal variations. However, values obtained for BH and SBH diets relative to other forages diets (Table 4.6) indicate that low CP content in BH (Table 4.1) might have an effect on the digestibility of DM, OM and the CP and minerals bound to the CWC as the NDF content was also relatively high (Table 4.1).

The digestibility of maize silage diets (MS and SMS) for DM, OM and N were similar to those reported by Sarwatt *et al.* (1989) for tropical maize silage and Bal *et al.* (1997) for temperate maize silage except that of N. The N digestibility for SMS was close to that reported by Bal *et al.* (1997) indicating that CP was the limiting factor to low digestibility in MS. Low CP digestibility in tropical maize silage was reported by Sarwatt *et al.* (1989) with higher CP (6.0-

10.8 % DM) than those reported by Bal *et al.* (1997) with more or less CP content (7.0-7.5 % DM), suggesting that in tropical maize silage CP was less available due to its N bound to the CWC than temperate silage. Another possible explanation to such differences is that tropical maize is physiologically more efficient in storage of carbohydrates in terms of starch than the temperate maize. This may lower MS digestibility because the proportion of starch in forages based diets have been found to have a negative effect on digestibility especially NDF (Stensig *et al.*, 1998a). This suggest that differences observed in tropical MS relative to that reported in the literature for temperate maize silage could be explained by differences in starch content.

Another reason for variation in digestibility of MS when compared to the literature value is the stage of cut. The maize crop in this study was cut at milky stage (post-anthesis). At this stage the DM and starch in cobs is normally high, at the expense of other qualities like CP, which is low, whereas NDF is high (Table 4.1). This agrees with the literature findings (Sarwatt *et al.*, 1989; Bal *et al.*, 1997) who attributed such differences in maize silage digestibility to be due to stage of cut (maturity) of the ensiled crop.

Processing procedure when ensiling the maize crop can be another source of variation in MS digestibility. In this study the maize for ensiling was cut manually and at this stage losses were minimum, but chopping was done mechanically (at approximately 2 - 4 cm) and it was observed that some losses of soluble fraction occurred during chopping maize for silage making. This may have increased the NDF fraction in the DM and hence digestibility.

Chopping of silage material during ensiling facilitates minimum losses of silage during feeding, but animals tend to eat the forage selectively. The rate of intake is also rather low as the forage look like small cubes. As observed, though not quantified, the selection was towards eating the cobs, which had the grains and leaves while stems were avoided. This selective eating and low level of intake that also showed high mean rumen retention time (Table 4.13) and low passage rate by rumen evacuation method (Table 4.10 and 4.11) resulted in higher digestibility coefficients than what has been observed in the literature (Stensig *et al.*, 1994a). Crushed (maceration) before chopping may result in higher intake and reduce digestibility than what was observed in this study. Silage used in this study had a cube like physical appearance that was as expected reduced intake and passage than when crushed.

Low intake of MS (Table 4.4) observed in this study indicate that fermentation quality were moderate and hence low consumption. Low level of feeding can explain why MS had high digestibility as digestibility increase with low level of intake. This observation is in agreement to what has been reported in the literature (Sarwatt *et al.*, 1989) where low intake of tropical silage were reported regardless of high digestibility coefficients in sheep.

There is little information on digestibility coefficients of DM, OM, NDF and N for LH, SLH and LHG forage diets, in the tropics. Therefore, comparison will be based on other tropical legume forages. The results obtained in this study (Table 4.6) showed higher digestibility coefficients than those reported by Mero and Udén (1998) for tropical legume forages. The differences can be explained to be due to high lignin and tannin content reported in the legumes studied by Mero and Udén (1998) and Shayo and Udén (1998) relative to LH and to a lesser extent LGH which have been reported (Acheampong-Boateng, 1998) to have less anti-nutritional factors like lignin and tannins.

Lower ND, higher NDFD and almost similar OMD found in LH (Table 4.6) than what has been reported in the literature can be attributed to the level of feeding, production level and diet composition (Stensig and Robinson, 1997; Holden *et al.*, 1994). Results by Stensig and Robinson (1997) where alfalfa was supplemented with fibre free concentrates (8 kg d⁻¹) for high producing cows the ND, OMD and NDFD of alfalfa silage was 74, 60 and 31 % respectively. Values which were higher (ND), similar (OMD) or lower (NDFD) than what was obtained in this study. This means with high producing cows (high level of feeding) and concentrates supplementation of alfalfa forage, lower digestibility of NDF was observed compared to the present study where the forage diets were fed either as sole diet except mineral supplementation (Expt.1) or supplemented with urea and FM (Expt.2).

Urea and FM supplementation normally have a positive effect on fibre digestibility (Silva and Ørskov 1988; Weisbjerg *et al.*, 1998), whereas concentrates with readily fermentable carbohydrates (RFC) have a negative effect on fibre digestion (Robinson *et al.*, 1987; Stensig and Robinson, 1997). The ND of LH was high as expected because the CP was also high (Table 4.1). Acheampong-Boateng (1998) reported high ND in alfalfa because the CP was not bound to the cell wall (CWC). In other studies with dry cows fed alfalfa hay, Holden *et al.* (1994) reported ND (75.2 %), DMD (72.8 %) OMD (74.3 %) and NDFD (60.2 %). In lactating cows fed similar hay, Holden *et al.* (1994) observed ND (67.5), DMD (68.0 %), OMD (68.4) and NDFD (46.4 %) values that were also different or similar to what was obtained in this study (Table 4.6). This difference can also be attributed to differences in the level of feeding, production level (dry and lactating cows) and diet composition (type and level of concentrate) as compared to animals used in this study (mature and non-pregnant heifers and fed almost sole forage diets). Differences or similarity in DMD, OMD, ND and NDFD for alfalfa forages reported in the literature (Holden *et al.*, 1994; Stensig *et al.*, 1994a;

Stensig and Robinson, 1997) relative to what was observed in this study can in general be associated to animal differences, feeding level, production level, CP content, NDF content and diet composition.

Digestibility coefficients of DM, OM and NDF for UTRS (Expt.1) and SUTRS (Expt.2) forage diets observed in this study are close to those reported by Djajanegara and Doyle (1989) by sheep at maintenance level and by Tuen *et al.* (1991) by goats at 85 % *ad libitum* intake. The little differences observed may suggest animal species differences, level of feeding and variations between species of rice straws used.

The nitrogen digestibility in UTRS was extremely low (6.5 %) and do not correlate to the protein content of UTRS when the following equation (Thomsen, 1979) is used:

$$\text{Digestibility coefficient (CP)} = 93 - \frac{300}{\% \text{ CP in DM}} \dots\dots\dots(\text{Equation 5.1})$$

Using equation 5.1 and CP contents of forages (Table 4.1), digestibility coefficients of CP can be calculated to be 46, 45, 66 and 53% DM for BH, MS, LH, LGH and UTRS respectively. When compared to the observed values (Table 4.6) ND are more or less similar for all forage diets except UTRS, taking into account that equation 5.1 was developed for sheep at maintenance level and digestibility in sheep is slightly higher than in cattle. In this study, the animals used were cattle and fed *ad libitum* and, therefore, the ND should be expected to be lower than calculated ND. The results suggest that chemical composition is a poor predictor of digestibility coefficients of feeds and therefore if routine analysis is to be developed to avoid the cumbersomeness of *in vivo* assays, biological assays like use of rumen liquor and enzymatic assays are inevitable. It can also be argued that, in this study where N intake was low for some

of the forage diets (Table 4.4) N digestibility is normally under-estimated due to N gained from N recycled (Weisbjerg *et al.*, 1998). Information about ND for UTRS is limited, but one could speculate that with high passage rate observed in UTRS (Table 4.10) relative to other forage diets the UTRS (Expt.1) N might have escaped rumen digestion and passed to the lower gut. In this study, urine was not collected. Therefore urine contamination when the urination and defecation occur at short intervals cannot, be ruled out, a situation that can also lead to under-estimation of N digestibility in all forage diets.

Urea-treatment usually solubilize the CWC in UTRS, and one could argue that there was intensive microbial fermentation at the hind gut that produced microbial protein which contributed to increased faecal N output that was not accounted for and resulted in low ND for UTRS than expected (Table 4.6).

As for SUTRS (Expt.2) however, the ND improved (46 % DM) but still not to the expected calculated (Equation 5.1) level (53 % DM). This is because of urea and fishmeal (FM) supplementation that improved the efficiency of microbial fermentation and thus rumen degradation rate of SUTRS straw diets even though the passage rate was still higher than other forages (Table 4.11). Improved rumen metabolism when urea is supplemented to rations deficient in rumen degradable protein has been reported by Weisbjerg *et al.* (1998). Also the potential of FM in provision of some essential nutrients important for optimum rumen functions which are deficient in other supplements (Silva and Ørskov, 1988; Mgheni *et al.*, 1994b) have been reported.

Low ash digestibility relative to the ash content of UTRS has been attributed to high content of silica as reported by Mgheni *et al.* (1993). Silica is indigestible and has been reported to lower digestibility (Van Soest, 1994) in feeds high in silica content. For all forages ash digestibility was rather on the lower side compared to other literature studies (Van Soest, 1994) relative to ash content of the forages (Table 4.1) except for LH. This may suggest other reasons than silica content in rice straw diets. Although supplemented minerals were accounted for in the calculation of ash digestibility in these forage diets, the low digestibility reported in this study for ash shows that either the minerals were bound to the CWC and, therefore not available to the animal (except LH diets), or the carriers added to the mineral supplements (Table 3.2) were also indigestible. Also endogenous minerals may have contributed to increased faecal ash output and hence under-estimation of ash digestibility (Table 4.6). During data collection the floor and the feeding troughs were quite new and animals had the tendency of licking the wall/floor and thus take in sand/cement. Such an accounted intake and faecal output usually results into incorrect estimate of ash digestibility.

Differences in digestibility coefficients between forages in this study (Table 4.6) could be attributed to species difference and preservation methods. If equation 5.1 holds true, then legumes are expected to have higher digestibility than grass forages because of their higher CP content (Van Soest, 1994). Thus, if legume forages are not high in lignin and tannin as reported by Achcampong-Boateng (1998) for lucerne, then digestibility is normally higher in legumes than in grass forages. In this study, higher digestibility was observed in LH than other forages (Table 4.6) for DM, OM, ash and N except the NDF. This may suggest that although LH had low NDF content (Table 4.1), partitioning of the NDF (biological availability) into total NDF, DNDF and INDF (Table 4.10 and 4.11) may have explained why LH had low NDF but its

NDFD difficult to explain *in vivo* (Table 4.6). The LH was found to have high INDF fraction but also high rate of digestion of DNDF, which compensate for the latter. However, if on the other hand the legume forage is high in lignin and tannin (Mero and Udén, 1998; Shayo and Udén, 1998) then legume forage will be less digestible despite its high CP content.

Forages may also show variation in digestibility depending on the quality obtained from the preservation method used. Good quality hay will have higher digestibility than bad quality hay obtained from mature grass or legume forage (Van Soest, 1994). Similarly maize silage made from maize cut at higher degree of maturity will have lower digestibility than one cut at an optimal or younger stage (Sarwatt *et al.*, 1989). Differences in the digestibility coefficients found in this study for all forages that were attributed to preservation methods have already been discussed. However, in other studies, results have shown that when optimal conditions for preservation are met, then forages have no differences in digestibility due to preservation methods (Huhtanen and Jaakkola, 1993). Therefore, one can speculate that perhaps differences found in the tropical forages relative to similar forages in the temperate region could be attributed to the fact that tropical animals which are consistently fed on forages of high fibre might have developed an adaptation mechanism that makes them more efficient in utilisation of fibrous forages than temperate animals. This area requires further research.

Degradability characteristics were found to be very different ($P < 0.0001$) between tropical forages estimated in the standard procedure (Table 4.2) and when estimated in the forage diets in expts. 1 and 2 (Table 4.3). Differences in degradability characteristics between tropical forages has also been reported in Tanzania (Kimambo *et al.*, 1994; Shem *et al.*, 1995; Mgheni *et al.*, 1996) and elsewhere (Stensig *et al.*, 1994a; Fonseca *et al.*, 1998). This difference in

degradability characteristics for tropical forages when evaluated by *in situ* method using the nylon bag technique was as expected as the forages varied in chemical composition (Table 4.1) and are of different species. In this study, legumes were expected to have higher degradability characteristics especially the rate constant (*c*) than grasses and straws because the CP was higher than in grass and crop residues (Table 4.1). Similar findings were reported for tropical grass, legumes and straw forages (Kimambo *et al.*, 1994; Shem *et al.*, 1995; Mgheni *et al.* 1996). In the current study, tropical forage degradability characteristics were further expected to be improved by urea and FM supplementation in expt.2 (Table 4.18). Supplementation improved the rate of degradation (*c*) significantly ($P<0.0001$) in all the forages. The degradability profiles (Fig.4.1 to 4.3) demonstrated that rate and extent of degradation of DM and N varied somewhat depending on the CP content of the forage up to 48 h. After 48 h the forages showed a trend that was very much related to the NDF content (Table 4.1) and NDF fractions, digestion and passage kinetics (Table 4.10 and 4.11).

Significant differences ($P<0.0001$) observed in these forages (standard procedure) and forage diets (Expts.1 and 2) clearly demonstrate that if the forages are to be ranked in terms of their degradability potential, it is important that their degradation characteristics are accurately determined in a standardised procedure (Table 4.2). This is very important because in this study degradability characteristics are the key variables (Model 3.15) in estimation of forage Fill values that were used to predict NDF intake (Model 3.16) and subsequent DM intake (Model 3.17).

The results showed short lag time in DM, N and NDF estimates (Table 4.2 and 4.3) but as suggested by Dhanoa (1988) lag time was included in the model for estimation of the

degradability characteristics (Model 3.3) to make sure that error of estimating the parameters was minimum. Studies with *in situ* methods (Stensig *et al.*, 1994a) indicated that lag time obtained in this study (Tables 4.2 and 4.3) may result in delayed degradation. This, however, is extremely of primary importance by allowing for adhesion and colonisation of the cellulolytic bacteria on feed particles compared to *in vitro* methods (Stensig *et al.*, 1994a). On the other hand too long a lag time may result in feed particles leaving the rumen before being degraded and this can introduce error in the calculation of effective degradability. Particle loss correction was done for NDF fraction (Model 3.2) according to Weisbjerg *et al.* (1990) but not for DM and N. This increased the standard error of estimate of the degradability characteristics in DM and N than in NDF fraction as seen in the asymptotic standard errors (Table 4.3).

As pointed out by other workers (Stensig *et al.*, 1994a; Madsen *et al.*, 1997; Adesogan *et al.* 1998; Hvelplund and Weisbjerg, 1998) the *in situ* method for predicting nutritive value has various analytical and mathematical problems which can sometimes lead to error in estimation of the degradability characteristics. In this study, the major problem observed was microbial contamination, which was found in LH forage samples. This led to incorrect estimate of the rate constant c (Tables 4.2 and 4.3) especially for N. The method used to remove microbial contamination (stomaching) was found not to be sufficiently effective. In spite of the procedure being applied to all forage samples after rumen incubation, the method was found not to be effective in removing all microbial contamination in LH. The LH was found to have a decreased degradation after 48 h (Appendices 3-6) and this decrease can be speculated to be due to microbial contamination which were attached in the inner side of the LH particles and “beating” using the stomacher was not effective enough to deal with the problem.

This is in contrast to the literature findings where microbial contamination has been reported to be more problematic in residues from feeds low in protein and high in fibre (Michalet-Doreau and Ould-Bah, 1992; Hvelplund and Weisbjerg, 1998). In this study, LH was found to be high in CP and low in NDF (Table 4.1). Since LH was found to have high INDF and high rate of DNDF digestibility (Tables 4.9 - 4.11), then after 48 h what was left was mostly INDF where microbes were still attached to the feed particles, thus, microbial contamination cannot be ruled out. As observed from degradation profiles (Fig 4.1-4.3), LH was degraded very fast up to 48 h, which implied that after 48 h the feed changed to having low protein and high fibre that was almost INDF (Table 4.10 and 4.11). Since the microbes were already attached to the feed particles, probably due to preference of the microbes to LH due to its high CP (Table 4.1). Then one could speculate that the microbes continued to be attached to LH particles even after degrading the digestible fraction. This problem made the stomaching technique to remove microbial contamination ineffective. Future work is needed to validate this behaviour of LH after 48 h.

To avoid further errors in estimation of the degradability parameters the values of LH after 48 h were omitted, as they were believed to be due to an artefact. This was to avoid further errors in estimating the *a*, *b* and *c* parameters by Model 3.3 (Table 4.2 and 4.3). Even with values of LH after 48 h being omitted, so as to make the data fit in Model 3.3, the rate constant (*c*) for DM may not be correct in LH as the estimated value gave the highest asymptotic standard error of estimate (± 3.9). The results suggest that incorrect estimate of degradation constants for LH cannot be ruled out.

Problems associated with microbial contamination include among other things, the washing procedure and effectiveness of stomaching (Michalet-Doreau and Ould-Bah, 1992). In this

study, washing procedure and stomaching were standardised according to Madsen and Hvelplund (1994). However, Michalet-Doreau and Ould-Bah (1992) found that after stomaching a certain proportion of bacteria DM was still attached to the feed particles, a situation that cannot be ruled out for LH.

The results showed that the degradability characteristics for NDF values of MS and LH were higher than those found in the literature Stensig *et al.* (1994a) This could be attributed to differences in analytical procedure as discussed previously. The problem of microbial contamination was not observed in the degradability characteristics for NDF in LH, suggesting that the NDF solution removed microbial and endogenous materials that were in DM and N. Similar findings were reported by Stensig *et al.* (1994a) who concluded that the NDF fraction is to be preferred for estimation of physical fill because it is devoid of microbial and endogenous material. Thus seems necessary to use NDF methods for LH after 48 h for removal of microbial contamination if correct estimate of degradability characteristics of the LH is to be achieved. This is because NDF procedure cannot be used at the beginning of the degradation process as this will also remove feed proteins that are still being degraded with time.

Problems associated with the *in situ* nylon bag technique in general have been reported elsewhere (Madsen and Hvelplund, 1994). In this study, even though similar problems like microbial contamination and lack of fit by Model 3.3 were observed, the *in sacco* procedure was able to describe the tropical forages in terms of their differences in which they were degraded in the rumen (Table 4.2 and 4.3). The parameters found have been used together with passage rates (Tables 4.10 and 4.11) to calculate the effective degradability (Model 3.10) and physical fill (Model 3.15) of these forages. Effective degradability (ED) estimates ruminal digestibility,

whereas fill describes the rumen capacity when physical regulation of intake is assumed. For tropical forages, rumen degradability is the most important factor describing the protein value of the feed protein as found in this study (Table 4.2 and 4.3) and reported earlier (Kimambo *et al.*, 1994; Mgheni *et al.*, 1994c and 1996). Tropical forages are mostly dependent on degradation in the rumen as the mobile bag technique has indicated that the intestinal digestibility often is very low (Kimambo *et al.*, 1994; Mgheni *et al.*, 1994c). This may suggest that there is no reason to estimate digestibility of rumen undegradable protein of tropical forages as it could correctly be assumed to be near zero. It is, therefore, important that tropical forages have their rumen protein degradation estimated as this value almost describes the protein value of tropical forages. This is because rumen degradability of feeds determines the supply of ammonia as well as branched-chain fatty acids for the rumen microbial growth. For concentrates and forages with reasonable intestinal digestibility of rumen undegradable protein, it also determines the supply of undegraded protein to the small intestine as a potential source for amino acid digested and absorbed in the small intestine (Moiro *et al.*, 1998).

The *in situ* method has demonstrated short lag time (Tables 4.2 and 4.3) but in other studies (Shem *et al.*, 1995) higher lag time was observed in tropical forages. The *in situ* method showed digestion rates markedly higher than those reported in the literature (Adegosan *et al.*, 1998) by *in vitro* methods indicating that *in vitro* methods under-estimate digestion. Thus, as demonstrated in this study, the *in situ* method is preferred to *in vitro* methods for estimation of potential digestion characteristics and estimation of ruminal digestion when weighted with passage rate (Table 4.14). Recently, with the use of rumen evacuation method and assuming a two pool model Stensig *et al.* (1998b) demonstrated that ruminal NDF digestibility can be obtained with values very close to *in vivo* digestibility using *in situ* methods. In the current study using the two

compartment model corrected for hind gut fermentation resulted in almost zero relationship (Table 4.17) even though numerically the ruminal NDF digestibilities were very close to *in vivo* NDFD (Table 4.14). The results suggest that there were no trends with individual observations (poor R^2) where ruminal digestibilities were closely related to *in vivo* NDFD data (Table 4.17).

Degradability characteristics from the *in situ* method, in this study, were used to estimate various parameters that described various NDF digestibilities of tropical forages. Potential rumen digestibility (b) for NDF (as NDF is not soluble) gives the proportion of NDF that can potentially be digested in the rumen assuming no passage to the lower tract. The values obtained (Table 4.6) simulate only the rumen digestion. For LH the values obtained at maximum rumen degradability after 192 h for NDF were close or slightly lower than *in vivo* values because of the behaviour of LH as discussed previously. The potential rumen digestibility (PRD) obtained either from long time incubation (30 days) or maximum rumen degradability (192 h) obtained *in situ* were higher as expected than *in vivo* data (Table 4.6) because of more resident time spent in the rumen (*in situ*) compared to *in vivo*.

For most forages the potential digestibility was higher than *in vivo* digestibility indicating that it cannot be directly compared to "true" *in vivo* digestion as the NDF cannot stay in the rumen that long (192 h) under normal feeding conditions. Digestion of food is a dynamic process and when it reaches a certain extent of digestion the food will be passed out of the rumen. It is, therefore, speculated that simulation of an *in vitro* process that fits the digestion process would give a better estimate of rumen digestion when compared with true *in vivo* data than what was estimated by Model 3.10 and 3.13 (Table 4.14).

Comparison of *in situ* degradability data to describe *in vivo* (Table 4.14) was found to have a very poor relationship (Table 4.17). The reliability of this method can always be questioned because of poor relationship when compared to true *in vivo* data (Stensig *et al.*, 1994a; Hvelplund and Weisbjerg, 1998; Adesogan *et al.*, 1998). This was also the case in this study (Table 4.17). In contrast to these findings Stensig *et al.* (1994a) reported a linear relationship ($R^2 = 0.77$) between ruminal digestibility across feedstuffs.

Like in protein evaluation, degradability characteristics of NDF can also be mathematically combined with information about rumen fractional outflow rate to estimate rumen digestibility (Ørskov and McDonald, 1979). In this study, methods for measuring passage rates were tested to give their ability to estimate ruminal digestibility or effective digestibility (ED) of NDF (Table 4.14). Passage rates measured either by rumen evacuation (RET) and chromium mordanted fibre (CR-MF) methods, or by assumed passage rates of 2 % h⁻¹ were compared in terms of their R^2 values (Table 4.17). The ED obtained with these methods were found to be somewhat inconsistency with literature findings (Stensig *et al.*, 1994a; Stensig *et al.*, 1998b). In their studies, the authors suggested that ruminal NDF digestibility could be estimated from degradability characteristics at a certain rate of passage measured by rumen evacuation method compared to passage rates obtained from chromium mordanted fibre.

In this study, the differences obtained in the calculated ED (Table 4.14), when the two methods of measuring passage rates were compared, could be attributed to the differences obtained in measurement of passage rates (Table 4.10 and 4.11). Although the ideal passage rates when tropical forages are fed to the animals has not been established, the results showed that CR-MF

over-estimated passage rates compared to RET method (Table 4.10 and Table 4.11). This is because when the precision of prediction of ruminal NDFD and DM intake were tested (Model 3.20) the correlation (Table 4.17) was higher for the RET method than when CR-MF was used to estimate passage rates. The results may suggest that, in CR-MF adhering of the chromium to the feed particles was different for different forages. This may imply that chromium migration to the liquid phase might have occurred and caused chromium to be found in the faeces much earlier than the particle mordanted to. Thus CR-MF was found to have higher passage rates than those estimated by RET. Also higher passage rates for MS were observed in the CR-MF method compared to when RET was used. This suggests that migration of the chromium from MS particles to the liquid phase was higher in MS than other forages. It seems, therefore, that when the CR-MF method of estimating passage rates is used, it is important to mordant each fibre separately rather than mordanting a common fibre e.g. alfalfa hay as suggested by Udén *et al.* (1980).

To improve the estimation of ruminal digestibility several approaches were used to calculate ED (Table 4.14) and test how the value corresponds to *in vivo* digestibility. It was observed that the ED gave poor relationship with *in vivo* data (Table 4.17) in expts. 1 and 2 when various methods of estimating passage rates were compared in estimating the ED. Several reasons can explain this poor relationship. Both methods assume that a constant part of the feed present in the rumen at one time is passing per time unit (first order kinetics). This in practice is not true as feed particles will pass out of the rumen at different rates with newly ingested feed in the rumen having a slower rate than feed that has already spent time in the rumen (Huhtanen, 1998). Two compartment models were fitted to improve the relationship (Model 3.13). The relationship numerically improved standard error of estimate although the R^2 did not improve (Table 4.17)

indicating that not all the observations showed similar relationship between the observed and the predicted ED. To improve the estimates further, the *in vivo* digestibility for NDF values were corrected for hind gut fermentation (Table 4.6). The relationship was further improved numerically and a low standard error of estimate obtained (Table 4.17) but still with a low R^2 . The reason for such a trend has been discussed previously.

The results are consistent with those reported by Stensig *et al.* (1994a) where *in situ* digestibility assume a one pool model, thus poor relationship where observed compared *in vivo* digestibilities (Stensig *et al.*, 1994a; 1998b). Rumen evacuation method made it possible to relate ruminal digestibility of NDF better than the *in sacco* procedure when a two-compartment model was assumed (Stensig *et al.*, 1998b). A two pool model explains better what happens in the rumen as feed particles are not static, but with time pass out of the rumen, or are digested and absorbed (See Fig. 2.3 and 2.4). The results also showed that, RET in contrast to other techniques, has the advantage that the obtained digestion and passage rates are related naturally to ruminal digestibility as they are derived from intake and flow data (Table 4.10 and 4.11). Consistent with these results, other studies also have shown that the *in situ* technique over-estimates *in vivo* NDF digestibility (Tamminga *et al.* 1989; Huhtanen and Khalili, 1991; Huhtanen *et al.*, 1995).

This study has demonstrated that ED calculated with the estimated passage rate from RET and assuming a two compartment model gave a better estimate of rumen digestibility (Table 4.14) when compared to *in vivo* data. The method is more robust and less dependent on exact curve fitting within the range of normal rate of passage. However, *in vivo* data are also difficult, cumbersome, expensive and difficult to execute and in most cases even more erroneous. Therefore, where the conditions are conducive enough to simulate *in vivo* situations, *in vivo*

procedures and also the *in situ* nylon bag technique can be replaced by *in vitro* and/or rumen evacuation and/or mathematical modelling with a relatively high degree of accuracy (Stensig *et al.* 1998b; Hvelplund *et al.*; 1998; Adesogan *et al.*, 1998; Danfær, 1998).

In general, the results showed that rumen degradability among the forages evaluated varied substantially in the standard procedure (Table 4.2) and in expts. 1 and 2 (Table 4.3) for DM, N and NDF. Therefore, estimation of degradability values for each feedstuff is an important task in feedstuff evaluation in the tropics. The results also showed that the degradability values obtained in the standard procedure (Table 4.2) and in expts.1 and 2 were quite similar numerically implying that the degradability characteristics can be estimated in either of the three rumen environments from which the forages were incubated without much error. The standard procedure is therefore recommended for use in the estimation of degradability characteristics if the parameters are to be used to estimate fill values (Model 3.15) which is an important parameter in prediction of intake (Model 3.16). This will make it possible for such values to be included in feed tables as they are estimated in a standardised procedure.

Passage rates are important parameters for estimating ED and for calculating fill value, an important predictor of NDF intake (Model 3.16). In this study, passage rates were found to be different depending on type of forage and method used to estimate passage rates. However, passage rates can also be influenced by level of feeding. Passage rates have a positive correlation with level of feeding and digestion rates. Forages that were digested at faster rate (Table 4.2 and 4.3) were passed out of the rumen quicker (Table 4.10 and 4.11) than those degraded at a slower rate. But this also depends on the level of feeding. The higher the level of feeding the higher the passage rates and vice versa. It is evident that the rate of passage and digestion found in expts.1

and 2 forage diets (Table 4.10 and 4.11) can partly be explained by level of feeding as forages were consumed at different amounts (Table 4.4) by the animals.

In the present study, the UTRS (Expt.1) and SUTRS (Expt.2) diets had exceptionally higher passage rates than other forages when estimated using the RET (Table 4.10 and 4.11). This behaviour could be due to a high level of silica in the diets. A review by Van Soest (1994) showed that silica content in forages reduced CWC digestibility. Reduction of CWC digestibility by silica may be due to increased specific gravity which accelerated passage out of the rumen as silica is a heavy and indigestible element which will always have the tendency of sinking down through the rumen mat into the reticulum or cranial sac where passage is facilitated.

The variation in passage rates found in the forage diets (Table 4.10 and 4.11) suggests that it is important to estimate the passage rates not only accurately but also for each forage if the parameter is to be used as a predictor of fill (Table 4.12) and ED (Table 4.14) It is assumed that the passage rate obtained from RET is closer to the "true" passage rate than to that obtained by CR-MF method. This is because of the condition which the RET is used to estimate passage rates were more practical to digestion and passage kinetics than when external markers (CR-MF) were used. The values obtained in this study are much lower than that estimated by other feed evaluation systems (Jarrige *et al.*, 1986; NRC, 1989; ARC, 1990; Madsen *et al.*, 1995). Passage rates obtained from CR-MF (Table 4.10 and 4.11), however, are comparable to those reported by Shem *et al.* (1995) for tropical forages but higher than passage rates obtained by RET.

Chromium markers have been reported to over-estimate passage rates (Udén *et al.*, 1980) especially when sampled from the duodenum (Stensig *et al.*, 1994a). In this study, when passage

rates obtained by CR-MF were compared to RET (Table 4.10 and 4.11) the values were found to be over twice the passage rates obtained by RET. As a particulate marker, however, CR-MF has been observed to be the best marker as it binds more strongly to the fibre fraction (Stensig, 1994a). On the other hand chromium makes the particle almost indigestible such that it gives passage rates close to the passage rate of the INDF (Table 4.10 and 4.11). Thus, as suggested by Tamminga *et al.* (1989) the marker is better in determining the passage rate of indigestible than the digestible fibre fraction.

Udén *et al.* (1980) suggested that when chromium is used as a particulate marker, it is important to apply relatively higher amounts in order to saturate all the binding sites. In this study, micro-labelling was adopted as suggested by Stensig *et al.* (1994a) as this minimised the physical influence of the feed particles. During analysis of chromium concentration, however, micro labelling may be problematic to analyse colourimetrically (Shem *et al.*, 1995) and, therefore, the method suggested by Stensig *et al.* (1994a) might require the use of Atomic absorption spectrophotometer for reading of samples of low chromium concentration.

Passage rates describe the amount a certain feed is digested or passed out of the rumen per hour (Table 4.10 and 4.11). Methods for estimating this parameters vary in accuracy and precision and yet no ideal method has so far been recommended. In this study, the passage rates were estimated by RET, CR-MF and calculated from *in vivo* digestibility and degradability characteristics from *in situ* methods. Among the methods used to estimate passage rates, the CR-MF gave the highest values of passage rates than RET and *in situ* methods. The *in vivo* methods gave the least and almost negligible values. This last method of estimating passage rate derived from *in vivo* and *in situ* potential digestibility and rate constant (c) may seem reasonable

for some of the feeds. For example, in LH maximum rumen degradability was close to that obtained *in vivo* (Table 4.6) meaning that passage was almost zero to most forages and even negative to LH (Table 4.6 and Table 4.10 and 4.11).

Although the RET and CR-MF methods both assume that a constant part of the feed present in the rumen at any time is passing per unit time (first-order kinetics), CR-MF tends to overestimate the passage rates. This is because the accuracy of the method was still inadequate and the results showed some outlier values that had to be omitted. In this study, samples were obtained from the faeces and not in the duodenum (Stensig *et al.*, 1994a) to avoid intermixing with pools from the lower tract and obtain a smooth dilution curve. The precision aimed at was not, however, achieved. Problems associated with use of external markers are well explained in the literature review (Udén *et al.*, 1980; Stensig, 1994a).

Compared to the CR-MF, rate of passage obtained from RET (faecal NDF output divided by the rumen pool size of NDF) has the advantage of having both the NDF pool size and NDF faecal output being derived from intake and flow data. In this study, although INDF in the feed was also measured the results obtained did not fit to the INDF content in faeces. In theory, INDF intake is supposed to be equal to INDF in faeces as INDF is indigestible. In the present study, differences of more than 50 % in some forages like LH and MS were observed and such differences were found unacceptable and were consequently omitted in subsequent calculations.

Possible reasons for this unacceptable differences can be explained by the omitted use of α -amylase in MS that is high in resistant starch and use sulphite in LH that is high in CP content as suggested by Van Soest *et al.* (1991). This is because the problem did not seem to show up in

faecal samples because of digestion through the total tract. The results are contrary to other findings (Huhtanen and Khalili, 1991; Huhtanen and Jaakkola, 1993; Stensig and Robinson, 1997; Stensig *et al.*, 1998a) who reported no discrepancies and the INDF obtained between the feed and faeces were within an acceptable range.

The INDF values obtained from the *in situ* long time incubation (30 days) method were lower than what has been obtained from other studies (Weisbjerg *et al.* 1998). Possible reasons were that the values in the literature were obtained from temperate regions and comparison may not be correct. Values obtained in this study showed DNDF values are higher than the maximum rumen degradability (192 h) and the asymptote ($a + b$) which is reasonable (Table 4.6). This may suggest that may be animals in the tropics that have been challenged to diets of high fibre of poor quality have adapted a better utilisation of fibre than temperate animals where similar experiments were conducted. Further research to validate this need to be conducted. This is because long incubation and rumen evacuation are important not only in estimating the passage rates but also important in the study of quantitative information about specific characteristics of various fibre sources to improve models of intake prediction as suggested by Mertens, (1987).

Feeds can also be described in terms of their pool sizes in the rumen and calculated physical fill using degradability characteristics and estimated passage rates. Different passage rates were estimated as described before and for the purpose of discussion focus will be mostly on the passage rates estimated from RET- total NDF. The pool sizes for DM were only given for comparisons (Table 4.8 and 4.9). The shortcoming of using rumen pool size of DM as predictor of VFI has been given in literature for tropical forages (Mgheni *et al.*, 1998) and for temperate forages (Stensig *et al.*, 1994b).

Although rumen pool size can also be an animal characteristic as described by Mould *et al.* (1982), the greatest variation was observed between forage diets (Table 4.8 and 4.9). Differences in pool sizes of NDF were related to the level of intake. In expt. 1, animals fed LGH had highest pool sizes of NDF, but also showed the highest intake of NDF. Animals fed MS had the lowest pool sizes of NDF and intake than other forage diets (Table 4.4 and 4.10). In expt. 2, the NDF pool size was highest in animals fed SBH and lowest in SMS and equal in SLH and SUTRS, indicating that the NDF pool was related to the level of intake (Table 4.4 and 4.11).

This high pool size of LGH relative to other forages at all evacuation times (Table 4.8) can be explained by high intake of this forage relative to other forages (Table 4.4). Low pool size of MS and SMS is also related to low level of intake. Similar findings of low intake of maize silage relative to other forages have also been reported by Stensig *et al.* (1994a). Numerically in expt. 2 SBH showed that supplementation increased intake and in response the rumen pool size of NDF was higher than UNBH. Similar findings were reported (Stensig *et al.*, 1994a) when concentrate feeding was found to increase NDF pool size for all rations. Low pool size of NDF in MS (Table 4.10) and SMS (Table 4.11) could be due to low palatability in MS that resulted from sub-optimal preservation methods of the MS *per se* as discussed previously.

The observed differences in the pool sizes obtained in the morning, mid-day and evening may suggest that more information is needed about optimal times for evacuation procedure. That is time of the day to evacuate the animal that gives the best estimate in pool size. The results are in agreement with other studies (Gasa *et al.*, 1991; Stensig *et al.*, 1994a) where it was observed that the lowest pool size was in the morning before feeding and the highest some few hours after

evening feeding. In this study, the mid-day seems to be close to the average of the three evacuations but it is not known whether, this would be the optimal measure of the rumen pool size. The variability obtained in the rumen pool size suggests also that this parameter has to be estimated for each forage if the parameter is to be considered in studies of passage and digestion rates kinetics (Model 3.6- 3.8) and as a predictor of intake (Model 3.16). Sampling technique so as to obtain the best representative sample of the rumen content need to be further evaluated to improve the accuracy of the estimate.

The NDF content of feed *per se* (Table 4.1) has been found to have a very poor correlation to the intake potential of forages in this study (Table 4.4) and other findings (Holden *et al.*, 1994; Stensig and Robinson, 1997). This is because of the differences in the NDF fractions (DNDF and INDF) and their rates of passage and digestion. In this study, fractionating the NDF into biological availability (Table 4.10 and 4.11) has been found to explain the relationship between the NDF and intake better than when the NDF content (Table 4.1) is used alone. Of interest to note from this approach, which is also consistent with the literature results (Shaver *et al.*, 1988; Stensig and Robinson, 1997), is a markedly higher INDF fraction (Table 4.10 and 4.11) a markedly faster rate of degradation (Table 4.2 and 4.3) and digestion (Table 4.10 and 4.11) of the LH and SLH diets compared to other forages. This is because although LH had a high proportion of INDF, the high rate of digestion of the DNDF fraction compensated for the high proportion of the INDF. As demonstrated in Table 4.10 and 4.11 the INDF is passed out of the rumen faster than other fibre fractions. This could be due to selective retention of large digesta particles before passage due to the fact that INDF/NDF is low in the first pool and high in the second pool (Fig.2.2). On the other hand the MS had the lowest pool size of INDF, low rates of passage and digestion of DNDF resulting in low intake despite high rate of passage of INDF

(Table 4.10). The LGH behaved somewhat similar to LH and this is because the forage contained 20 % LH. In UTRS the amount of INDF pool sizes was similar to other forages except the MS and BH. This is reasonable because they were consumed at a lower amount. Similar trend was observed in expt.2.

The major focus in studies of fibre kinetics was to describe tropical feeds in terms of their physical fill. The calculated fill (Table 4.12) using the passage rates obtained from all methods showed high variation and was related to the passage rates. A small change in passage rates showed a big change in physical fill ascribed to each forage. The accuracy of fill value, therefore, depended on the accuracy of estimating the passage rates. It is not easy to give precisely which passage rate is correct as all methods were found to have problems. However, since intake parameters were obtained from animals from similar experiments where passage rates were measured, then the best estimate of passage rate will be that which will explain the differences obtained in the predicted VFI for forage diets in terms of R^2 with least error of estimate. In this study, the fill estimated from RET- total NDF (Fill-2, Table 4.12) was found to be most accurate and for this reason the discussion will focus more on this method. The fill value obtained by this method was able to explain the differences in intake for the forages in both experiments. Forages of high fill were found to be eaten in lower amounts (Table 4.4) than those of low fill.

Physical regulating of intake means that the rumen is so much filled with indigestible material that the animal cannot take more and hence has to stop eating. The relationship is also reflected by high mean rumen retention time (Table 4.13). Forages of high mean rumen retention time (MRRT) had high fill and because MRRT is the reciprocal of passage rate it means that the

passage rates were also low for forages of high fill. In this study, some forages like LGH and UTRS (expt.1) and SUTRS (expt.2) were found to have high fill even though their passage rates were high, suggesting that fill was not only a function of passage rate but also of the rate at which *b* fraction was digested (Table 4.2 and 4.3). The NDF concentration in forages (Table 4.1) and total intake (Table 4.4) also contributed to high fill. This might also explain why diets calculated to be low and high in fill based on degradation characteristics, but assumed same passage rates (Miller *et al.*, 1990) have failed to elicit the predicted intake responses. In other words the source of fibre has an important impact on the intake potential of forages. Similar findings were reported in alfalfa and grass hay and silage (Shaver *et al.*, 1988; Weiss and Shockey, 1991; Holden *et al.* 1994; Stensig and Robinson, 1997).

Differences in passage and digestion rates, fill value and subsequently intake have also been attributed to level of feeding (Holden *et al.*, 1994) and the proportion of starch and sugar in the diet (Robinson *et al.*, 1987; Huhtanen and Jaakkola, 1993; Stensig *et al.*, 1998a) as reviewed previously (Table 2.3, 2.4, and 2.5). Since the results from this study were from either sole forage (Expt.1) or supplemented with urea and FM (Expt.2) which are all believed to be fibre free (FM fibre from contamination assumed to be negligible), there is every reason to believe that there was no confounding effect on the results obtained. Interpretation of the results should, therefore, reflect the effect of source of fibre and level of intake on the variations observed in all the parameters measured.

In the present study, starch was not estimated in MS and SMS diets, but one could speculate that MS had higher starch/sugar content than other forages which may have influenced fibre digestion as found by other workers (Robinson *et al.*, 1987; Stensig *et al.*, 1998a) when

starch/sugar was added at different proportions in forage-based diets. The results obtained for passage and digestion kinetics studies (Table 4.10 and 4.11) and subsequent calculations of physical fill (Table 4.12) and predicted intakes (Table 4.15 and 4.16) support the idea suggested earlier by Mertens (1987) and later confirmed by Stensig and Robinson (1997) that it is important to incorporate quantitative information on the digestion and passage characteristics of NDF source into models of physical fill for prediction of intake.

5.2 Description of animal characteristics, rumen environment and intake parameters

Digestion (extent and rates), passage rates and pool sizes are not only influenced by feed characteristics as discussed previously but also by the animal and the rumen environment where the parameters were studied. Although, animal variation was accounted for by running both experiments in a 5 x 5 Latin square differences in initial body weights and changes in weights during the experiments (Appendices 7 and 8) may have influenced the observed differences in intake and pool sizes. This is clearly demonstrated by the very highly significant difference ($P < 0.0001$) obtained when the intake potential was expressed to constant weight ($\text{g kg}^{-1} \text{M}^{0.75}$). In this study, other conditions inside the rumen e.g. rumen pH and NH_3 concentration may give differences in the parameters measured. These are extrinsic factors apart from those of feed that influence digestion and passage of fibre. In the present study, the final measure of the nutritive value of the forage diets studied has been shown by the response of the animals when the diets were fed to the animals, thus, reflecting the maximum intake potential (capacity) when these forages are fed *ad libitum*.

5.2.1 Rumen fermentation

The degradability characteristics for DM and NDF did not seem to be affected by the different environments in which they were incubated (Table 4.2 and 4.3). This can be explained by the fact that in both experiments including the standard procedure there was optimum rumen environment for microbial fermentation (Table 4.7). The results suggest that the rumen environments were highly buffered for optimum cellulolytic activity. These findings are similar to those reported in other studies (Silva and Ørskov, 1988; Mgheni *et al.*, 1994b). The environment was expected to be even better in standard procedure as the concentrates (Table 3.2) might have supplied more energy and protein for better microbial activity. In this connection higher rumen ammonia was observed (Table 4.7) in expt.2 than in expt.1 because of lack of enough energy to utilise the excessive ammonia produced from urea and FM for microbial synthesis. It is evident that in expt.2 supplementation of urea and FM was in excess of what the microbes were able to utilise given the fact that no energy supplementation was done together with the extra supplied protein. In expt.1 rumen ammonia and volatile fatty acids produced from fermentation of forage were utilised/absorbed at the same rate at which they were produced and hence diurnal variations (Fig. 4.4 and 4.5) were not as conspicuous as it was observed in expt.2 where urea and FM were supplemented. Optimum cellulolytic activity was also achieved in both experiments as the pH values were within the range recommended in the literature (Mould *et al.*, 1983; Ørskov and Ryle, 1990). This is because the animals were fed *ad libitum* and, therefore, the rumen environment was highly buffered by production of saliva. Saliva was high with high intake of forage a process that is desirable for normal rumen function ((Nørgaard, 1993). With high level of feeding and where high amounts of concentrates have been used, reduction in pH and fibre utilisation have been reported (Robinson *et al.* 1987; Stensig and Robinson, 1997).

Urea and FM were supplemented on the assumption that the forage intake would be limited by inadequate N a case that was not observed in expt.1 as the NH_3 observed was not critical for optimal rumen microbial fermentation (Preston, 1995). This may suggest that sole forage diets were adequate for animals that were not producing with minimum growth. It is therefore important that similar studies are conducted in other animal categories where forages can be supplemented for both energy and protein for high production level. Such studies will quantify the NDF digestion and passage kinetics from different fibre sources, proportion of starch and/or sugar and the level of feeding. This will highlight the optimum rumen condition where fibre digestion and passage rates are reasonable but at the same time the animals are fed at production requirement levels.

5.2.2 Feed intake and animal performance

Intake of DM, OM, N, NDF and water (Table 4.4) varied substantially between the forages studied in expts.1 and 2. In this study, variability in feed intake by the animals fed different forage diets has been attributed to physical limitations caused by differences in digestion and passage rates, fill, MRRT and different intake potentials. As discussed previously, it has been difficult to use a single parameter to explain differences obtained in intake. In the present study, and for practical purposes, it has been necessary to study those pertinent factors believed to limit intake of tropical forages under specified feeding situation. Forages used in this study were expected to be eaten to maximum rumen fill to give "fill value" for each forage. Due to specific feed characteristics the levels achieved were very different for each forage diet in both experiments even though all the forages were fed *ad libitum*. The reason for this variation will be discussed for each forage diet separately.

The LGH and LH were preserved at optimum conditions as they were produced under irrigation during the dry season and this made it possible to cut them at the right stage of maturity (when 50 % of the crop had flowered). Preservation methods (as hay) were also good because the drying procedure did not show any mouldy conditions. During feeding, weeds observed in LGH did not seem to affect intake as no selection against the weeds was observed. However, it is not known if absence of the weeds would have improved intake. Also storage of the hay for one year cannot be quantified to have reduced intake as the animals were well covered for vitamin deficiency (Table 3.1) that might have occurred due to destruction of β -carotene and other precursors for vitamin A and other vitamins after such a long storage. It can only be speculated that storage for one year may have reduced forage palatability and the animals could only eat the forage because there was no choice.

In UTRS diets, intake was comparable to other forages studied (Table 4.4). It has been reported that in all the improvement methods applied to rice straw diets, urea treatment resulted in marked increase in intake, digestibility and growth (Djajanegara and Doyle, 1989; Tuen *et al.*, 1991; Mgheni *et al.*, 1993). In this study, increased intake can be attributed to high passage rates as demonstrated by all methods used in expts.1 and 2 except CR-MF (Table 4.10 and 4.11). Compared to the silage quality reviewed by Van Soest (1994), MS observed in this study was found to be moderate and to some attributes even poor (See section 3.2.2 for MS description). Silage of such low quality, as observed in this study has been reported (Sarwatt *et al.*, 1989; Bal *et al.*, 1997) to be of low palatability and, therefore, poorly accepted by the animals. The quality show that the fermentation process was not optimal as when compared to results shown in the literature (Van Soest, 1994). The volatile fatty acids showed a reasonable proportion, lactic acid was also on the lower side (see description of forages in section 3.2.2). Bal *et al.* (1997)

reported pH of maize silage at different stages of growth as 3.73, 3.98, 4.11 and 4.10. A review by Van Soest (1994) showed that good silage has a pH of 4.4. From these results the pH of the MS (4.26) did not seem to limit its quality and thus intake. During feeding MS was slightly heated, brown and mouldy on the sides. Heated silage forms Maillard reactions (browning) that causes caramel a darkening colour which reduces palatability an important quality in intake of silage. Heated silage is not uncommon in the tropics and with the concrete silo used one cannot rule out the possibility of slightly heated silage in this study. Wet silage material is also susceptible to growth of mould as it is difficult to make proper compaction (to eliminate the O₂). In this study, moulds were observed on the sides of the silo (See section 3.2.2). Although during collection of MS from the silo for feeding selection was made to avoid the mouldy silage, possibility of collecting some mouldy silage can not be ruled out. Mouldy silage lower feed value through loss of digestible nutrients and decrease palatability because of the musty odour it produces and thus lower the intake potential. Silage DM content (Table 2.6) and silage fermentation quality (Table 2.7) have such an important effect on intake that DM and fermentation quality have been included as among the important factors in most models for prediction of intake developed in Denmark (Kristensen and Ingvarsten, 1986) and in UK (Rook and Gill, 1990; Rook *et al.*, 1990a)

High DMI due to high CP intake from forages of high CP content (Table 4.1) was because protein intake is important for efficient extent and rate of degradation of nutrients by the rumen microbes. Feeds of low CP will be eaten in small amounts and feeds of high CP content will be consumed in large amounts. It is also pertinent to note that high NDF content of tropical forages (Table 4.1) reduced DMI (Table 4.4). This is because NDF is highly correlated with the bulkiness of the diet (Mertens, 1987) and, thus, represents the dietary ruminal fill, a parameter that limits DMI but at the

same time is important for proper rumen function (Nørgaard, 1993). Low DMI in some forages may also be associated with fibre source. As found in this study, LH had relatively high fill (Table 4.12) and low NDF content (Table 4.1) but reasonable high intake due to its favourable fibre characteristics. Similarly, MS had low NDF (Table 4.1) and high fill (Table 4.12) but on the contrary to LH, MS had low intake a situation that can be due to its DM and fermentation quality rather than its NDF fractions. It can be speculated that its physical form (cube like) may have provoked high intake of cobs, that are high in starch and depressed digestion of fibre resulting in high MRRT (Table 4.13) and fill (4.12).

In the present study, rumen fill reduced DMI as the animals' response to intake (Table 4.4) was related in most cases to fill value (Table 4.12). The forages with high fill value were eaten at a low intake (MS) and those of low fill were consumed at a high amount (UTRS and SUTRS). This may be associated with low passage rate when the rumen is filled with fibre in the rumen and reduce intake. Thus, differences obtained in intake showed that the major reasons were related to differences in fibre source, passage and digestion rates. Specific characteristics of various fibre sources are, therefore, important information to incorporate in the study in order to improve models of intake predictions. The differences in characteristics of fibre sources obtained in this study (though not estimated), are most probably due to the degree of lignification (Van Soest, 1994; Stensig and Robinson, 1997) of the various forages and the negative effect of starch/sugars as discussed previously. Forage NDF content generally reduced DMI in the current study. This is because the forages used in this study formed over 70 % of DM and hence at high intake of DM, the NDF intake should also be expected to be high. This is consistent with other studies (Robinson *et al.*, 1987; Weiss and Shockey, 1991; Holden *et al.*, 1994; Stensig and Robinson, 1997).

High NDF intake was demonstrated by high NDF pool sizes in rumen (Tables 4.10 and 4.11). This may suggest that high pool sizes were not only a result of high fill caused by low passage but also a result of high intake of forage. Similar to these findings, (Holden *et al.*, 1994) reported intake to contribute more to fill than passage. In other studies (Shaver *et al.*, 1988) passage was attributed to the rate at which feed particles were degraded to small size and increased specific gravity that facilitated passage out of the rumen. Mathison *et al.* (1995) speculated that the animal controls digesta out of the rumen. In the present study, UTRS and SUTRS diets were found to have exceptionally high intake and higher passage than all the forages. Since none of the parameters measured could explain why UTRS diets had the highest passage rates which lead to low fill and high intake one could speculate that the silica content in rice straw (Mgheni *et al.*, 1993) might have caused changes in specific gravity that increased passage. High silica content in rice straw resulted in siliceous straw that might have irritated the animal and caused stimulus that made the animal to pass the feed out of the rumen and eat more.

Low intake by the animals for other forages like MS that was not attributable to “fill” can have other explanations. It can be speculated that the animals were discomforted and learned to eat less (Forbes 1995b) because MS showed highest MRRT (Table 4.13) in both experiments a situation that indicated depressed digestion and passage rates. This means that animals may stop eating to maximum fill due to indigestible food that cause discomfort to the animal even though they have not reached maximum intake as observed in MS. Other possible reasons for low intake in MS and BH diets in this study could be due to low CP content (Table 4.1) that reduced rate of digestion as reported by Kimambo *et al.* (1994) for similar tropical forages. In prediction of intake, problematic feeds like MS could be ascribed a correction factor to improve precision.

In all feed evaluation systems, feeds are described in terms of their feeding value to predict the performance of the animals offered the feed. Appendices 7 and 8 showed that in general all the animals gained weight. This may suggest that if the animals were fed a combination of the forages *ad libitum* they would gain weight to some extent. Since this can not be related to intake (7 days estimate) it is not possible to quantify if the animals were fed to the requirement or not as weights were made on the basis of 30 days period. In this study, intake cannot, therefore, be related to the body weight changes of the animals. For example in expt.2 (Table 4.5), SLH forage diets, the animals ate a total DM of 6.12 kg d⁻¹ and gained 940 g per day. Danish Feed Table suggest that, 1 kg of gain require 4 FU (Strudsholm, 1995). The FU for maintenance calculated from the formula: $W/200 + 1.5 = \text{FU for maintenance}$ suggest that with the animals body weights of 261-288 kg (Expt.1) and 257-283 kg (Expt.2), and with the amount of forage consumed (Table 4.4) it was not possible for the animals to have any FU left after maintenance to be utilised to such an efficiency of being able to gain 940 g d⁻¹. Based on the these arguments the gains observed in this study (Table 4.5) are not realistic and could only be used to characterise the forages in terms of whether they were able to meet the animals maintenance requirement or not when fed *ad libitum* (plus minerals) with or without FM and urea supplementation.

To characterise these forages in terms of their potential to support animal production, organic matter intake (OMI) was related to the intake of total digestible nutrients (TDN) This made it possible to relate intake obtained in this study (Table 4.4) with values given in feed tables (NRC, 1989). This can test if the animal's intake (Table 4.4) was to its requirements (in this case maintenance) or not. In expt. 1 calculated digestible organic matter (DOM) intake was 2.59, 2.27, 3.64, 3.29 and 3.11 kg d⁻¹ for BH, MS, LH, LGH and UTRS respectively. In expt 2 calculated DOM intake was 2.54, 2.40, 2.54, 3.39 and 3.10 kg d⁻¹ for UNBH, SBH, SMS, SLH and SUTRS respectively. Assuming that

DOM intake will be equal to TDN, as fat content of the tropical forages was almost negligible (Kimambo *et al.*, 1994; Mgheni *et al.*, 1996). Then intake in the present study was slightly above/below maintenance in terms of DM, CP and DOM intake in both experiments (Tables 2.6 and 4.4). This may suggest that the tropical forages in the present study did not have similar potential to support animal production. Feeding them in combination *ad libitum* could achieve maintenance allowance. Some forages like LH, LGH and UTRS could even lead to gain in weights (Table 4.5) when fed *ad libitum*. With urea and fishmeal (FM) supplementation the animals had even better performance (Table 4.5) as the CP intake was above the requirement for SLH and SUTRS. Under tropical conditions, DM intakes slightly lower (2.2- 4.7 kg d⁻¹) than what has been obtained in this study has been reported (Shem *et al.*, 1995) in growing steers fed tropical forages. The animals, however, were also of lower body weights (117-209 kg) and forages used were of lower feeding value than what was used in the present study.

Similar effects in all forage diets (Table 4.18) when FM and urea was supplemented to the animals may suggest that it was important to supplement some of the forage diets with protein (Table 5.3). Urea and FM supplementation to increase rumen metabolism, has been reported to improve intake of forages low in protein (Weisbjerg *et al.*, 1998; Mgheni *et al.*, 1993). However, urea and FM supplementation showed accumulation of NH₃ in the rumen (Table 4.7) an indication that there was lack of enough digestible carbohydrates for utilisation of NH₃ for microbial protein synthesis. Similar findings were reported (Mgheni *et al.*, 1993) in rice straw diets fed to dairy goats. Taking into account the high price of FM and urea, supplementation of the forages studied may not seem necessary for the animal category used. To improve the intake of both forages a feeding strategy may seem necessary. For example feeding MS in combination with other forages may improve intake (Bal *et al.*, 1997). The BH could be improved in intake by cutting at optimum stage (Mgheni

et al., 1996). In practice, the results may form the basis for proper feeding and supplementation strategy for a certain level of production. This is by taking into consideration that it is not possible to meet the animals requirements especially at high level production by sole forage based diets (Nkya *et al.*, 1998).

5.3 Prediction of intake

In feed evaluation the best prediction model is one which can give the amount of food the animal can consume at an expected level of production with a reasonable degree of accuracy. Accuracy seems to make models more complicated. When the farmer (end user) wants to understand the models, then complicated models can be unpopular to the farmer. On the other hand if the farmer wants to understand the outcome of the model then it does not matter how complicated the model is. The goal is to be as precise as possible, but at the same time the model has to have a practical application and easy to improve when more information becomes available.

The prediction models obtained in this study (Table 4.17) predicted forage DM intake with variable degrees of accuracy depending mostly on how accurate the variables used to predict intake were estimated. Models developed indicated that the DMI could be predicted most accurately using fill that was estimated from RET-total NDF with standard error of the mean of 0.7 kg (Expt.1) and 0.5 kg (Expt.2). The models were also able to explain 0.70 (Expt.1) and 0.75 (Expt.2) of the variations observed for intake and only 0.25 and 0.30 were due to other factors not accounted for. Such a model can be accepted as the animal factors like body weights and other feed factors like palatability and preferences were not accounted for. Most important factors regulating VFI considered in these models was the NDF fraction which contributed to the fill value of forages (Table 4.12) which assumed a physical regulation of feed intake.

Use of rumen NDF pool instead of rumen pool size of DM used previously (Mgheni *et al.*, 1998), is recommended because this fraction is easier to handle and devoid of microbial and endogenous material. The rumen DM pool consists of undegraded feeds, microbes, and products from microbial metabolism and endogenous DM especially that from saliva. The total DM pool size in the rumen can not, therefore, be used as an estimate of the rumen capacity truly available from intake unless corrections are made. This suggestions confirms the results reported by Mgheni *et al.* (1998) who obtained poor correlation ($r = 0.53$) when the DM pool size was used as an estimate of rumen capacity without correction for microbial matter. These results are consistent with other studies (Stensig *et al.*, 1994b) which reported improved R^2 and low standard error of estimate when NDF parameters were used to predict DM intake instead of using DM parameters that were not corrected for microbial DM. Similar findings have been reported by Weisbjerg *et al.* (1998).

Thus, NDF parameters measured as degradability characteristics (Table 4.3), rumen pool size of NDF (Table 4.8 and 4.9) and passage rates (Table 4.10 and 4.11) were used as key parameters that predicted NDF intake (Model 3.16) and finally DM intake (Model 3.17). As shown in Table 4.17 the standard error of the predicted DMI when total-NDF was used to estimate passage rates was within the acceptable level for both experiments, whereas poor relationship and high error of estimate were observed when other methods were used. Low precision was observed when passage rates were estimated from CR-MF, RET-DNDF plus INDF and a constant passage rate of $2\% \text{ h}^{-1}$ (Table 4.17) was used, compared to RET-total NDF. This may suggest that if passage rates is to be used to calculate fill (Model 3.15) then this parameter has to be estimated with reasonable precision. The results further suggests that measure of passage rate for each forage may be necessary as indicated by the low value of R^2 with high error of estimate when a constant

passage rate of 2 % h⁻¹ was used. In general the results indicated that if the NDF analysis procedures and methods for estimating passage rates could be improved upon, the models could also be improved to a reasonable precision. From the present study, the prediction models varied substantially (Table 4.17) in terms of R^2 and root mean square errors (RMSE) suggesting that some methods used to estimate passage rates, especially that of CR-MF were not good enough to explain the differences observed in intake and may be erroneous to be used in the prediction of intake.

In my own opinion a model that can provide biologically acceptable interpretation of the differences obtained in forage intake by 70 to 75 % (Table 4.17) should be adequate enough to predict the dry matter intake of tropical forages under zero grazing conditions. The models that used passage rate obtained from RET-total NDF was able to predict DM intake with RMSE of 0.83 kg (Expt.1) and 0.71 kg (Expt.2). This error of estimate seems reasonable, although it is higher than error of estimate (RMSE of 0.58 kg) obtained by Stensig *et al.* (1994b) using similar method.

Although high correlations were obtained ($R^2 = 0.70$) in expt.1 and ($R^2 = 0.75$) in expt.2, their practical application may be difficult. Estimate of passage rates has been found to be labour intensive and expensive procedure (Huhtanen, 1998), yet it has been difficult to obtain the required precision. In this study, passage rates estimated using markers were difficult to achieve the required precision and yet there is no single marker that fulfils the criteria of an ideal marker. The rumen evacuation method suggested by Stensig *et al.* (1998b) and used in the present study may seem appropriate, but like CR-MF used in the present study it is labour intensive and may be in practice difficult to be used as routine laboratory analysis as it requires use of fistulated

animals. Thus, for practical purposes, it may be possible to use a constant passage rate of 2 % h⁻¹ with the argument that by using LSMcans for the measured and predicted DM intake (Table 4.16), the R^2 were improved (Table 4.19). The calculations indicated that animal differences were an important factor contributing to the variation in intake and when considered in the Model 3.18 and 3.19 using LSMcans instead of individual observations the precision improved. Also the number of animals used in this study may seem to be an important factor in improving the prediction models since the R^2 improved when LSMeans from the two experiments were considered (Table 4.19). However, since this study was looking at feed evaluation *per se* and the design of the experiments was a 5 x 5 Latin square that took care of animal differences the variation between animals were not considered important. It may be also difficult, in this aspect, to use a mathematical approach to remove biological variations completely.

From the calculation shown in Table 4.19 one can argue that by using a constant passage rate of 2 % h⁻¹ instead of measured passage rate using RET-total NDF that maximise R^2 (Table 4.17) the approach may be more practical. This can be cheaper and more practical in using the model developed in this study. The model can even be improved further if more animals are used to test the model to improve its precision.

Considering predicted intake observed from individual treatment diets (Table 4.16), the results showed that in general voluntary DM intake was under-estimated. The results are similar to those obtained by Stensig *et al.* (1994b). Various reasons could explain this under-prediction relative to the observed intakes. The major reasons was in the difficulty of measuring accurately

the variables used as inputs to the prediction model (Model 3.16) viz: rumen pool size of NDF (kg) and Fill (day).

According to results obtained by Gasa *et al.* (1991) on diurnal variations in the rumen pool size, the three evacuation times in the present experiments varied and the sampling of the rumen content may not represent the true rumen content. This may reflect the source of error that might lead to under-estimation of mean diurnal rumen pool size. Since the rumen pool size of NDF has been used as an estimate of rumen capacity it can lead to an under-estimate of intake as obtained in this study.

Fill was calculated from degradability characteristic obtained from the nylon bag technique and the data fitted by Model 3.3. The problem of the nylon bag technique and problem of fit for the data by Model 3.3 in general has been discussed previously and can be another source of error. In estimating ruminal digestibility that combine degradability characteristics and passage rates, methods to improve the *in situ* nylon bag technique that over-estimate ruminal digestibility of NDF has been studied (Tamminga *et al.*, 1989; Huhtanen et 1995; Huhtanen and Khalili, 1991; Stensig *et al.*, 1994a; Hveplund and Weisbjerg, 1998; Stensig *et al.*, 1998b). Like in this study, the ruminal digestibility decreased with increased passage rates (Table 4.13) as indicated by different passage rates obtained by different methods. Other reasons were associated with the error of estimating the *b* and *c* values by Model 3.3 that assume a steady state as discussed previously.

The use of a two-compartment model from parameters derived from rumen evacuation (Model 3.13) improved ruminal digestibility of NDF (Table 4.14). This may suggest that if the method for estimating physical fill proposed by Madsen *et al.* (1994) is calculated using similar approach (assuming a two-pool model) the method can be more reliable and more useful tool in understanding and predicting changes in intake of tropical forages. The model focuses on digestion as a dynamic process. Measure of diurnal variations in intake associated with changes in digestion and passage rates (assuming a physical regulation of intake) has the advantage that the obtained parameters are connected naturally with the rumen digestibility as they are derived from intake and flow data.

The results have demonstrated that intake of tropical forages can adequately be described from physical fill based on degradability characteristics, rumen pool size and passage rate of NDF. For the system to be used in practice it is necessary to have accurate estimates of the degradability characteristics, rumen pool sizes and passage rates. The models utilised a range of input variables and this provides the basis for a flexible approach to intake prediction in practical situations where characterisation of the forages varied substantially. The study showed a large variation in degradability characteristics, rumen pool sizes and passage rates, suggesting that prediction in practice may be difficult, a situation that was reflected by poor R^2 when a constant passage rate was used.

In a way the system of describing physical fill of forages is simple and flexible to build on by making correction that modifies the system as more information becomes available. The model, seems to be inadequate in the sense that the system only takes into account physical fill and does not reflect the true complexity of intake regulation (description of the physiological process

inside the animal) in the tropics and consequently intake. Thus, before the system is put into use it is important to test the models using independent data, different animals, and large number of animals with more commonly used forages by smallscale dairy farmers and define the variations. It is emphasised that since other factors affecting intake were not accounted for in the present study, the use of the developed models are still limited to the animal category developed for and cannot be used as a general model for predicting intake for all animal categories. Also the variations found between different fibre sources may suggest that it may be necessary to construct a model for specific forages or diets under defined management situations rather than developing a general model.

6 CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

- It can be concluded that the most important factor-limiting intake of tropical forages is the physical fill of NDF in the rumen due to either passage and digestion rates and/or intake. Fill of the rumen was found to make the animal eat less at high fill or eat more at low fill. Thus, description of "Fill value" and rumen pool size of NDF of forages can be used in feed evaluation systems to describe physical fill of feeds. Maize silage was found to deviate from the assumption that intake was regulated physically by indigestible residue and rumen pool size of NDF. It was revealed that intake of MS was low, a situation that may be required to be corrected for in the system using MS fermentation quality.
- The system of describing the physical fill of tropical forages obtained from passage rate estimated from RET-total NDF was found to be adequate in predicting DMI in mature non-pregnant dairy heifers fed *ad libitum* under a zero-grazing system with an accuracy of $R^2 = 0.70$ (RMSE = 0.83) in expt.1 and $R^2 = 0.75$ (RMSE = 0.71) in expt.2.
- For practical purposes it may be necessary to work for a constant "Fill" for tropical forages so as to avoid parameters needed to calculate fill values. It is also necessary to calibrate the system in standardised experiments using large numbers of animals before the system is released for use by farmers.
- For the system to be used in practice it is necessary to have accurate estimates of the important input factors to the model viz: degradability characteristics, rumen pool sizes and

passage rates. The *in situ* nylon bag technique for estimating degradability characteristics was found to have few shortcomings that were distinct and specific to the present study. This was poor fit of the data by Model 3.3 when removal of the microbial contamination was ineffective even when stomaching procedure was used for LH forage, thus giving inaccurate estimates of the degradability constants.

- The *in situ* nylon bag technique long incubation (30 days) made it possible to fractionate the fibre fraction into digestible and indigestible fractions which are more reasonable with respect to biological availability rather than further chemical fractions as clearly demonstrated by LH. Thus, the system was able to incorporate the quantitative information of the digestion and passage kinetics of individual fibre sources without any confounding effect of the fibre diets. This made it possible to evaluate the potential digestion characteristics and passage rates of individual forage fibre at a defined feeding (*ad libitum*) level.
- The methods for estimating passage rates were found to be inadequate in terms of accuracy (poor R^2). The rumen evacuation method (total-NDF), however, was found to be relatively more accurate compared to chromium-mordanted fibre which was found to over-estimate the passage rates and, thus, the predicted intake. The rumen evacuation method in contrast to the chromium-mordanted fibre has the advantage that the obtained digestion and passage rates are naturally associated with rumen digestibility, as they are derived from the intake and flow data.

- The results have demonstrated that intake of tropical forages can adequately be described from physical fill based on degradability characteristics estimated using the *in situ* nylon bag technique, rumen pool size and passage rate of NDF measured by rumen evacuation technique (RET). The study showed a large variation in degradability characteristics, rumen pool sizes and passage rates, suggesting that prediction in practice may be difficult, a situation that was reflected by poor R^2 when a constant passage rate was used.
- The system of describing physical fill showed a biologically more acceptable interpretation of the relationships of differences in intake of different forages by the animals. The models that described the system utilised a range of input variables estimated in the same experiments. Thus, the results form the basis for a flexible approach to prediction of intake in practical situations where feed characteristics vary substantially.

6.2 Recommendations

- Further evaluation is required to improve and/or replace the methods and procedures used for estimating degradability characteristics, rumen pool size of NDF, passage and digestion rates in order to have accurate estimates of the important and pertinent input parameters to the model that were also used to describe the physical fill of tropical forages and finally used to predict dry matter intake.
- The evaluation should be able to choose the most important factor to be included in the model considering the accuracy of the individual feed analysis, their costs and sustainability in the tropics. As far as possible the analysis should be standardised at least within a

laboratory and made such that it can be used as a routine analysis that can be tabulated in feed tables. The model needs to be tested using a larger number of animals and forages, different animal categories and under defined management systems.

- On prediction of intake future models should focus on dynamic, mechanistic models of the total digestive tract of the animal in order to reflect the complexity of intake regulation. With adequate data/information mathematical equations using dynamic, mechanistic models can be more important in understanding the mechanism involved in feed intake regulation. With such understanding a novel system that can result in more satisfactory prediction models of feed intake in ruminants under different tropical production systems can be developed.

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APPENDICES

Appendix. 1 Ambient temperature (temp) and humidity (RH) for July, August and September (1997) as recorded daily from the Meteorological Station SUA main campus, Morogoro.

Day	Temp (°C)		RH (%)		Temp (°C)		RH (%)		Temp (°C)		RH (%)	
	July				August				September			
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
1	16.9	28.7	51	98	14.3	27.8	55	83	18.7	28.8	49	90
2	17.3	28.8	63	96	16.6	28.5	50	97	18.0	29.2	47	98
3	15.2	28.4	51	96	17.6	27.6	56	98	17.2	30.9	42	97
4	16.0	28.8	54	96	17.0	28.7	50	96	16.9	30.8	40	98
5	16.6	29.3	53	95	17.4	29.0	50	91	18.1	29.9	42	95
6	16.2	27.5	53	99	14.2	30.3	42	96	16.6	30.6	40	98
7	17.8	30.0	90	96	14.9	29.0	49	99	17.2	30.8	39	95
8	18.4	25.6	62	86	15.0	28.5	59	98	18.0	30.7	42	95
9	17.7	27.0	54	94	18.2	29.2	45	87	16.4	27.7	47	95
10	19.0	28.2	45	87	17.2	27.7	49	93	16.5	29.5	43	95
11	17.5	25.7	55	98	18.6	27.5	47	93	16.2	31.0	34	90
12	15.1	27.4	53	77	16.8	28.9	50	96	17.2	30.7	41	90
13	17.8	26.0	56	91	15.5	28.4	48	96	18.0	29.0	32	94
14	18.0	27.2	47	73	15.2	29.5	39	96	18.2	30.0	43	93
15	14.0	27.0	49	96	18.2	27.6	49	97	17.5	29.2	49	97
16	14.8	27.4	49	93	17.7	28.8	47	97	16.8	29.0	46	95
17	16.5	27.0	71	92	16.9	27.7	37	96	17.1	28.2	49	95
18	16.9	26.6	63	93	17.0	29.5	47	95	18.6	31.5	41	94
19	19.8	29.2	45	94	17.0	29.1	54	97	17.1	31.8	39	96
20	16.9	29.3	50	90	17.2	29.8	48	96	16.0	31.0	39	95
21	17.0	28.0	50	100	16.2	31.2	43	97	17.3	32.0	38	93
22	15.0	27.3	52	97	15.0	30.4	40	97	18.1	31.6	37	90
23	14.8	27.9	51	96	12.4	30.8	71	94	18.0	31.4	35	99
24	15.3	28.0	67	96	14.5	29.5	39	94	18.1	31.7	37	91
25	16.0	28.5	83	95	14.4	29.0	39	89	16.5	33.0	37	97
26	15.5	28.0	51	95	18.0	27.4	55	88	16.5	34.3	33	97
27	12.3	27.3	40	99	17.2	28.0	48	97	18.6	33.0	36	93
28	15.4	24.4	64	94	16.5	29.3	47	98	18.4	31.5	35	93
29	14.5	24.5	75	98	15.8	28.8	45	93	18.0	31.2	41	90
30	15.5	28.5	74	96	17.5	27.8	47	95	19.0	31.2	42	97
31	14.8	29.0	45	91	16.8	28.4	58	98	xxx	xxx	xxx	xxx
M ¹	16.3	27.5			16.4	28.8			17.5	30.7		

¹Mean temperatures and humidity for the month.

Appendix. 2 Ambient temperature (temp) and humidity (RH) for October and November (1997) as recorded daily from the Meteorological Station SUA main campus, Morogoro.

Day	Temp (°C)		RH (%)		Temp (°C)		RH (%)	
	October				November			
	Min	Max	Min	Max	Min	Max	Min	Max
1	19.7	30.6	39	90	21.0	29.8	49	99
2	18.4	31.2	41	91	20.3	29.0	75	96
3	18.8	30.5	33	81	20.8	25.9	87	97
4	18.2	31.1	33	79	21.0	30.1	59	99
5	18.2	32.6	35	80	20.5	31.1	49	98
6	21.5	27.4	80	99	20.5	30.3	55	97
7	20.6	29.8	58	99	19.7	30.4	55	98
8	21.7	31.3	49	99	20.2	31.2	49	98
9	20.2	29.0	63	97	19.8	30.7	50	85
10	19.0	30.3	53	95	19.7	31.7	54	97
11	18.6	29.8	43	92	19.3	30.8	54	97
12	19.0	32.2	42	97	21.5	32.8	42	96
13	18.9	32.1	37	98	20.8	32.6	92	98
14	20.1	32.5	41	98	20.5	31.7	62	97
15	19.0	31.5	48	97	21.7	30.5	87	93
16	20.4	31.2	46	95	20.8	31.5	53	98
17	20.4	29.3	65	89	23.0	31.9	60	89
18	20.9	29.7	51	96	21.1	32.2	52	96
19	20.5	26.4	66	95	21.5	34.6	49	98
20	20.4	25.7	63	92	21.5	29.7	61	95
21	20.0	27.8	67	99	22.1	26.6	82	98
22	21.0	30.0	55	99	21.5	31.3	58	99
23	20.5	30.5	48	99	21.5	31.9	58	98
24	18.5	30.1	62	95	22.5	31.8	53	97
25	19.6	31.1	51	95	21.5	32.0	47	87
26	20.4	30.7	47	96	20.6	32.0	46	95
27	18.5	30.8	51	98	21.8	30.2	68	95
28	19.1	32.0	48	100	21.9	31.6	54	98
29	21.3	31.2	87	93	21.0	29.7	77	98
30	21.6	29.6	89	99	21.4	28.5	91	99
31	21.1	29.5	71	98	xxx	xxx	xxx	xxx
Mean ¹	19.9	30.2			21.0	30.8		

¹Mean temperatures and humidity for the month.

Appendix. 3 LSMeans dry matter (DM), nitrogen (N) and neutral detergent fibre (NDF) degradability values at different incubation time of tropical forages done in a standard procedure (% DM)

Type of forage and feed fractions	Incubation time (h)									
	0	2	4	8	16	24	48	96	144	192
Dry matter (DM):										
BH	22.4	26.8	28.8	31.7	38.0	49.8	63.8	71.5	73.3	75.0
MS	36.3	40.0	43.0	47.2	50.3	60.9	74.0	81.5	83.6	84.7
LH	33.9	51.0	56.5	63.5	64.7	67.9	73.1	64.2	67.6	68.7
LGH	18.8	28.6	30.4	36.7	43.3	50.7	61.5	64.2	67.6	68.7
UTRS	15.9	21.9	22.6	30.5	36.4	45.6	62.1	68.1	70.7	72.2
Nitrogen (N):										
BH	28.9	36.0	46.6	60.7	68.6	78.4	86.1	90.4	92.1	93.4
MS	68.1	71.8	74.9	78.1	80.8	90.9	95.8	97.2	97.9	98.2
LH	57.9	69.6	76.0	84.9	87.1	89.4	92.3	86.9	88.7	89.7
LGH	55.2	65.3	68.9	72.2	76.2	80.2	85.2	86.9	88.7	89.7
UTRS	39.8	50.4	57.9	65.2	70.6	76.0	84.4	88.2	90.5	92.2
Neutral detergent fibre (NDF):										
BH	0.0	8.6	8.5	15.8	20.4	34.5	55.4	65.2	71.9	71.9
MS	0.0	5.9	11.4	17.4	28.1	42.9	63.9	74.4	79.2	79.2
LH	0.0	24.1	21.4	27.7	35.7	39.6	42.2	47.7	47.3	47.3
LGH	0.0	9.8	10.7	12.4	26.9	32.7	49.7	56.8	60.0	59.0
UTRS	0.0	9.8	5.9	15.7	21.0	38.0	56.1	65.3	75.9	75.9

Appendix. 4 LSMeans dry matter (DM) degradability values at different incubation time as incubated in animals fed tropical forages in experiment 1 and 2 (% DM)

Type of forage	Incubation time (h)									
	0	2	4	8	16	24	48	96	144	192
Experiment 1:										
BH	22.3	23.9	25.0	30.4	35.9	42.2	60.8	69.5	72.8	74.2
MS	34.1	37.0	38.6	43.8	49.8	58.4	71.0	80.9	84.7	86.7
LH	28.4	44.1	46.3	57.0	64.9	68.6	70.9	68.1	70.8	73.0
LGH	20.1	27.0	29.1	35.4	47.5	55.0	62.8	66.4	67.2	69.0
UTRS	17.2	20.4	22.5	28.3	37.9	47.0	59.6	67.9	70.5	72.6
Experiment 2:										
UNBH	19.7	23.7	24.8	31.2	42.9	42.9	57.8	69.0	74.1	75.0
SBH	20.6	23.0	24.9	30.6	46.7	46.7	62.8	70.8	73.2	74.5
SMS	32.1	36.8	39.1	46.3	63.2	63.2	73.7	82.5	84.7	88.1
SLH	30.9	46.9	52.8	60.3	69.3	69.3	71.3	69.0	59.9	51.9
SUTRS	17.2	19.5	21.0	29.1	46.4	46.4	57.5	65.6	71.4	70.1

Appendix. 5 LSMeans nitrogen (N) degradability values at different incubation time as incubated in animals fed tropical forages in experiment 1 and 2 (% DM)

Type of forage	Incubation time (h)									
	0	2	4	8	16	24	48	96	144	192
Experiment 1:										
BH	37.5	42.1	44.5	51.0	57.0	64.8	76.2	82.9	85.8	87.3
MS	63.6	66.5	71.1	74.7	78.5	82.9	88.5	94.5	96.1	96.9
LH	40.6	54.9	68.9	78.5	85.8	87.6	89.0	87.5	89.3	90.8
LGH	27.4	38.4	45.8	53.8	65.8	72.9	79.0	83.6	85.0	86.9
UTRS	46.8	50.1	53.9	58.8	65.9	73.4	80.6	85.6	89.0	89.0
Experiment 2:										
UNBH	35.7	41.8	43.8	50.6	53.6	62.2	73.5	81.8	83.3	88.0
SBH	36.5	41.5	44.1	49.6	58.7	65.0	75.8	81.5	83.3	85.1
SMS	62.2	67.5	69.8	74.6	77.8	83.7	89.0	93.5	94.7	96.4
SLH	44.2	59.7	67.7	79.8	85.5	89.0	90.6	88.1	81.1	76.3
SUTRS	41.8	46.6	48.9	55.6	61.9	68.5	73.7	82.3	86.5	85.3

Appendix. 6 LSMeans neutral detergent fibre (NDF) degradability values at different incubation times as incubated in animals fed tropical forages in experiment 1 and 2 (% DM)

Type of forage	Incubation time (h)									
	0	2	4	8	16	24	48	96	144	192
Experiment 1:										
BH	0.0	4.0	6.1	13.9	23.4	37.6	58.1	66.9	72.7	71.8
MS	0.0	0.3	2.2	9.7	15.3	26.4	41.0	61.0	67.5	73.0
LH	0.0	12.1	17.1	25.4	31.4	35.8	43.4	46.6	49.7	52.5
LGH	0.0	6.4	11.3	14.8	29.0	42.0	53.6	60.4	64.5	65.3
UTRS	0.0	3.0	6.5	10.5	22.4	34.0	54.2	66.5	70.4	72.6
Experiment 2:										
UNBH	0.0	2.6	6.3	14.9	17.8	30.1	49.0	61.8	64.6	69.6
SBH	0.0	2.3	8.0	15.1	24.5	30.1	41.3	52.2	55.5	61.1
SMS	0.0	0.6	3.6	16.8	24.4	37.9	52.1	67.3	69.1	74.3
SLH	0.0	17.4	23.2	33.2	41.3	44.5	52.0	53.5	54.1	56.1
SUTRS	0.0	1.0	3.6	13.1	26.4	40.9	57.0	68.9	74.7	75.3

Appendix. 7 **Livebody weight (kg) of the animals as weighed at beginning of the experiments and at the end of each period (1-5) regardless of their forage diets (Experiment 1)**

Measured at:	Animal identification number				
	9248 (1)	9238 (2)	9067 (3)	58 (4)	0129 (5)
Beginning of the experiment	258	255	226	238	228
End of period 1	259	258	248	226	253
End of period 2	257	303	259	231	275
End of period 3	284	294	261	262	275
End of period 4	308	324	265	274	281
End of period 5	292	348	249	313	300

Appendix. 8 **Livebody weight of the animals as weighed at beginning of the experiments and at the end of each period (1-5) regardless of their forage diets (Experiment 2)**

Measured at:	Animal identification number				
	9232 (1)	9070 (2)	9063 (3)	9064 (4)	78 (5)
Beginning of the experiment	279	213	249	220	259
End of period 1	297	214	257	225	258
End of period 2	314	226	242	239	272
End of period 3	330	255	237	259	276
End of period 4	323	264	244	257	311
End of period 5	313	247	299	273	332

Appendix. 9

LSMeans rumen pH and ammonia (NH₃) diurnal variations measured in animals fed tropical forage-based diets (Experiment.1)

Time	Type of diet					SEM	P-value forage
	BH	MS	LH	LGH	UTRS		
pH:							
00:30	6.8	6.9	6.6	6.7	6.5	0.1	0.2758
02:30	6.8	6.8	6.7	6.6	6.6	0.8	0.3805
04:30	6.8	7.0	6.7	6.7	6.5	0.1	0.0078
06:30	6.9	7.0	6.8	6.8	6.9	0.1	0.3484
08:30	6.9	7.1	7.1	6.9	6.9	0.1	0.1233
10:30	7.0	7.0	7.0	7.0	7.0	0.1	0.9451
12:30	6.8	7.0	6.8	6.8	6.8	0.1	0.6171
14:30	6.8	7.0	6.9	6.8	6.9	0.1	0.1066
16:30	6.6	6.9	6.8	6.8	6.8	0.1	0.5175
18:30	6.6	6.8	6.7	6.5	6.6	0.1	0.4427
20:30	6.6	6.8	6.7	6.5	6.5	0.1	0.2598
22:30	6.7	6.9	6.6	6.6	6.4	0.3	0.5261
Mean	6.7	6.9	6.8	6.7	6.7	0.1	0.3558
NH₃ (mg l⁻¹)							
00:30	44.5	47.0	198.7	90.1	85.2	17.4	0.0003
02:30	83.8	63.7	198.5	92.9	84.7	23.2	0.0105
04:30	54.4	60.1	265.7	108.5	98.2	19.3	0.0001
06:30	50.9	55.9	183.3	72.5	86.6	17.2	0.0012
08:30	45.8	54.3	125.0	101.2	89.0	14.7	0.0232
10:30	86.6	71.3	146.1	136.8	116.7	16.0	0.0405
12:30	53.1	55.8	126.1	104.0	103.2	18.6	0.0614
14:30	61.2	72.5	176.5	135.4	102.8	32.5	0.1433
16:30	129.3	67.0	108.9	163.4	126.0	20.7	0.0692
18:30	55.2	44.2	130.3	81.8	86.5	13.8	0.0120
20:30	49.8	46.2	148.7	99.6	82.5	28.4	0.1346
22:30	51.2	61.5	188.8	72.6	83.7	19.1	0.0064
Mean	63.8	58.7	169.0	105.3	95.4	12.6	0.0003

Appendix. 10 **LSMeans rumen pH and ammonia (NH₃) diurnal variations measured in animals fed tropical forage-based diets supplemented with FM and urea (Experiment 2)**

Time	Type of forage					SEM	P-value forage
	UNBH	SBH	SMS	SLH	SUTRS		
pH:							
00:30	6.8	6.8	6.7	6.7	6.6	0.1	0.2972
02:30	6.8	6.7	6.8	6.6	6.8	0.1	0.2519
04:30	6.9	6.8	6.7	6.8	6.7	0.1	0.5337
06:30	6.8	6.8	6.9	6.8	6.6	0.1	0.4574
08:30	6.9	7.0	7.0	7.1	6.8	0.1	0.0837
10:30	6.9	6.9	6.7	6.9	6.9	0.1	0.6290
12:30	6.8	6.8	6.8	6.7	6.8	0.1	0.7587
14:30	6.8	6.9	6.9	6.9	6.8	0.1	0.8639
16:30	6.6	6.8	6.7	6.7	6.8	0.1	0.6113
18:30	6.5	6.6	6.7	6.5	6.7	0.1	0.5007
20:30	6.7	6.6	6.8	6.4	6.5	0.1	0.0174
22:30	6.8	6.6	6.7	6.5	6.6	0.1	0.3530
Mean	6.8	6.8	6.8	6.7	6.7	0.1	0.7193
NH₃ (mg l⁻¹)							
00:30	39.1	50.1	134.9	230.2	170.8	27.8	0.0101
02:30	39.8	71.0	138.1	228.1	190.3	32.7	0.0228
04:30	49.1	75.7	122.2	226.8	132.7	20.9	0.0163
06:30	47.7	60.1	160.8	171.6	171.5	22.0	0.0194
08:30	32.8	67.3	63.0	152.0	111.6	11.6	0.0003
10:30	111.7	114.5	56.1	261.8	202.5	26.3	0.0117
12:30	45.5	97.5	80.4	218.0	180.8	24.9	0.0062
14:30	48.8	75.2	88.9	124.4	181.2	10.7	0.0011
16:30*	-	-	-	-	-	-	-
18:30	47.0	69.9	135.0	172.3	137.8	34.6	0.4600
20:30	43.4	41.8	120.3	137.1	44.2	30.4	0.1474
22:30	40.2	102.4	84.8	174.0	164.6	30.7	0.1906
Mean	50.9	79.0	96.6	196.3	157.9	13.9	0.0002

*The SAS Proc. GLM could not estimate the value because there was too few values left after eliminating those considered to be outliers or absolutely not possible estimate of rumen ammonia as they were too high to be true.