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IN MEMORY OF MY BELOVED LATE MOTHER

Summary

The first ruminants evolved about 50 million years ago and were small forest dwelling omnivores. Today there are about 200 species of ruminants which include both wild and domestic species. Cattle, sheep, and goats account for about 95% of the total population of domestic ruminants. The present thesis aimed at studying various comparative aspects of feed intake and digestibility among different domestic ruminant species, therefore, this work was structured in two major parts. The first part dealt with dataset on voluntary feed intake, digestibility and composition of basal diets and supplements of the domestic ruminant species, i.e., sheep, goats, cattle and buffaloes by pooling data from previously published studies. A meta-analysis of these studies was performed to determine whether there is a common scaling exponent for dry matter intake (DMI) among domestic ruminant species or if this exponent is species specific, and to investigate the influence of dietary nutrient composition on DMI and digestibility. Distinguishable, i.e. species-specific, scaling factors for the relationship between DMI and body weight were estimated, and the difference was pronounced between small and large ruminants with lower exponents for sheep and goats and higher for cattle and buffaloes. Across all ruminant species, crude protein (CP) had a positive influence on intake and digestibility while fibre fractions influenced DMI negatively except for buffaloes who responded positively to acid detergent fibre (ADF). Digestibility was also negatively influenced by ADF in all species, whereas neutral detergent fibre had a negative effect in cattle only. However, the magnitude of the response of feed intake and digestibility to varying concentrations of dietary constituents differed among the ruminant species. Whereas, second part of the study focused on evaluation of digestibility of wheat silage-based diets harvested at different stages of maturity in cattle and sheep. The diets were fed at maintenance or *ad libitum* intake. Two digestibility methods were compared, the total faecal collection method and titanium(IV)-oxide marker method. The influence of species and diet type was significant on diets digestibility. No significant differences between the methods as well as species and diets for marker recovery except with significant impact of species on titanium(IV)-oxide at *ad libitum* feeding were recorded. Also non-significant differences among variables' interactions except for significant effect of species and diet interaction on CP digestibility at *ad libitum* intake were observed. This trend confirmed that titanium(IV)-oxide is a robust external marker and can be used in digestion studies across different animal species and diet types.

Zusammenfassung

Die ersten Wiederkäuer, die sich vor circa 50 Millionen Jahren entwickelten, waren kleine, waldbewohnende Omnivore. Heute gibt es ungefähr 200 Wiederkäuerspezies, die sowohl wilde als auch domestizierte Arten einschließen. Rinder, Schafe und Ziegen machen dabei 95 % der Gesamtpopulation der Hauswiederkäuer aus. Die vorliegende Dissertation untersucht verschiedene vergleichende Aspekte der Futteraufnahme und -verdaulichkeit bei unterschiedlichen domestizierten Wiederkäuerspezies und wurde dazu in zwei Hauptteile gegliedert. Der erste Teil befasst sich mit einem Datensatz zu freiwilliger Futteraufnahme, Verdaulichkeit und Zusammensetzung von Grundrationen und Supplementen bei Hauswiederkäuerspezies, namentlich Schafen, Ziegen, Rindern und Büffeln. Daten bereits veröffentlichter Studien wurden zusammengefasst und eine Meta-Analyse durchgeführt, um zu bestimmen, ob es bei den Hauswiederkäuerspezies für die Trockenmasseaufnahme (TMA) einen gemeinsamen normierbaren Exponenten gibt oder ob dieser Exponent speziesspezifisch ist, und um den Einfluss der Nährstoffzusammensetzung einer Ration auf TMA und Verdaulichkeit zu untersuchen. Unterscheidbare, das heißt speziesabhängige Scalingfaktoren der Beziehung zwischen TMA und Körpergewicht wurden geschätzt. Der Unterschied zwischen kleinen und großen Wiederkäuern wurde durch niedrigere Exponenten für Schafe und Ziegen und höhere für Rinder und Büffel ausgedrückt. Auf alle untersuchten Wiederkäuerspezies bezogen hatte das Rohprotein einen positiven Einfluss auf die TMA und Verdaulichkeit, wohingegen die Faserfraktionen – außer bei Büffeln, welche positiv auf die Säure-Detergenzien-Faser (ADF) reagierten – die TMA negativ beeinflussten. Die Verdaulichkeit wurde bei allen Spezies ebenfalls durch die ADF negativ beeinflusst, wohingegen die Neutral-Detergenzien-Faser nur beim Rind einen negativen Effekt hatte. Jedoch unterschied sich das Ausmaß des Effekts auf die Futteraufnahme und -verdaulichkeit bei unterschiedlichen Konzentrationen der Nahrungsbestandteile zwischen den Wiederkäuerspezies. Demgegenüber konzentrierte sich der zweite Teil der Studie auf die Untersuchung der Verdaulichkeit von Weizenganzplanzensilage basierten Rationen bei Rindern und Schafen. Der Weizen wurde zu unterschiedlichen Reifestadien geerntet und die Rationen entweder entsprechend dem energetischen Erhaltungsbedarf oder zur Aufnahme *ad libitum* angeboten. Mit der Kot-Totalsammlung und der Titan(IV)oxid-Markermethode wurden zwei Methoden zur Verdaulichkeitsbestimmung verglichen. Der Einfluss der Spezies und des Rationstyps auf die Verdaulichkeiten war signifikant. Außer einer signifikanten Wirkung der Spezies auf die Titan(IV)-oxid-Wiederfindung bei *ad libitum*-Futteraufnahme wurden zwischen den Methoden sowie zwischen Spezies und Ration keine signifikanten Effekte auf die Markerwiederfindung und die Verdaulichkeiten verzeichnet. Außer signifikanten Interaktionen zwischen Spezies und Ration für die Rohprotein-Verdaulichkeit bei Futteraufnahme *ad libitum* gab es keine signifikanten Interaktionen zwischen den einzelnen Variablen. Dieser Trend bestätigte die Tatsache, dass Titan(IV)-oxid ein robuster externer Marker ist, der in Verdaulichkeitsstudien bei unterschiedlichen Spezies und Rationstypen angewendet werden kann.

Table of contents

Figures

Chapter 3

Tables

Chapter 3

Chapter 4

Chapter 6

Abbreviations

ADF	Acid detergent fibre
ADL	Acid detergent lignin
AIA	Acid insoluble ash
BW	Body weight
CP	Crude protein
CPD	Crude protein digestibility
$CuSO_4$	Copper sulphate
DM	Dry matter
DMD	Dry matter digestibility
DMI	Dry matter intake
ED	Early dough stage of wheat grain maturity
HD	Hard dough stage of wheat grain maturity
H_2O	Water
H_2O_2	Hydrogen peroxide
H_3PO_4	Phosphoric acid
K_2SO_4	Potassium sulphate
LM	Late milk stage of wheat grain maturity
MBS	Metabolic body size
Na_2SO_3	Sodium sulphite
NDF	Neutral detergent fibre
NRC	National Research Council
OMD	Organic matter digestibility
rDMI	Relative dry matter intake expressed in relation to body weight
TC	Total collection of faeces
TiO_2	Titanium(IV)-oxide

General introduction

The first ruminants evolved about 50 million years ago and were small forest dwelling omnivores (Hackmann and Spain, 2010). Today there are about 200 species of ruminants which include both wild and domestic species (Nowak, 1999). Nine species have been domesticated during the last 10,000 years. Among these domestic ruminant species, cattle were originally identified as three separate species. Recently these three species have increasingly been grouped as one species "*Bos primigenius*" (Opinions, 2003). The population size of domestic species numbers 3.57 billion nearly 50 fold greater than that of wild ruminants which are about 75 million. Cattle, sheep, and goats account for about 95% of the total population of domestic ruminants (Hackmann and Spain, 2010).

Most research for the assessment of digestion and utilisation of feed by ruminants has focused on sheep and cattle and, usually the results obtained from these species are implicated to evaluate the feed intake and digestibility in other ruminant species (Südekum et al., 1995; Kawashima et al., 2007). However, some studies can be found in the literature which have compared these variables between large ruminants like cattle and buffaloes (Ichinohe et al., 2004; Lapitan et al., 2008) and relatively few studies have dealt with this issue for the sake of comparisons among more than two species simultaneously (Sharma and Rajora, 1977; Burns et al., 2005).

The comparative evaluation of feed digestibility and intake among ruminant species can be conducted by direct method i.e. through quantitative measurements of feed intake and collection of faecal outputs. But it requires a lot of time and labour input. To avoid such time consuming laborious activities certain digestibility markers (either internal or external) have been established which are commonly used in nutrition studies to estimate faecal output without necessitating time and labour consuming quantitative faecal sampling schedules. For example, titanium(IV)-oxide (TiO_2), like other metal oxides, bares potential as a digestibility marker (Owens and Hanson, 1992) and has successfully been used in rats (Lloyd et al., 1955; Krawielitzki et al., 1987), rabbits (Marks, 1959), swine (Jagger et al., 1992), chicken (Short et al., 1996), sheep (Brandt et al., 1987) and cattle (Hafez et al., 1988). Titgemeyer et al. (2001) found faecal recovery of TiO_2 93% for steers fed a forage-based diet and 95% and 90% for restricted and *ad libitum* consumption, respectively, for steers fed corn based diets. Glindemann et al. (2009) observed differences in faecal recovery of titanium(IV)-oxide for sheep with hay diets higher than in diets containing hay and concentrate. Other markers have also been used to determine nutrients digestibility in different species. For example, acid insoluble ash (AIA) is one of the naturally occurring markers commonly used for the determination of feed digestibility in monogastric as well as ruminant animals. It has been used to predict diet digestibility in swine (Ly et al., 2002), poultry (Vogtmann et al., 1975), sheep (Van Keulen and young, 1977) and cattle (Block et al., 1981). Similarly, acid detergent lignin (ADL) is also used as a marker which is naturally found in feedstuffs for ruminants; it is often regarded as being indigestible because there are no known mammalian or anaerobic microbial enzymes capable of degrading lignin (Van Soest, 1982). The rare earth (RE) elements are used as particulate markers in nutrition studies (Allen and Van Soest, 1984; Turnbull and Thomas, 1987). They are the most abundant ones along with chromium used for this purpose (Stefanon et al., 1992; Bernard and Doreau, 2000). Ferret et al. (1999) found 97% recovery of chromium in ryegrass hay and 105% in alfalfa hay fed to dairy ewes.

However, whatever the method is applied for measurements of digestibility and intake, inconsistencies appear in the studies dealing with the comparison of feed intake and digestibility across various ruminant species. For example, Quick and Dehority (1986) observed no apparent differences between feed intake of sheep and goats. Huston et al. (1988) mentioned that sheep and goats were similar in terms of DMI when higher quality diets were fed, inconsistencies mostly occurred with low quality feeds. However, several published reports contradict this pattern. In a review, Brown and Johnson (1984) highlighted that in most trials, sheep showed greater DMI of good quality diets and goats exhibited greater relative DMI of high fibre diets. Also for the digestibility variables, contrasting reports of digestive efficiencies of feed nutrients by ruminant species can be found in the literature. Mostly researchers noticed goats being more efficient for utilizing poor quality diets (Al Jassim et al., 1991). Nonetheless, some studies exist in the literature where goats were found better in terms of their ability to digest good quality diets (Brown and Johnson, 1985). Puppo et al. (2002) observed that cattle had significantly higher digestibility for NDF and cellulose than buffaloes when fed lucerne hay or maize silage with concentrate. But on the other hand, buffaloes have also been reported to utilize feed nutrients better than cattle when fed on poor quality rations containing higher levels of cellulose (Katiyar and Bisth, 1988).

Different factors may contribute to such kinds of inconsistencies mentioned above for comparative studies of different ruminant species. Some of the important factors contributing substantially to the differences observed for feed intake and digestibility in farm animal species are described below.

1.1. Environmental factors

Changes in the surrounding climatic environment also influence feed intake and digestibility of ruminants. MacDonald and Bell (1958) indicated that a raise in ambient temperature led to decrease in hay intake, and Wayman et al. (1962) suggested that part of this effect might be due to a decreased rate of passage of digesta through the rumen. Conversely, a decrease in temperature is associated with an increase in hay intake. Phillips et al. (1982) reported that environmental temperature has indeed an influence on digestibility of ruminants and that there is a physiological basis for the response. A hot environment reduces voluntary feed intake and increases maintenance requirements (Blaxter, 1967). On the other hand, Graham et al. (1982) showed in their study that cold exposure resulted in the increased amount of DM in the hind gut which was probably due to the higher level of feed intake in the cold. The existence of a 'thermostatic' mechanism in hypothalamus affecting feed and water intake has been demonstrated in ruminants (Andersson and Larsson, 1961). Dry matter intake and water intake are linearly related to each other (Silanikove, 1987b) and water restriction reduces voluntary feed intake (Silanikove, 1985).

Photoperiod and timing of feeding also influence feed intake and eating activities. Light (L) to dark (D) ratios affect eating patterns (Tucker et al., 1984). Sheep and heifers have been shown to consume up to 13% more feed and grow faster when the ratio is 16L to 8D than when the ratio is 8L to 16D or continuous light (Peters et al., 1980). Similarly, Brosch et al. (1988) observed that Bedouin goats maintained outdoors during the summer and given water once every four days, their voluntary intake was depressed during the hot hours of the day and it was resumed in the afternoon. The level of expansion of rumen volume was mainly dependent on the stage of dehydration and the quality of the feed. When ruminants are given a free choice for feeding, mostly they prefer to eat during cooler hours i.e., during the afternoon or at night (Brosh et al., 1988).

1.2. Dietary factors

Rumen contents contain about 85% water. Water added to the rumen has little effect on dry matter intake since it is rapidly absorbed and excreted (Van Soest, 1982). Nonlactating cattle consume an average of 3 parts water to 1 part dry matter up to 4.4 °C environmental temperature and then an increased amount of water proportional to increases in the ambient temperature (Winchester and Morris, 1956). So, water restriction causes a reduction in feed intake and an increase in feed utilization in various ruminant species (Kijora et al., 1989). The increase in digestibility seems to be related to the increase in the mean retention time of feed particles in the gut (Kijora et al., 1989). Likewise, heat stress also negatively affects the feeding activities of the animals. For example, metabolism is reduced and this was associated with a restriction in thyroid secretion and in gut motility, and thus an increase in gut fill (Lu, 1989). Reduction in appetite under heat stress is also a result primarily of the elevated body temperature and secondly it may be related to an increase in gut fill. Slower rate of passage of digesta in the gastrointestinal tract under heat load reflects the reduced ruminal activity and rumen motility (Lu, 1989). In reviewing the relevant literature, Brosh et al. (1988) indicated that quality of feed also influences intake of animals. They found that goats maintained on low quality roughages such as wheat straw will consume less feed and require less water than when fed lucerne hay (high quality roughage).

Diet digestibility and thus rate of passage is reduced if nitrogen requirements of rumen bacteria are not met (Van Soest, 1982). Diet protein solubility and degradability influence dietary protein availability to meet microbial nitrogen needs. Thus, the level of nitrogen needed in the rumen to support the maximum rate of passage would be expected to vary with carbohydrate digestibility in the rumen. Also reducing particle size and collapsing of the cell structure by finely grinding and pelleting fibrous feeds reduces rumination time and increases the rate of passage and thus feed intake (Van Soest, 1982). The NRC (1996) concluded that intake was improved most with processing where roughage was the major constituent, and the impact increased with increasing concentrations of plant cell wall and with alkali, ammoniation, or other treatments that increased the potential for cell wall digestion. Increasing the rate of passage of indigestible material can improve intake of roughages high in cell wall content by up to 50 percent. Generally, however, intake is reduced if grains are processed and if digestibility is increased.

1.3. Species differences

Niche separation in sympatric herbivores is accompanied by morphological and physiological adaptations. These adaptations have been used to categorize ruminants into concentrate selectors, intermediate feeders and grass/roughage feeders (Hofmann, 1988). According to his classification, concentrate selectors differ from grass/roughage feeders by having narrower, more prehensile muzzels; larger salivary (particularly parotid) glands; smaller mass of gastrointestinal tract relative to body weight and larger livers. These morphophysiological differences enable concentrate selectors to quickly pass roughage through the alimentary tract, resulting in rapid digestion of cell solubles and passage of undigested cell walls. However, the term “concentrate selectors” used by Hofmann (1988) for classification of herbivores may be misleading as it may correspond to browsers which actually include both diet selective and unselective species (Demment and Longhurst, 1987).

In the literature herbivores have also been classified as browsers, grazers and intermediate feeders based on their feeding type (Hummel et al., 2006). Grazing ruminants usually retain the ingesta in the gastrointestinal tract for a longer period of time and digest fibre more efficiently than browsing ruminants (Pérez-Barbería et al., 2004). Hummel et al. (2006) supported the hypothesis of shorter retention time of feed in the digestive tract of browsing ruminants based on the observation of fermentation patterns of herbs and browse plant leaves used in their study. Along with these possible feeding strategy differences among different classes of animals, body mass also plays an important role for their feed selection (Clauss et al., 2008). Demment and Van Soest (1985) in their remarkable publication dealing with body size patterns of herbivores highlighted in detail the influence of various body masses on feed selection and intake of animals. They demonstrated that, theoretically, grazing by ruminants is feasible at greater body masses than browsing. They also suggested that large ruminants may get their energy requirements even by eating relatively low quality diets due to long retention time of feed particles in their big rumen and small ruminants having supposedly shorter passage times consume high quality feeds or increase their feed intake to meet the metabolic requirements. Therefore, it is not only the feeding type but also body mass that has a significant role in animals’ diet selection. However, along with these possible species differences among various classes of ruminants in their diet selectivity, different animal production classes, age, sex and breed (Brown and Johnson, 1984) may also account for the inconsistencies observed in the comparative studies of different ruminant species.

Therefore, this research was structured in two major parts to add scientific knowledge in ruminant nutrition. In the first part, a broad based literature survey was carried out across different studies worldwide to contribute a useful and informative addition to the limited literature to investigate the influence of different dietary factors on voluntary intake and digestibility of more than two domestic ruminant species simultaneously. While in the second part a comparative study based animals trial of sheep and cattle was performed to evaluate the accuracy of external marker titanium(IV)-oxide (TiO_2) through calculating the digestibility of wheat silage diets harvested at different stages of maturity (i.e. late milk, early dough and hard dough) in two different ruminant species, i.e. cattle and sheep. The diets were fed at either maintenance or *ad libitum* intake. Two digestibility methods were compared, the total faecal collection method and TiO_2 marker method.

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Scope of the thesis

This is a cumulative thesis composed of two papers directly or indirectly addressing the problems mentioned in the general introduction. The third and fourth chapters compile manuscripts that are formatted according to the regulations of the journal chosen for submission.

The third chapter deals with dataset on voluntary feed intake, digestibility and composition of basal diets and supplements of the domestic ruminant species i.e. sheep, goats, cattle and buffaloes by pooling data from previously published studies. Since relatively few studies are available for comparison of feed intake and digestibility among more than two ruminant species. Therefore, a meta-analysis of these studies was performed to determine whether there is a common scaling exponent for DMI among domestic ruminant species or if this exponent is species specific, and to investigate the influence of dietary nutrient composition on DMI and digestibility. Species-specific, scaling factors for the relationship between DMI and BW were estimated, and the difference was pronounced between small and large ruminants with lower exponents for sheep and goats and higher for cattle and buffaloes. Across all ruminant species, CP had a positive influence on intake and digestibility while fibre fractions influenced DMI negatively except for buffaloes who responded positively to ADF. Digestibility was also negatively influenced by ADF in all species, whereas NDF had a negative effect in cattle only.

The fourth chapter focuses on evaluation of wheat silage-based diets in cattle and sheep. The total faecal collection and titanium(IV)-oxide marker methods were compared. Animal species and diet type had significant influence on diet digestibility. No significant differences between the methods as well as species and diets for marker recovery except with significant impact of species on titanium(IV)-oxide at *ad libitum* feeding were recorded. Also non-significant differences among variables' interactions except significant effect on CPD in species and diet interaction for marker recovery and digestibility were observed. This trend confirms the fact that titanium(IV)-oxide is a robust external marker and can be used across different animal species and diet types for digestibility studies.

Voluntary feed intake and digestibility of four domestic ruminant species as influenced by dietary constituents: A meta-analysis

Riaz, M.Q., Südekum, K.-H., Clauss, M., Jayanegara, A., 2014. Voluntary feed inatake and digestibility of four domestic ruminant species: A meta-analysis. Livest. Sci. 162, 76-85.

Abstract

This meta-analysis was performed to evaluate whether voluntary feed intake and digestibility of forage-based diets differ between four domestic ruminant species, *i.e.* sheep, goats, cattle and buffaloes, and secondly, whether dietary constituents, *i.e.* protein and fibre influence the respective variables. A dataset on voluntary feed intake, digestibility and composition of basal diets and supplements of the respective domestic ruminant species was compiled by pooling data from previously published studies. A total of 45 studies were found to meet the required criteria. Data were analysed by mixed model regression methodology. Discrete (domestic ruminant species) and continuous predictor variables (chemical composition of diet) were treated as fixed effects, while different studies were considered as random effects. Significant linear relationships were observed between log-transformed body weight and log-transformed dry matter intake (DMI) for all ruminant species ($P<0.05$). Within species, this scaling factor was lower for sheep and goats than for cattle and buffaloes. Crude protein (CP) concentration affected DMI of ruminants positively with variations among the species; buffaloes were more responsive to CP, followed by sheep, goats and cattle. In contrast, acid detergent fibre (ADF) negatively influenced DMI across all species except buffaloes, and had a much stronger effect on DMI of sheep and cattle than on DMI of goats. The impact of CP on DM digestibility (DMD) was similar to its influence on DMI. The strongest effect was observed in cattle and was only significant in cattle and buffaloes ($P<0.05$). Neutral detergent fibre reduced DMD only in cattle, while sheep were positively influenced and goats tended to be positively affected. The ADF lowered DMD in sheep, goats and cattle with significant effect for sheep and goats.

Keywords: Crude Protein; Digestibility; Fibre; Intake; Meta-analysis; Ruminant

3.1. Introduction

Numerous studies have compared feed intake and digestibility of various nutrients between sheep and goats (e.g. Molina Alcaide et al., 2000; Yañez-Ruiz and Molina Alcaide, 2008; Abidi et al., 2009) and between sheep and cattle (e.g. Südekum et al., 1995; Mulligan et al., 2001; Kawashima et al., 2007). Fewer studies have made comparisons between cattle and buffaloes (e.g. Pearson and Archibald, 1990; Ichinohe et al., 2004; Lapitan et al., 2008). Also relatively few published studies are available for comparison of feed intake and digestibility among more than two ruminant species (e.g. Sharma and Murdia, 1974; Sharma and Rajora, 1977; Burns et al., 2005). Therefore, we assumed that it may be a useful and informative addition to the limited literature to investigate the influence of different dietary factors on voluntary intake and digestibility of more than two domestic ruminant species simultaneously.

For comparisons of voluntary feed intake across ruminant species of varying body weights (BW), a reference scaling unit is needed to achieve comparability, because large ruminants will usually eat less relative to BW than small ones. Thus, different scaling factors have been applied to compare feed intake among ruminants of various sizes. Traditionally, for sheep and cattle feed intake comparisons in Europe, metabolic body size (MBS, i.e. $BW^{0.75}$; Kleiber, 1961) is used as a scaling factor and researchers in North America usually express dry matter (DM) intake (DMI) related to $BW^{1.0}$ (Mertens, 1994). Researchers in Australia and New Zealand frequently use the reference unit of $BW^{0.90}$ based on the recommendations of Graham (1972) for feed intake comparisons. The scaling unit of $BW^{0.90}$ has been verified by several other researchers, supporting its use for feed intake comparisons among different livestock species (Minson and Whiteman, 1989; Reid et al., 1990; Hackmann and Spain, 2010). These different scaling factors have also been found in datasets comparing mammalian herbivores beyond ruminants. Across all available species ranging from small rodents to elephants, dry matter intake scales more or less to MBS (reviewed in Clauss et al., 2007, Meyer et al., 2010). If, in contrast, only large species with a BW above 10 kg are considered, the scaling exponent is higher at $BW^{0.84}$ (Müller et al., 2013). The relevance of these different scaling exponents lies in their use when comparing data on DMI between animals of different BW within and between species. If for example a lower scaling exponent (e.g. $BW^{0.75}$) is used for comparisons than the actual one (e.g. $BW^{0.84}$), then the relative intake of the larger animals (expressed per unit $BW^{0.75}$ in this example) will be artificially increased compared to that of the smaller animals. For the same reason, it is important to know whether the same scaling exponents can be used in inter- and intraspecific comparisons.

Inconsistencies between the outcomes of individual studies may result from differences in the specific experimental conditions, the diets used and their chemical composition. Combining data from various reports into a meta-analysis can be a useful tool to deal with the inconsistencies exhibited across a variety of experimental conditions of different studies (Charbonneau et al., 2006; Sauvant et al., 2008). Therefore, we performed a meta-analysis of various studies to determine whether there is a common scaling exponent for DMI among domestic ruminant species or if this exponent is species specific, and to investigate the influence of dietary nutrient composition on DMI and digestibility.

3.2. Materials and methods

3.2.1. Description of database

A dataset summarizing voluntary feed intake, digestibility, and composition of basal diets and supplements of forage-based diets fed to domestic sheep, cattle, goats and buffaloes was compiled by pooling data from scientific literature (references listed in Appendix). The total number of studies meeting the inclusion criteria was 45, which were divided into 3 main categories that comprised comparisons between sheep and cattle (n=10), sheep and goats (n=25), and cattle and buffaloes (n=10). The corresponding numbers of individual observations for sheep, goats, cattle and buffaloes were 139, 78, 91 and 30, respectively. Detailed composition of diets evaluated in the present study can be obtained from the corresponding author upon request. The prerequisites for a study to be included in the dataset was that DM digestibility (DMD, in g/kg), BW of animals (individual BW (kg) of animals used in an experiment or mean value of a group of animals given for a certain trial, and feed intake (expressed as DMI, g/day) of any two or more of the above mentioned domestic ruminant species was reported for ad libitum feeding conditions. Chemical characteristics of the diets (i.e. neutral detergent fibre (NDF), acid detergent fibre (ADF) and/or crude protein (CP)) were included as available. Feed intake data given as kg/day, % of BW or g/kg $BW^{1.0}$, g/kg $BW^{0.90}$ or g/kg $BW^{0.75}$ were converted to g/day.

An allometric relationship between DMI and BW was constructed according to the following model:

$$DMI = aBW^{b},$$

where a is a constant and b is the scaling factor. The respective model was transformed into its logarithmic equation to obtain a linear relationship between DMI and BW, where the scaling factor is the slope of the equation:

log DMI = log a + b log BW

In a first step, scaling factors were estimated for each ruminant species separately. The scaling factor was then used to obtain species-specific MBS, i.e. $BW^{scaling\ factor}$ for each species. Feed intake was then expressed as g DMI per unit of species-specific MBS. To know whether there is a common scaling factor for all four ruminant species or not (i.e. each species has its specific scaling factor), interaction between species and log BW on log DMI was statistically tested.

3.2.2. Statistical analyses

Data were analysed using mixed model regression methodology (St-Pierre, 2001; Sauvant et al., 2008). Models with either discrete a predictor variable (domestic ruminant species) or continuous predictor variables (chemical composition of diets: CP, NDF or ADF) were assessed individually. The respective predictor variables were considered as fixed effects. Different studies were considered as random effects. The model statistics used for this study was Akaike's information criterion (AIC). The AIC was applied in model selection to measure the relative goodness of fit of a statistical model. In this study, AIC was used to select whether a model is quadratic or linear (lower AIC is better model), together with the P-value (explained below). Accordingly, for the continuous predictor variable (chemical composition of diet), the following model was used:

$$Y_{ij} = B_0 + B_1X_{ij} + B_2X_{ij}^2 + s_i + b_iX_{ij} + e_{ij},$$

where Y_{ij} = the dependent variable, B_0 = overall inter-study intercept (fixed effect), B_1 = the overall linear regression coefficient Y on X (fixed effect), B_2 = the overall quadratic regression coefficient Y on X (fixed effect), X_{ij}= the value of the continuous predictor variable, s_i = the random effect of the i^{th} study, b_i = the random effect of study on the regression coefficient of Y on X, and e_{ij} = the residual error. When a quadratic model did not significantly explain the relationship between independent and dependent variables, the model was modified into a linear model by taking out the $B_2X_{ij}^2$ term. For the discrete predictor variable (domestic ruminant species), the following model was applied:

$$Y_{ijk} = \mu + s_i + \tau_j + s\tau_{ij} + e_{ijk},$$

where Y_{ijk} = the dependent variable, μ = overall mean, s_i = the random effect of the i^{th} study, τ_j = the fixed effect of the j^{th} level of factor τ, $s\tau_{ij}$ = the random interaction between the i^{th} study and the j^{th} level of factor τ, e_{ijk} = the residual error.

Data were weighted by the number of animals in each study. Tukey's test was applied as a post hoc test to compare the differences among means in the case of discrete predictor variables.

3.3. Results

In some studies not all the variables of interest were reported, therefore, the number of observations across variables was not uniform (Table 1). There were large differences between minimum and maximum values in the database for dietary constituents (NDF, ADF and CP) between buffaloes and the other three species; for these three species, however, the nutrient ranges of the diets were relatively similar.

Table 1: Statistical description of the dietary and response variables in the database

Species	Variables[a]	n[b]	Mean	SD[c]	Minimum	Maximum
Sheep						
	Body weight, kg	139	41.6	17.3	10.2	82.6
	Feed nutrients, g/kg DM					
	NDF	69	520	168	134	768
	ADF	53	364	154	94	870
	CP	126	124	68	16	422
	DMI, g/kg MBS	139	898	435	139	2530
	DMD, g/kg DM	92	580	95	243	815
Goats						
	Body weight, kg	78	26.0	15.0	7.0	67.8
	Feed nutrients, g/kg DM					
	NDF	35	457	184	134	764
	ADF	25	347	164	94	870
	CP	78	121	75	25	422
	DMI, g/kg MBS	78	600	300	150	1520
	DMD, g/kg DM	45	611	102	312	869
Cattle						
	Body weight, kg	91	391.0	136.5	103.0	674.0
	Feed nutrients, g/kg DM					
	NDF	38	603	83	406	768
	ADF	43	403	128	221	661
	CP	68	114	66	16	313
	DMI, g/kg MBS	91	6857	3166	1680	19870
	DMD, g/kg DM	67	555	87	366	717
Buffaloes						
	Body weight, kg	30	329.0	137.8	150.0	722.0
	Feed nutrients, g/kg DM					
	NDF	5	606	54	510	632
	ADF	15	450	65	350	578
	CP	26	76	66	22	255
	DMI, g/kg MBS	30	5539	2055	2390	11200
	DMD, g/kg DM	15	478	79	366	610

[a]NDF = neutral detergent fibre; ADF = acid detergent fibre; CP = crude protein; DM = dry matter, DMI = DM intake; DMD = DM digestibility; MBS = Metabolic body size.
[b]n = Number of data used.
[c]SD = Standard deviation. References used to construct the data base are given as a separate list at the end of the reference section.

Significant linear relationships were observed between log-transformed BW and log-transformed DMI of all domestic ruminant species in this study (Fig. 1). Individual regression equations for each ruminant species as shown in the footnote of Fig. 1 demonstrated that the scaling exponent for relative DMI (rDMI; intake expressed in relation to BW) is lower in small ruminants than in in large ruminants.

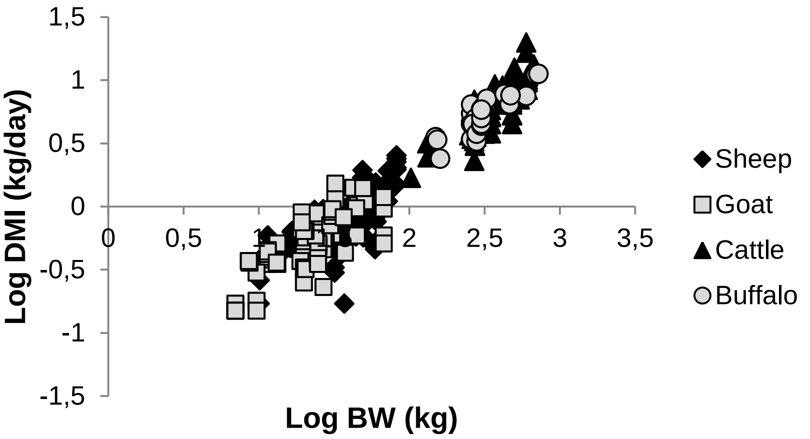


Fig. 1. Relationship between log body weight (BW) and log dry matter intake (DMI). The regression equation for each ruminant species is as follows (mean ± 95% confidence interval): Sheep: log DMI = –1.105 (± 0.290) + 0.639 (± 0.187) log BW; P<0.001; r^2 = 0.49. Goat: log DMI = –1.231 (± 0.290) + 0.714 (± 0.212) log BW; P<0.001; r^2 = 0.55. Cattle: log DMI = –1.461 (± 0.445) + 0.883 (± 0.175) log BW; P<0.001; r^2 = 0.71. Buffalo: log DMI = –1.316 (± 0.602) + 0.818 (± 0.246) log BW; P<0.001; r^2 = 0.75. P-values: species, P<0.01; log BW, P<0.001; species × log BW, P<0.01.

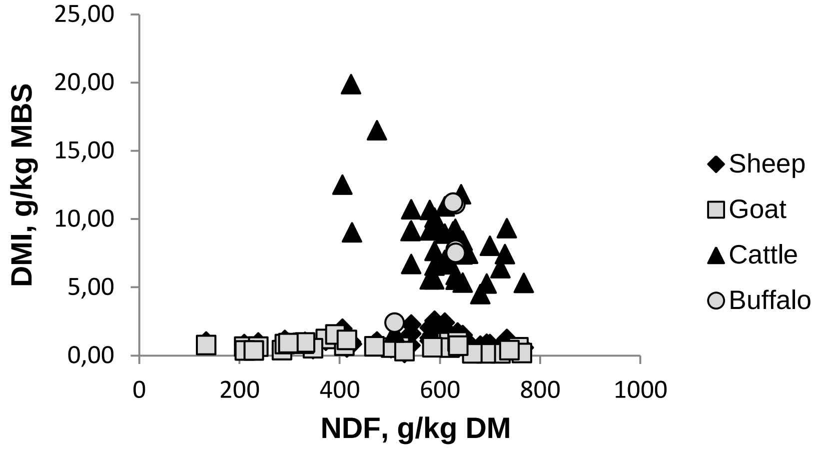
The differences for scaling factors among species were significant for each individual factor as shown by the significant interaction between species and log BW (P<0.05). The regression analysis showed that CP concentration impacted positively on DMI of ruminants with variations among the species (Table 2). Quite large differences were found for slope values of regression equations among all four ruminant species. The impact of feed constituents on DMI of these four ruminant species is also shown in Fig. 2. Overall buffaloes were found to be more responsive to CP with slope value of 0.364, followed by sheep, goats and cattle, and this response was significant for all species.

Table 2: Equations for linear regression between chemical composition of feeds (independent variable; in g/kg dry matter) and dry matter intake (response variable; g/kg metabolic body size) of sheep, goats, cattle and buffaloes.

Independent				Parameter estimates[d]						Model statistics[e]
Variables[a]	Species	Model[b]	n[c]	Intercept	95% CI	$P_{Intercept}$	Slope	95% CI	P_{Slope}	AIC
CP	Sheep	Q	126	57.3	14.1	<0.001	0.289	0.161	<0.001	
							–0.0005	0.0004	0.014	1157.1
	Goats	Q	78	43.9	12.3	<0.001	0.211	0.125	0.002	
							–0.0004	0.0003	0.013	680.0
	Cattle	Q	74	22.9	7.0	<0.001	0.199	0.092	<0.001	
							–0.0005	0.0003	<0.001	531.3
	Buffaloes	Q	26	32.1	7.0	<0.001	0.364	0.152	<0.001	
							–0.0012	0.0005	<0.001	190.3
	All	Q	304	42.4	11.4	<0.001	0.266	0.139	<0.001	
							–0.0005	0.0004	0.008	2917.0
NDF	Sheep	L	67	106.5	25.1	<0.001	–0.041	0.045	0.085	612.1
	Goats	L	34	69.3	19.1	<0.001	–0.012	0.032	0.472	287.8
	Cattle	L	38	75.1	21.3	<0.001	–0.060	0.035	0.002	260.9
	Buffaloes	n.d.	5	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	All	L	144	95.5	19.4	<0.001	–0.050	0.036	0.008	1406.8
ADF	Sheep	L	53	99.4	23.3	<0.001	–0.032	0.055	0.263	485.0
	Goats	L	25	59.6	16.0	<0.001	–0.005	0.033	0.787	205.1
	Cattle	L	43	46.8	17.7	0.002	–0.023	0.036	0.224	306.9
	Buffaloes	L	15	42.3	22.4	0.034	0.004	0.049	0.868	107.0
	All	L	136	75.8	20.3	<0.001	–0.031	0.048	0.214	1330.4

[a]CP = crude protein; NDF = neutral detergent fibre; ADF = acid detergent fibre.
[b]Q = quadratic; L = linear; n.d. = not determined; number of data for buffaloes was <10.
[c]n = number of data used.
[d]CI = confidence interval.
[e]AIC = Akaike's information criterion.

a



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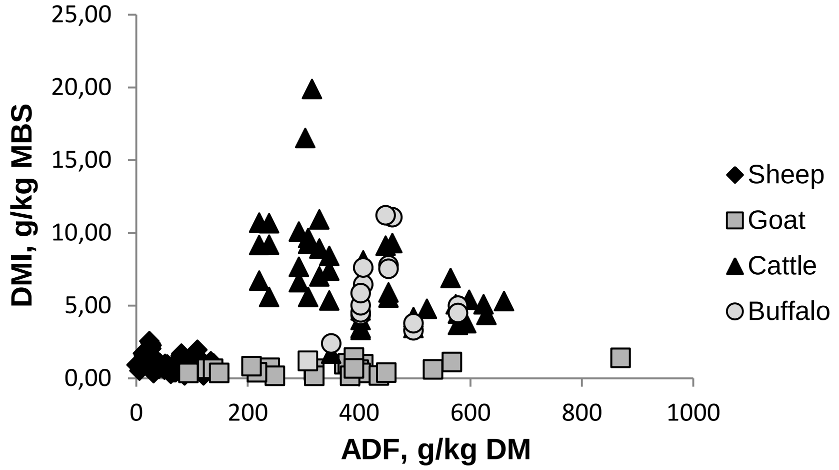

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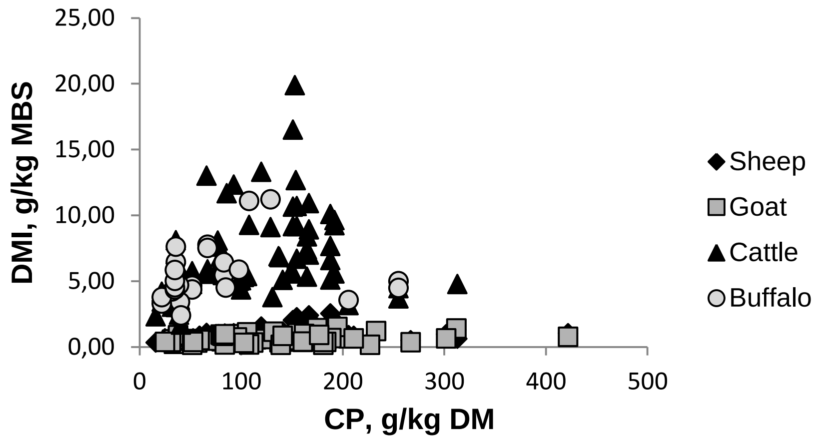


Fig. 2. The influence of various dietary constituents on dry matter intake (DMI) of sheep, goat, cattle and buffalo. MBS, metabolic body size.

In case of NDF, the number of observations for buffaloes was low; therefore, it was not possible to include this continuous predictor variable in the analysis. However, NDF negatively affected DMI of the other three species yet with a significant effect in cattle only. In contrast, ADF negatively influenced DMI of all species except buffaloes, showing the strongest effect on DMI of sheep and cattle with slope values of -0.032 and -0.023, respectively. The DMI of goats was less influenced by ADF with a slope value of -0.005 (Table 2).

The regression analysis for the effect of dietary factors on digestibility of animals showed that CP was positively correlated to DMD across species. The effect was much greater in cattle than the other three ruminant species, and it was significant only for cattle and buffaloes (P<0.05; Table 3). The database of buffaloes for NDF and ADF was small. Therefore, only sheep, goat and cattle data could be analysed for these chemical entities. The NDF depressed DMD only in cattle, whereas it positively influenced DMD in sheep and goats (Table 3; significant effect in sheep only). On the other hand, ADF lowered DMD in sheep, goats and cattle with a significant effect observed for sheep and goats.

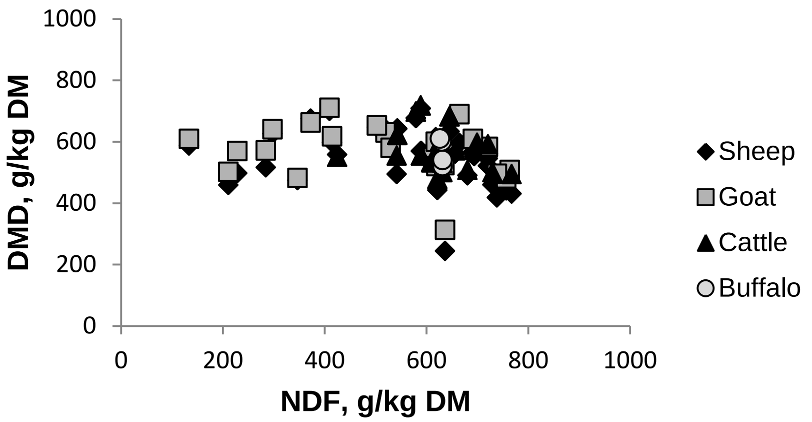
Table 3: Equations for linear regression between chemical composition of feeds (independent variable; g/kg dry matter) and dry matter digestibility (response variable; g/kg dry matter) of sheep, goats, cattle and buffaloes.

Independent				Parameter estimate[d]						Model statistics[e]
Variables[a]	Species	Model[b]	n[c]	Intercept	95% CI	$P_{Intercept}$	Slope	95% CI	P_{Slope}	AIC
CP	Sheep	L	82	545	47	<0.001	0.21	0.21	0.059	943.6
	Goats	L	45	553	59	<0.001	0.31	0.32	0.065	531.1
	Cattle	Q	53	374	66	<0.001	2.34	0.87	<0.001	
							–0.0052	0.0026	<0.001	615.2
	Buffaloes	L	15	400	51	<0.001	0.83	0.63	0.030	159.9
	All	Q	195	478	48	<0.001	1.01	0.46	<0.001	
							–0.0019	0.0011	0.001	2239.1
NDF	Sheep	Q	51	413	203	0.002	0.90	0.80	0.035	
							–0.0011	0.0008	0.008	587.2
	Goats	Q	23	437	236	0.007	0.94	1.02	0.094	
							–0.0012	0.0010	0.0041	276.7
	Cattle	L	32	590	321	0.037	–0.02	0.52	0.946	363.5
	Buffaloes	n.d.	4	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	All	Q	110	414	155	<0.001	0.92	0.60	0.004	
							–0.0011	0.0006	<0.001	1257.9
ADF	Sheep	L	44	709	95	<0.001	–0.36	0.21	0.002	484.3
	Goats	L	18	752	118	<0.001	–0.49	0.31	0.012	199.9
	Cattle	L	34	656	225	0.011	–0.25	0.46	0.288	396.0
	Buffaloes	n.d.	8	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	All		104	726	82	<0.001	–0.44	0.17	<0.001	1173.4

[a]CP = crude protein; NDF = neutral detergent fibre; ADF = acid detergent fibre.
[b]Q = quadratic; L = linear; n.d. = not determined; number of data for buffaloes was <10.
[c]n = number of data used.
[d]CI = confidence interval.
[e]AIC = Akaike's information criterion.

The species-specific response of DMD to dietary constituents is also highlighted in Fig 3.

a



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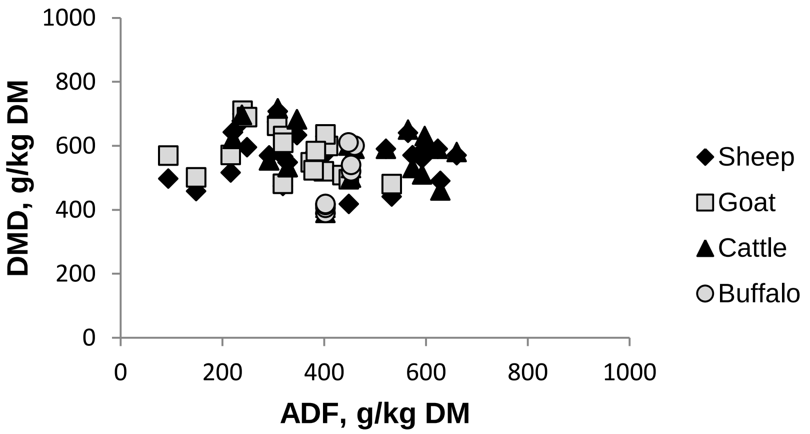

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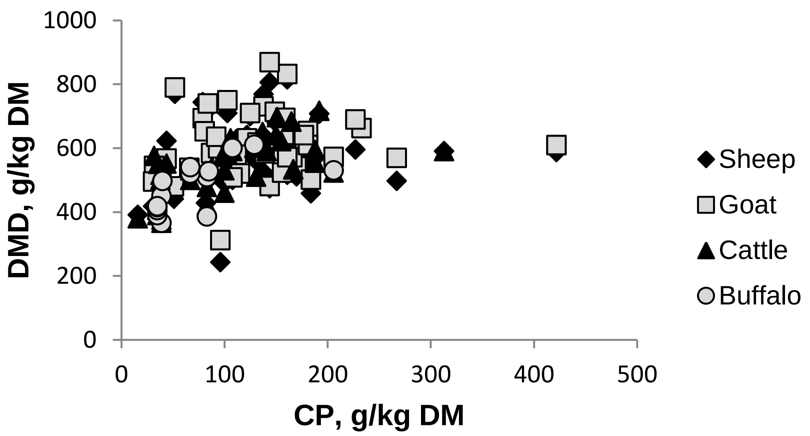

Fig. 3. The influence of various dietary constituents on dry matter digestibility (DMD) in sheep, goat, cattle and buffalo.

3.4. Discussion

3.4.1. Relationship between dry matter intake and body weight of animals

Voluntary feed intake is generally recognised as one of the most important factors influencing performance. Domestic ruminant species have substantially different BW, ranging from about 30 to 600 kg for matured dwarf female goat and cattle, respectively (Adejumo and Ademosun, 1991). Different opinions with regard to the effect of size on intake may be found in the literature. Kleiber (1961), for instance, stated that feed conversion in herbivores is dependent of body size because intake is directly proportional to maintenance requirement. As with increasing size, maintenance requirements per unit of BW decrease, feed intake relative to BW will decrease to the same extent. On the other hand, Van Soest (1982) argued that gut size of animals acts as a limiting factor, and that, because gut capacity scales linearly with BW, intake of a given diet will be a constant fraction of BW irrespective of species size. In the present study, we obtained an allometric relationship between DMI and BW of animals confirming the findings of other researchers who also described the relationship between feed intake and BW (Peyraud et al., 1996; Faverdin, 1999). The different scaling factors were found species-specific with lower values for small ruminants (sheep, goats) and higher values for large ruminants (cattle, buffalo), supporting previous studies on ruminant and non-ruminant herbivores (Clauss et al. 2007; Meyer et al., 2010).

More recently, Müller et al. (2013) suggested that the scaling of DMI is higher in larger as compared to smaller (<10 kg BW) mammalian herbivores. Given the finding of the present study that the scaling factor was lower in goats and sheep than in cattle and buffaloes, it may be reasonable to suggest that potentially there even are differences in the intake scaling among the larger herbivores (>10 kg BW) themselves.

When comparisons are intended to compare across different domestic ruminant species, various scaling factors are suggested by different researchers. For example, the use of 0.90 as scaling exponent for interspecies comparisons was suggested by Graham (1972), which has later been endorsed by other scientists (Minson and Whiteman, 1989; Reid et al., 1990; Hackmann and Spain, 2010). In contrast, if comparisons are to be made within species, other scaling factors may be more appropriate, which is supported by the results of the present study with lower scaling factors for small ruminants (sheep and goats) and greater exponents for large ruminants (cattle and buffalo).

The relevance of the magnitude of the scaling exponent was explained by Hackmann and Spain (2010) and Müller et al. (2013): The fact that rDMI scaling in large herbivores is higher than the scaling of energy requirements (which scale to about 0.75, e.g. Müller et al., 2012) suggests that larger herbivores cannot compensate for the poorer diet quality they have to accept in the wild by increasing digestive efficiency, but by increasing intake.

3.4.2. Dependency of voluntary dry matter intake of ruminants on dietary constitu

The CP concentration had a positive effect on DMI, whereas, fibre fractions of diets depressed DMI of the animals. This trend is consistent with previous studies (Molina Alcaide et al., 2000; Kawashima et al., 2007; Abidi et al., 2009). Overall, buffaloes appeared to be more responsive to CP content of diets at a given CP level than the other three ruminant species. The low quality diets with very low content of CP fed to the buffaloes used in the present study may be responsible, resulting in the positive response to increasing CP concentration. However, it is difficult to draw a concrete conclusion as the data size is small. The other three ruminant species responded similarly to an increase of CP concentration which has also been reported previously. For example, Quick and Dehority (1986) observed only small differences between feed intake of sheep and goats. However, the authors also mentioned that there would probably be selectivity differences if the animals were kept under natural grazing conditions. Similarly, Molina Alcaide et al. (2000) found equal response of these species when fed medium to good quality diets in the absence of feed selection.

Goats appeared less responsive to increases in fibre fractions (NDF and ADF) than the other species such that these feed fractions had a less negative impact on their DMI. Huston et al. (1988) mentioned that sheep and goats were similar in terms of DMI when higher quality diets were fed; inconsistencies mostly occurred when low quality feeds were given with higher intake shown by goats and this observation is in agreement with the findings of the present study. In a review, Brown and Johnson (1984) indicated that intake was higher in sheep than in goats in most studies, with relatively greater intake by goats fed high fibre diets.

3.4.3. Dependency of digestibility on dietary constituents

Dietary CP had a positive influence on digestibility. The effect of CP on DMD in cattle was significant and higher than for the other species which may be partly be due to the structure of the data set which encompassed not only a range of diets but also different breeds within species which may also play vital role in feed selection of animals (Huston, 1978). Of the other three species, DMD of buffaloes responded stronger to an increase of CP, however, this observation should be interpreted cautiously as the available dataset for buffaloes was small. The CP influenced DMD in sheep and goats almost in the same manner though non-significantly showing no large differences between the slope values of these species which is in contradiction to the generally accepted theory that goats are able to digest poor quality diets with high cell and low CP content better than other domestic ruminant species (Gihad, 1976; Adebowale, 1988; Domingue et al., 1991). McCabe and Barry (1988) suggested that goats are vastly superior to sheep in utilizing highly lignified diets. Similarly, Al Jassim et al. (1991) and Domingue et al. (1991) found that goats showed superiority over sheep when fed on low quality diets. The better utilization of fibrous diets by goats than other ruminant species may be due to higher fermentation rate (El Hag, 1976), higher rate of salivary excretion (Seth et al., 1976), or higher activity of cellulolytic bacteria (Gihad et al., 1980). Also Doyle et al. (1984) suggested that a greater ability of goats compared with sheep to digest low quality forages resulted from longer ruminal digesta retention times and possibly a higher capacity to recycle and conserve N within the body.

The content of NDF negatively influenced digestibility only in cattle, whereas sheep and goats responded positively with almost the same magnitude to this feed constituent. This finding is in contradiction to the generally accepted idea of reduced digestibility of high-fibre compared with low-fibre diets (Poppi et al., 1980; Woods et al., 1999). Our observations on the effect of NDF on DMD should be observed carefully, since data selection can have an impact – data was collected across different studies conducted in different parts of the world with large variations of environmental conditions, animal breeds and feeds.

The ADF negatively influenced DMD. This effect was most pronounced in goats followed by sheep and cattle. Usually goats are considered more robust to digest low quality diets with high fibre concentrations. Nonetheless, several authors have stated that digestibility of high quality diets is either similar among domestic ruminant species or goats are even superior to other domestic ruminant species. Jones et al. (1972) reported that goats digested CP better than dairy steers. Huston (1978) suggested that, in contrast to the general assumption of greater digestibility of low quality forages by goats, that goats would be less efficient in digesting low quality forages because of differences in the dynamics of the gastrointestinal systems between goats and sheep. This author proposed that this occurs because goats have a relatively smaller reticulo-rumen and shorter ruminal retention times, and therefore, satisfy their nutrient requirements by higher daily forage DMI. Brown and Johnson (1985) found that digestibility of NDF and ADF was higher in sheep than in goats and suggested that goats can better exploit their potential on higher quality feeds. Again, the deviation of the outcome of the present data evaluation from the general trend – goats digesting fibrous diets better than other ruminants – may be due to data structure which encompassed different goat breeds;

digestive efficiency of goats varies considerably with breed and strain (Huston, 1978).

For the other two species, cattle appeared to digest fibrous diets better than sheep. There are other studies which are in agreement with this finding. Prigge et al. (1984) reported that sheep showed a tendency to consume greater percentage of dietary CP which, vice versa, indicates that cattle do better on low quality diets which are typically low in CP. Similarly, Südekum et al. (1995) reported that cattle digested DM, NDF and ADF better than sheep. Also Woods et al. (1999) revealed that cattle digest fibre better than sheep. The ability of cattle to digest low quality rations better can be linked to the observation that they retain digesta longer in their rumen which may result in a greater digestive efficiency compared with sheep (Poppi et al., 1980).

3.5. Conclusions

Feed intake of ruminants is dependent upon their BW. Distinguishable, i.e. species-specific, scaling factors for the relationship between DMI and BW were estimated, and the difference was pronounced between small and large ruminants with lower exponents for sheep and goats and higher for cattle and buffaloes. Across all ruminant species, CP had a positive influence on intake and digestibility while fibre fractions influenced DMI negatively except for buffaloes who responded positively to ADF. Digestibility was also negatively influenced by ADF in all species, whereas NDF had a negative effect in cattle only. However, the magnitude of the response of feed intake and digestibility to varying concentrations of dietary constituents differed among the ruminant species.

Conflicts of interest statement

The authors declare that they have no conflict of interest.

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Digestibility of wheat silage diest harvested at different stages of maturity in cattle and sheep fed at maintenance or *ad libitum* intake: Total collection and titanium(IV)-oxide marker methods

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Abstract

Markers are commonly used in nutrition studies to estimate faecal output without necessitating time and labour consuming quantitative faecal sampling schedules. Internal and external markers both possess advantages and disadvantages and at present it seems that no ideal markers have been found. The purpose of this study was to evaluate the digestibility of wheat silage diets harvested at different stages of maturity (i.e. late milk, early dough and hard dough) in two different ruminant species, i.e. cattle (steers) and sheep (wethers). The diets were fed at either maintenance or *ad libitum* intake. Two digestibility methods were compared, the total collection method and titanium(IV)-oxide (TiO_2) marker method. Six yearling Angler Rotvieh cattle and nine adult crossbred sheep (German Blackface x German Whiteface) were used. The marker TiO_2 was determined photometrically in a Kjeldahl-digested TiO_2-solution (40 mg/L TiO_2 in 1.3 M sulphuric acid) and in Kjeldahl-digested samples of concentrate and faeces. For both intake levels digestibility of DM, OM and CP and the marker recovery were analysed by a general linear model procedure. The influence of species and diet type was significant on digestibility. No significant differences between the methods as well as species and diets for marker recovery except with significant impact of species on titanium(IV)-oxide at *ad libitum* feeding were recorded. Some numerical differences were noted among individual magnitudes of digestibility within and between species fed various forms of wheat silage diet. No significant differences among interactions of variables except for CPD with species × diet interaction effect were recorded for marker recovery and feed digestibility which indicated that titanium(IV)-oxide is a robust external marker and can be used in site and extent of digestion studies across different animal species as well as various diet types.

Keywords: Ruminants; Digestibility; Wheat silage diets; Titanium(IV)-oxide; Intake levels; Methods.

4.1. Introduction

Markers are commonly used in nutrition studies to estimate faecal output without necessitating time and labour consuming quantitative faecal sampling schedules. In addition to minimal time and labour requirement, quantitative measurements of feed intake and faecal output are not required and measurements can be made on single feed and faecal samples. Internal and external markers both possess advantages and disadvantages and at present it seems that no ideal markers have been found. Titanium(IV)-oxide (TiO_2), like other metal oxides, bares potential as a digestibility marker (Owens and Hanson, 1992) and has successfully been used in rats (Lloyd et al., 1955; Krawielitzki et al., 1987), rabbits (Marks, 1959), swine (Jagger et al., 1992), chicken (Short et al., 1996), sheep (Brandt et al., 1987) and cattle (Hafez et al., 1988). Titgemeyer et al. (2001) found 93% faecal recovery of TiO_2 for steers fed a forage-based diet and 95% and 90% for restricted and *ad libitum* consumption, respectively, for steers fed maize grain based diets. Glindemann et al. (2009) observed differences in faecal recovery of TiO_2 for sheep with hay diets higher than in diets containing hay and concentrate.

Other markers have also been used to determine nutrients digestibility in different species. For example, acid insoluble ash (AIA) is one of the naturally occurring markers commonly used for the determination of feed digestibility in monogastric as well as ruminant animals. It has been used to predict diet digestibility in swine (Ly et al., 2002), poultry (Vogtmann et al., 1975), sheep (Van Keulen and young, 1977) and cattle (Block et al., 1981). Similarly, acid detergent lignin (ADL) is also used as a marker which is naturally found in feedstuffs for ruminants; it is often regarded as being indigestible because there are no known mammalian or anaerobic microbial enzymes capable of degrading lignin (Van Soest, 1982). However, inconsistencies in the ability to quantitatively recover ADL have also been reported (Fahey and Jung, 1983). Muntifering et al. (1981) found 101% faecal recovery of acid detergent lignin in lambs fed Kenhy tall fescue and suggested that determination of ruminal digestibility could be corrected to 100% lignin recovery with faecal lignin.

The purpose of this study was to evaluate the digestibility of wheat silage diets harvested at different stages of maturity (i.e. late milk, early dough and hard dough) in two different ruminant species, i.e. cattle (steers) and sheep (wethers). The diets were fed at either maintenance or *ad libitum* intake. Two digestibility methods were compared, the total collection method and TiO_2 marker method.

4.2. Materials and methods

The experimental design, sampling schedules and standard analytical methods have been described in detail by Südekum et al. (1995). Briefly, materials and methods for the present study are given below.

4.2.1. Animals

Six yearling Angler Rotvieh cattle were each surgically prepared with a large rumen fistula, closed by a silicone cannula. Three months elapsed between cannulation and experimental work. The cattle were kept in individual tie stalls on wooden floors in a temperature-controlled room (18°C). Water was provided from automatic water bowls. Nine adult crossbred sheep (German Blackface x German Whiteface) were kept in elevated mesh bottom pens in the same room as the cattle. Water was available for *ad libitum* intake. At the beginning of the experiments, sheep were treated with levamisole (5 mg/kg BW; Citarin®-L; Bayer AG, Leverkusen, Germany) to control helminths and closely shorn at 3 months intervals.

4.2.2. Diets and Feeding

Winter wheat (*Triticum aestivum* L., variety Ares) was grown at the Experimental Farm of the Federal Dairy Research Centre in Schädtbek near Kiel, Germany. Whole crop wheat was harvested at late milk, early dough and hard dough stages of maturity. The treatments were direct cut with a precision chop forage harvester equipped with a multiple-knife drum (48 knives). The cutter bar height was 18 cm. A dry inoculant, containing specific strains of *Lactobacillus plantarum* and *Streptococcus faecium* (1177; Pioneer Hi-Bred, Microbial Genetics Div. Johnston, IA, USA), was applied in accordance with manufacturers recommendations at the rate of 1×10^8 lactic acid-producing bacteria/g of fresh forage by means of an automatic feeder (M 904; Gandy, Owatonna, MN, USA) mounted on the forage harvester. Direct cut forage was ensiled in 10 m^3 (3.5 m × 1.9 m; height × internal diameter) cylindrical concrete tower silos (two silos per treatment). During filling, glucose was applied at the rate of 15 g/kg of fresh forage to provide sufficient fermentable carbohydrates for all maturities. Silage was stored for a minimum of 120 d prior to initiation of the animal trial.

Silage was assumed to contain 9% CP and balanced to approximately 13% CP in dietary DM with concentrates containing a soy protein concentrate (70.6% CP in DM; DANPRO A; Aarhus Oliefabrik, Aarhus, Denmark). The soy protein concentrate was blended with a digestibility marker, titanium(IV)-oxide, and mineral and vitamin mixes. Blends were formulated to supply minerals for maintenance plus 1 kg of daily BW gain (cattle) and for maintenance of 70 kg of BW (sheep) according to Agricultural Research Council (1980). During *ad libitum* intake, additional soy protein concentrate was given to maintain the CP concentration constant at 13% of dietary DM. The diets were designated LM, ED, and HD to denote late milk, early dough, and hard dough stages of wheat grain maturity, respectively (Table 4 for cattle and table 5 for sheep).

Table 4: Composition of diets prepared from whole crop wheat silage with late mile (LM), early dough (ED) and hard dough (HD) satges of maturity fed to cattle.

	Maintenance feeding			Ad libitum feeding		
Diet[a]	LM	ED	HD	LM	ED	HD
Ingredients	(% of DM)					
Whole crop wheat silage	89.65	89.73	89.28	90.82	90.76	89.94
Soy protein concentrate	7.43	7.37	7.70	7.38	7.51	8.36
Mineral-vitamin mix[a]	2.60	2.58	2.69	1.60	1.54	1.51
Titanium(IV)-oxide	.32	.32	.33	.20	.19	.19
Nutrients composition (%)						
DM	39.0	44.3	55.1	39.8	41.8	50.1
OM	92.5	92.9	93.0	93.9	94.2	94.5
CP (N *6.25)	13.1	12.7	13.5	13.2	13.0	13.8
NDF	42.6	38.8	38.5	43.2	37.6	37.2
ADF	26.2	23.8	22.9	26.4	22.7	22.7
Hemicellulose	16.4	15.0	15.6	16.8	14.9	14.5
Lignin	3.17	2.99	2.98	3.16	2.62	2.89
Starch	8.1	15.8	20.1	10.6	16.2	22.5

[a]Mineral-vitamin mixture composition given in detail by Südekum et al., 1995; DM, dry matter; OM, organic matter; CP, crude protein; NDF; neutral detergent fibre; ADF, acid detergent fibre.

Table 5: Composition of diets prepared from whole crop wheat silage with late mile (LM), early dough (ED) and hard dough (HD) satges of maturity fed to sheep.

	Maintenance feeding			Ad libitum feeding		
Diet[a]	LM	ED	HD	LM	ED	HD
Ingredients	(% of DM)					
Whole crop wheat silage	89.78	89.74	89.60	91.00	90.35	90.02
Soy protein concentrate	8.04	8.06	8.17	7.90	8.50	8.85
Mineral-vitamin mix[a]	2.04	2.06	2.08	1.03	1.08	1.05
Titanium(IV)-oxide	.14	.14	.15	.07	.07	.08
Nutrients composition (%)						
DM	39.2	44.3	54.8	40.7	41.0	50.7
OM	93.4	93.7	94.0	94.6	94.7	95.1
CP (N *6.25)	14.0	13.7	14.2	13.2	13.7	14.3
NDF	42.4	38.7	38.8	41.9	37.5	36.0
ADF	26.3	23.4	23.2	25.5	22.6	22.0
Hemicellulose	16.1	15.3	15.6	16.4	14.9	14.0
Lignin	3.20	3.03	3.06	2.90	2.64	2.85
Starch	7.5	16.4	21.3	10.6	16.9	22.8

[a]Mineral-vitamin mixture composition given in detail by Südekum et al., 1995; DM, dry matter; OM, organic matter; CP, crude protein; NDF; neutral detergent fibre; ADF, acid detergent fibre.

Feed was offered at 07.00 and 18.00 h in individual feeding troughs. Prior to feeding, portions of the silage (1.5 kg for cattle and 0.5 kg for sheep) were mixed by hand with the concentrate portion of the diet. To prevent losses of the dusty soy protein concentrate, 0.5 L (cattle) or 0.2 L (sheep) of a 0.2% flavour solution (Cuxarom Coconut 100; Lohmann-LTE-GmbH, Cuxhaven, Germany) was added and the mixture was given at the beginning of each feeding, followed by the remainder of the silage within 10 min.

4.2.3. Faecal Collection

Total faecal collections were made over 7 d at both intakes. Faecal collections started and finished at 07.00 h. Cattle and sheep faeces were collected in plastic pans. Animals carried faecal plastic bags, which were attached to the pans. Wet cattle faeces were weighed twice daily to the nearest 10 g and mixed, and an aliquot of 10% (maintenance intake) or 5% (*ad libitum* intake) on a wet weight basis was transferred to an accumulative sample container and immediately stored at -20ºC. Sheep faeces also were collected twice daily, weighed to the nearest 1 g, transferred to an accumulative sample container, and stored at -20°C. The aliquot for each steer and the total faecal output for each wether during the digestion trial were used for laboratory methods. Orts, if any, were collected twice daily, stored under vacuum during the digestion trials, and composited over the collection period. Feed samples were taken daily during the digestion trials and also composited over the collection period.

4.2.4. Laboratory Methods

Silages, orts, and faeces were mixed and DM was estimated by freeze-drying and subsequent oven-drying at 105ºC overnight. The DM contents of silages and orts were corrected for losses of volatiles during drying (Weissbach and Berg, 1977). Freeze-dried material of silages, orts, and faeces was used for all other analyses. Concentrates, orts, and freeze-dried silages and faeces were successively ground in mills with 3- and 1-mm screens and, for starch analysis, with a 2-mm screen. The NDF and ADF were analysed according to the German Handbook of Agricultural Experimental and Analytical Methods (VDLUFA, 2007).

4.2.5. Analysis of TiO_2

The marker TiO_2 was determined photometrically in a Kjeldahl-digested TiO_2-solution (40 mg/L TiO_2 in 1.3 M sulphuric acid) and in Kjeldahl-digested samples of concentrate and faeces (Brandt and Allam, 1987). A detailed laboratory procedure used for this analysis is described as below:

1. Principle

Titanium(IV)-oxide is slowly soluble in hot, concentrated sulfuric acid (H_2SO_4) and forms a stable yellow complex compound with hydrogen peroxide (H_2O_2) in sulfuric solutions. This complex is quantified spectrophotometrically at 405 nm.

II. Kjeldahl-digestion

a. Freeze-dried or fresh digesta and faeces are weighed into cleaned Kjeldahl flasks. If N is determined in the same flasks, fresh matter or defrosted fresh matter of ileal digesta and faeces must be used to prevent losses of volatile N compounds during drying.
b. Initial weights: Duodenal digesta 4 g dry matter (DM), Ileal digesta 2 g DM; Faeces 2 g DM or the respective fresh matter. Initial weights were calculated to contain approx. 10 mg TiO_2/g DM.
c. Add 10 g potassium sulfate (K_2SO_4) and 2.5 ml of a 10% solution (w/v) of copper sulfate ($CuSO_4$) as a catalyst.
d. The Kjeldahl digestion is performed after adding 50 ml (+ 5 ml/g digesta or faeces DM) 96% H_2SO_4 (extra pure). If digesta or faeces contain > 10 mg TiO_2/g DM, more sulfuric acid is needed to bring TiO_2 completely into solution.
e. After becoming clear, the solution is boiled for additional 3 h. The solution is cooled down once during this time and the sides of the flask are rinsed with deionised water.
f. Subsequently, the solution is transferred into a 500 ml volumetric flask, after cooling (room temperature) made up to volume with deionised water, and then filtered through "Black ribbon" ashless filter paper (e. g. Ref. No. 300 012, Schleicher & Schuell, 3354 Dassel, Germany). The first 30 ml of the filtrate are discarded. Kjeldahl-solutions used as measuring solutions should have a normality between 1.5 and 4 and contain 20 to 60 mg TiO_2/L.

III. Measuring of the TiO_2-complex

Reagents:

Mixture I: 40 ml 35 % H_2O_2, extra pure (= 46.66 ml 30% H_2O_2); 120 ml 85 % H_3PO_4, extra pure; 200 ml 96 % H_2SO_4, extra pure and 360 ml H_2O, deionised.

Mixture II: 120 ml 85 % H_3PO_4 extra pure; 200 ml 96 % H_2SO_4 extra pure and 400 ml H_2O, deionised.

Mixtures I and II contain H_3PO_4 to prevent decomposition of H_2O_2 which would give small bubbles. The phosphoric acid (H_3PO_4) gives a slight bleaching of the complex compound, which can be standardized, but keeps the complex stable in the sulfuric acid solution over a wide range of normalities.

a. 10 ml of the diluted Kjeldahl-solution are pipetted into a test-tube. 1 ml of solution "mixture I" are added and
b. The test-tube is vigorously shaken.
c. The absorbance is read at 405 nm against deionised water at the earliest after 30 min.
d. The colour of the sample + reagents without the complex compound is measured simultaneously. 1 ml of mixture II is added to 10 ml of the diluted Kjeldahl-solution. Then continue as under 3b and 3c. The absorbance of 3d is substracted from the absorbance of the sample (3a to 3c).

IV. Measuring design

a. Each sample is measured with two replicates.
b. Basically, samples are measured animal by animal, and within animal the following order is kept: standard solution, faeces.
c. Standard solution is the Kjeldahl digested TiO_2. The standard solution contains 20 mg TiO_2/500 ml solution, which corresponds to an absorbance of ≈ 0.330.
   Preparation of the standard solution:
   40 mg TiO_2 + 80 ml H_2SO_4 + 10 g K_2SO_4 + 2.5 ml 10% $CuSO_4$-solution are brought to 1 l with deionised water.
d. The absorbance of all TiO_2-containing solutions within one series should be in the same range, preferably around the absorbance of the standard solution

V. Calculation of the daily dose of TiO_2 for estimating digestibility of DM and DM constituents

The following has to be considered:
DM intake of the animal, apparent digestibility of dietary DM, sample weight for Kjeldahl-digestion and the Kjeldahl-digest which is used as measuring solution should contain 20 to 60 mg TiO_2/L (measuring range 0.100 - 0.450 absorbance units).

4.2.5. Statistical methods

For each intake (maintenance and *ad libitum* intake), digestibility of DM, OM and CP and the recovery of TiO_2 were analysed by a general linear model according to the following model:

$$Y_{ijklm} = \mu + S_i + P_{ij} + A_{ik} + D_l + M_m + (S\times D)_{il} + (S\times M)_{im} + (D\times M)_{lm} + (S\times D\times M)_{ilm} + e_{ijklm}$$

where

Y_{ijklm} = observed response (e.g. OM digestibility),
μ = overall mean,

S_i = effect of species i,

P_{ij} = effect of period j within species i,

A_{ik} = effect of animal k within species i,

D_l = effect of diet l,

M_m = effect of method of determining digestibility,

$(S\times D)_{il}$ = effect of interaction between species i and diet l,

$(S\times M)_{im}$ = effect of interaction between species i and method of determining digestibility m,

$(D\times M)_{lm}$ = effect of interaction between diet l and method of determining digestibility m,

$(S\times D\times M)_{ilm}$ = effect of interaction between species i and diet l and method of determining digestibility m, and

e_{ijklm} = residual error.

The level of significance was declared at $P<0.05$. All the statistical analyses were performed by using SPSS software version 16.0 (SPSS Inc., Chicago, USA).

4.3. Results

4.3.1. Influence of diets and determination method on feed digestibility of cattle and sheep fed at maintenance intake

The digestibility of DM, OM and CP differed significantly for species and diet types ($P<0.05$; Table 6). These variables had no significant influence on the recovery of titanium(IV)-oxide. The impact of method used for calculating digestibility was also non-significant ($P>0.05$).

Table 6: Feed digestibility and TiO_2 recovery of wheat silage diets in cattle and sheep fed at maintenance intake level.

Species	Diet[a]	Method	DMD (%)	OMD (%)	CPD (%)	TiO_2 recovery (%)
Cattle	LM	TC	70.4	72.5	72.0	na
Cattle	LM	TiO_2	69.3	71.5	71.0	96.6
Cattle	ED	TC	74.0	76.1	72.1	na
Cattle	ED	TiO_2	73.5	75.6	71.5	98.1
Cattle	HD	TC	73.7	76.0	74.4	na
Cattle	HD	TiO_2	73.3	75.7	74.2	99.1
Sheep	LM	TC	68.3	70.1	74.8	na
Sheep	LM	TiO_2	68.4	70.3	74.9	100.4
Sheep	ED	TC	71.7	73.7	74.9	na
Sheep	ED	TiO_2	68.8	71.1	72.3	93.9
Sheep	HD	TC	73.4	75.4	78.1	na
Sheep	HD	TiO_2	72.6	74.7	77.5	97.1
SEM			0.375	0.368	0.375	1.185
P-value						
Species			0.012	0.005	0.006	0.584
Diet			<0.001	<0.001	<0.001	0.645
Method			0.156	0.158	0.183	na
Species*Diet			0.156	0.160	0.490	0.379
Species*Method			0.695	0.699	0.759	na
Diet*Method			0.667	0.671	0.686	na
Species*Diet*Method			0.534	0.525	0.612	na

[a]Diets fed to animals prepared from whole crop wheat silage of different stages of maturity. LM, late milk; ED, early dough: HD, hard dough; DMD, dry matter digestibility; OMD, organic matter digestibility; CPD, crude protein digestibility; na, not applicable; TC, total collection method.

Non-significant differences were recorded among nutrients digestibility of both species fed different wheat silage diets. For cattle, digestibility of DM was almost similar when fed HD diet but for LM and ED diets differences were noted between DMD determined by either total collection (TC) or with marker. It was higher when measured with TC method for both diet types (Table 6). The OMD was found higher for all diet types when measured by TC method and also CP demonstrated higher digestibility for LM and ED diets with TC but it was similar for HD without any effect of determination method. The digestibility of DM was the same for sheep when LM diet was fed to animals and similar trend was observed for OM and CP digestibility as well. The differences were observed between digestibility of these nutrients for ED and HD diets measured with TC and TiO_2 where DM demonstrated higher digestibility determined with TC method. Nearly similar trends were recorded for OM and CP digestibility (Table 6). The interactions of species with diet and method as well as between diet and method were non-significant. It was also not significant for interaction among species, diet type and method for feed digestibility. Similarly, the interaction of species and diets did not significantly influence TiO_2 recovery.

4.3.2. Influence of diets and determination method on feed digestibility of cattle and sheep fed at ad libitum intake

Digestibility of DM, OM and CP was significantly influenced by species and diet type for *ad libitum* feeding intake as well ($P<0.05$; Table 7). Similar to maintenance intake level, determination method applied did not significantly affect the nutrients digestibility ($P>0.05$).

Table 7: Feed digestibility and TiO_2 recovery of wheat silage diets in cattle and sheep fed at *ad libitum* intake level.

Species	Diet[a]	Method	DMD (%)	OMD (%)	CPD (%)	TiO_2 recovery (%)
Cattle	LM	TC	68.7	70.7	67.1	na
Cattle	LM	TiO_2	68.7	70.7	67.2	100.6
Cattle	ED	TC	70.0	72.1	65.4	na
Cattle	ED	TiO_2	69.8	71.9	65.4	99.7
Cattle	HD	TC	68.8	70.7	68.0	na
Cattle	HD	TiO_2	67.5	69.5	66.8	96.5
Sheep	LM	TC	68.3	69.8	71.8	na
Sheep	LM	TiO_2	67.8	69.3	71.3	98.5
Sheep	ED	TC	68.3	70.1	69.9	na
Sheep	ED	TiO_2	69.2	71.0	70.8	103.2
Sheep	HD	TC	67.2	68.9	69.5	na
Sheep	HD	TiO_2	67.8	69.5	70.0	102.0
SEM			0.251	0.249	0.371	0.907
P-value						
Species			0.002	<0.001	<0.001	0.020
Diet			0.006	0.002	0.014	0.568
Method			0.846	0.857	0.925	na
Species*Diet			0.793	0.822	0.026	0.215
Species*Method			0.305	0.324	0.414	na
Diet*Method			0.696	0.717	0.729	na
Species*Diet*Method			0.442	0.431	0.505	na

[a]Diets fed to animals prepared from whole crop wheat silage of different stages of maturity. LM, late milk; ED, early dough: HD, hard dough; DMD, dry matter digestibility; OMD, organic matter digestibility; CPD, crude protein digestibility; na, not applicable; TC, total collection method.

In contrast to maintenance intake, animal species had significant impact on recovery of titanium(IV)-oxide. Some numerical differences were noted among individual magnitudes of digestibility within and between species fed various forms of wheat silage diet. For example, DMD in cattle was same for LM diet but it was higher for ED and HD diets when measured through TC method. The same observation was noticed in OMD and CPD except for ED where CPD was also similar showing no effect of method used for digestibility measurement (Table 7). Sheep had higher DMD for LM and lower for ED and HD diets measured with TC method. Nearly the same trends were observed for OM and CP digestibility with all three diet types. The interaction effect among two or more variables i.e. species, diet and method was non-significant for digestibility of diets as well as marker recovery as it was the case with maintenance intake except for significant species and diet interaction effect on CPD ($P<0.05$; Table 7).

4.4. Discussion

Feed intake and digestibility are considered one of the most important factors influencing performance of animals. Feed digestibility by ruminants can be determined by direct method i.e. through quantitative measurements and total faecal collection. But it requires a lot of time and labour input. Therefore, to avoid such time consuming laborious activities certain digestibility markers have been established which are commonly used in nutrition studies to estimate faecal output without necessitating time and labour consuming quantitative faecal sampling schedules (Ly et al., 2002). In the present study, the influence of species and diet type was significant on digestibility. No significant differences between the methods as well as species and diets for marker recovery except with significant impact of species on titanium(IV)-oxide at *ad libitum* feeding were recorded. Also species × diet interactions at both intake levels for marker recovery as well as nutrients digestibility were non-significant except for CPD with *ad libitum* feed intake. Similarly, no significant species × method and diet × method interactions were noted for digestibility at either intake level which is in agreement with the findings of Titgemeyer et al. (2001) who also noticed no differences between digestibility calculated with TiO2 and from those based on total faecal collections. In our study no significant effect of species, diet and method interactions was recorded for digestibility at both feed intakes. So the trends observed in this research support the idea that TiO_2 is a good external inert marker to estimate feed digestibility (Myers et al., 2006).

This marker has been used successfully by many researchers for various animal species and variety of diets and showed quite promising results obtained with TiO_2. Glindemann et al. (2009) used titanium(IV)-oxide to measure faecal excretion in sheep and observed differences in faecal recovery of marker with hay diets higher than in diets containing hay and concentrate. They noted that variation in faecal TiO_2 is less and proposed the use of titanium (IV)-oxide as a reliable marker for estimation of faecal excretion in sheep which is consistent with the results of our study where no significant species × diet interactions were recorded for TiO_2 recovery in both species. Myers et al. (2006) compared titanium(IV)-oxide and chromium oxide (Cr_2O_3) to examine differences in excretion patterns between the markers in ewes fed forage based diets and found TiO_2 a better and acceptable alternative to Cr_2O_3 for its use in digestion studies in ruminants. Also Brandt et al. (1987) and Hafez et al. (1988) applied TiO_2 as a digestibility marker in their studies for sheep and cattle respectively and found it a good marker to calculate the digestibility. In addition, TiO_2 has been reported to be a reliable digestibility marker in studies conducted with several non-ruminant species as well such as rats (Lloyd et al., 1955; Krawielitzki et al., 1987), rabbits (Marks, 1959), fowls (Peddie et al., 1982) swine (Jagger et al., 1992) and chicken (Short et al., 1996). Also in the present study neither species × diet nor species × method interactions were found significant which indicated that TiO_2 is a robust and reliable external marker and can be used across different species and diet types.

4.5. Conclusions

In the present study, commonly used external marker titanium(IV)-oxide was applied to estimate nutrients digestibility of two ruminant species at either maintenance or *ad libitum* intake. The influence of species and diet type was significant on digestibility. No significant differences between the methods as well as species and diets for marker recovery except with significant impact of species on titanium(IV)-oxide at *ad libitum* feeding were recorded. Some numerical differences were noted among individual values of digestibilit within and between species fed various forms of wheat silage diet. No significant differences among variables' interactions except for CPD with species × diet interaction were noticed for marker recovery and feed digestibility which indicated that titanium(IV)-oxide is a robust external marker and can be used in site and extent of digestion studies across different animal species as well as various diet types.

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General discussion and conclusions

The present thesis aimed at studying various comparative aspects of feed intake and digestibility among different domestic ruminant species. For this purpose, this work was structured in two major parts.

5.1. Comparative voluntary feed intake and digestibility of four domestic ruminant species

Numerous studies have compared feed intake and digestibility of nutrients between sheep and goats (e.g., Yañez-Ruiz and Molina Alcaide, 2008; Abidi et al., 2009), and between sheep and cattle (e.g., Mulligan et al., 2001; Kawashima et al., 2007). Few studies have made comparisons between cattle and buffaloes (Ichinohe et al., 2004; Lapitan et al., 2008). Also relatively few studies are available for comparisons of feed intake and digestibility among more than two ruminant species (Sharma and Rajora, 1977; Burns et al., 2005). Therefore, we assumed that it would be worth studying the influence of different dietary factors on voluntary intake and digestibility of more than two domestic ruminant species simultaneously. For comparisons of voluntary feed intake across ruminant species of varying body weights (BW), a reference scaling unit is needed to achieve comparability, because large ruminants will usually eat less relative to BW than small ones. Thus, different scaling factors have been applied to compare feed intake among ruminants of various sizes.

Inconsistencies between the outcomes of individual studies may result from differences in the specific experimental conditions and characteristics of, the diets used, e.g., chemical composition, forage to concentrate ratio and structure value. Combining data from various reports into a meta-analysis can be a useful tool to deal with the inconsistencies exhibited across a variety of experimental conditions of different studies (Sauvant et al., 2008). Therefore, we performed a meta-analysis of various studies to determine whether there is a common scaling exponent for DMI among domestic ruminant species or if this exponent is species specific, and to investigate the influence of dietary nutrient composition on DMI and digestibility. Detailed composition of diets used in this meta-analysis is described in the appendix tables of chapter 6.

Domestic ruminant species have substantially different BW, ranging from about 30 to 700 kg for matured dwarf female goat and cattle, respectively (Adejumo and Ademosun, 1991; Heinrichs and Hargrove, 1987). Different opinions with regard to the effect of size on intake can be found in the literature. Kleiber (1961), for instance, stated that feed conversion in herbivores is dependent of body weight because intake is directly proportional to maintenance requirement. On the other hand, Van Soest (1982) argued that gut size of animals acts as a limiting factor, and that, because gut capacity scales linearly with BW, intake of a given diet will be a constant fraction of BW irrespective of species size.

In our own study, an allometric relationship was obtained between DMI and BW of animals confirming the findings of other researchers who also described the relationship between feed intake and BW (Peyraud et al., 1996; Faverdin, 1999). Different scaling factors were reported and appeared to be species-specific with lower values for small ruminants (sheep, goats) and higher values for large ruminants (cattle, buffaloes), supporting previous studies on ruminant and non-ruminant herbivores (Clauss et al. 2007; Meyer et al., 2010). More recently, Müller et al. (2013) suggested that the scaling of DMI is higher in larger as compared to smaller (< 10 kg BW) mammalian herbivores. Given the finding of the present study that the scaling factor was lower in goats and sheep than in cattle and buffaloes, it may be reasonable to suggest that potentially there even are differences in the intake scaling among the larger herbivores (> 10 kg BW). When comparisons are made across different domestic ruminant species, various scaling factors are suggested by different researchers. For example, the use of 0.90 as scaling exponent for interspecies comparisons was suggested by Graham (1972), which has later been endorsed by other scientists (Reid et al., 1990; Hackmann and Spain, 2010). In contrast, if comparisons are to be made within species, other scaling factors may be more appropriate, which is supported by the results of the present study with lower scaling factors for small ruminants (sheep and goats) and greater exponents for large ruminants (cattle and buffaloes).

The relationship between dietary constituents and voluntary DMI was such that CP had a positive effect on DMI, whereas, increasing fibre fractions of diets lowered DMI of the animals which is in line with previous studies (Kawashima et al., 2007; Abidi et al., 2009). Overall, buffaloes appeared to be more responsive to CP content of diets than the other three ruminant species. Perhaps, poor quality diets with very low content of CP fed to the buffaloes used in the present study may be responsible, resulting in the positive response of DMI to increasing CP concentration. However, it is difficult to draw a concrete conclusion as the data size was small. The other three ruminant species responded similarly to an increase of CP concentration which has also been reported previously.

Quick and Dehority (1986) observed only small differences between feed intake of sheep and goats. Goats appeared less responsive to increases in fibre fractions (NDF and ADF) than the other species such that these feed fractions had a less negative impact on their DMI. Huston et al. (1988) mentioned that sheep and goats were similar in terms of DMI when higher quality diets were fed; inconsistencies mostly occurred when low quality feeds were given with higher intake shown by goats and this observation is in agreement with the findings of the present study.

Similarly, dietary CP showed a positive influence on digestibility which was also observed for DMI. The effect of CP on DMD in cattle was significant and greater than for the other species which may be partly due to the structure of the data set which encompassed not only a range of diets but also different breeds within species, which may also play a vital role in feed selection of animals (Huston, 1978). Of the other three species, DMD of buffaloes responded stronger to an increase of CP, however, this observation should be interpreted cautiously as the available dataset for buffaloes was small. The CP concentration affected DMD in sheep and goats almost in the same manner though non-significant showing no large differences between the slope values of these species which is in contradiction to the generally accepted theory that goats are able to digest poor quality diets with high cell-wall and low CP content better than other domestic ruminant species (Domingue et al., 1991). McCabe and Barry (1988) suggested that goats are vastly superior to sheep in utilizing highly lignified diets. Similarly, Al Jassim et al. (1991) and Domingue et al. (1991) found that goats showed superiority over sheep when fed on low-quality diets e.g., wheat straw, prairie grass etc. The better utilization of fibrous diets by goats than other ruminant species may be due to higher fermentation rate (El Hag, 1976), higher rate of salivary excretion (Seth et al., 1976), or higher activity of cellulolytic bacteria (Gihad et al., 1980).

The content of NDF negatively influenced digestibility only in cattle, whereas sheep and goats responded positively with almost the same magnitude to this feed nutrient. This finding is in contradiction to the generally accepted idea of lower digestibility of high-fibre than low-fibre diets (Poppi et al., 1980; Woods et al., 1999). However, this trend should be observed carefully, since data selection can have an impact – data was collected across different studies conducted in different parts of the world with large variations of environmental conditions, animal breeds and feeds. The ADF negatively influenced DMD and it was most pronounced in goats followed by sheep and cattle. Usually goats are considered more robust to digest low quality diets with high fibre concentrations. Nonetheless, several authors have stated that digestibility of high quality diets is either similar among domestic ruminant species or goats are even superior to other domestic ruminant species. Jones et al. (1972) reported that goats digested CP better than dairy steers. Huston (1978) suggested that, in contrast to the general assumption of greater digestibility of low quality forages by goats, that goats would be less efficient in digesting low quality forages because of differences in the dynamics of the gastrointestinal systems between goats and sheep. Again, the deviation of the outcome of the present data evaluation from the general trend – goats digesting fibrous diets better than other ruminants – may be due to data structure which encompassed different goat breeds; digestive efficiency of goats varies considerably with breed and strain (Huston, 1978). And for the other two species, cattle appeared to digest fibrous diets better than sheep. There are other studies which are in agreement with this finding. Prigge et al. (1984) reported that sheep showed a tendency to consume greater percentage of dietary CP which, vice versa, indicates that cattle do better on low quality diets which are typically low in CP. Also Südekum et al. (1995) reported that cattle digested DM, NDF and ADF of wheat silage rations better than sheep. The ability of cattle to digest low quality rations better can be linked to the observation that they retain digesta longer in their rumen which may result in a greater digestive efficiency compared with sheep (Poppi et al., 1980).

5.2. Digestibility of wheat silage diets harvested at different stages of maturity in cattle and sheep fed at maintenance or *ad libitum* intake

Markers are commonly used in nutrition studies to estimate faecal output without necessitating time and labour consuming quantitative faecal sampling schedules. In addition to minimal time and labour requirement, quantitative measurements of feed intake and faecal output are not required and measurements can be made on single feed and faecal samples. Internal and external markers both possess advantages and disadvantages and at present it seems that no ideal markers have been found. The purpose of this study was to evaluate the digestibility of wheat silage diets harvested at different stages of maturity (i.e. late milk, early dough and hard dough) in two different ruminant species, i.e. cattle (steers) and sheep (wethers). The diets were fed at either maintenance or *ad libitum* intake. Two digestibility methods were compared, the total collection method and titanium(IV)-oxide marker method.

In the current research, species × diet interactions at both intake levels for marker recovery as well as digestibility of DM, OM and CP was non significant except for CPD with *ad libitum* feed intake. Similarly, no significant species × method and diet × method interactions were noted for nutrient digestibility at either intake level which is in agreement with the findings of Titgemeyer et al. (2001) who also noticed no differences between digestibility calculated with titanium(IV)-oxide (TiO_2) and from those based on total faecal collections. Also no significant influences of species, diet and method interactions were recorded for digestibility at both feed intakes. So the trends observed in our research support the idea that TiO_2 is a good external inert marker to estimate feed digestibility.

Titanium(IV)-oxide has been used by many researchers for various animal species and diets. Glindemann et al. (2009) used TiO_2 to measure faecal excretion in sheep and observed differences in faecal recovery of marker with hay diets higher than in diets containing hay and concentrate. They noted that variation in faecal TiO_2 is less and proposed its use as a reliable marker for estimation of faecal excretion in sheep which is consistent with the results of our study where no significant species × diet interactions were recorded for TiO_2 recovery in both species. Brandt et al. (1987) and Hafez et al. (1988) applied TiO_2 as a digestibility marker in their studies for sheep and cattle respectively and found it a good marker to calculate the digestibility. On the other hand, TiO_2 has been applied as a digestibility marker in many studies conducted with several non-ruminant species as well such as rats (Krawielitzki et al., 1987), fowls (Peddie et al., 1982) swine (Jagger et al., 1992) and chicken (Short et al., 1996). In the present study, also neither species × diet nor species × method significant interactions were noticed which confirmed the fact that TiO_2 is a robust and reliable external marker and can be used across different species and diet types.

5.3. General conclusions

General conclusions of this thesis dealing with different comparative aspects of feed intake and digestibility of ruminant species drawn are:

1) Feed intake of ruminants is dependent upon their BW. Distinguishable, i.e. species-specific, scaling factors for the relationship between DMI and BW were estimated, and the difference was pronounced between small and large ruminants with lower exponents for sheep and goats and higher for cattle and buffaloes.

2) Across all ruminant species, CP had a positive influence on intake and digestibility while fibre fractions influenced DMI negatively except for buffaloes who responded positively to ADF. To prove this trend observed for buffaloes, a much larger data set is required as data size available for this species in the meta-analysis was quite small.

3) Digestibility was also negatively influenced by ADF in all species, whereas NDF had a negative effect in cattle only. However, the magnitude of the response of feed intake and digestibility to varying concentrations of dietary constituents differed among the ruminant species.

4) For marker evaluation, a commonly used external marker, namely titanium(IV)-oxide was applied to estimate nutrient digestibility of two ruminant species at either maintenance or *ad libitum* intake and some numerical differences were noted among individual values of digestibility within and between species fed various forms of wheat silage diet at both intake

levels.

5) No significant differences between the methods as well as species and diets for marker recovery except with significant impact of species on titanium(IV)-oxide recovery at *ad libitum* feeding were recorded.

6) Also no significant differences among variables' interactions except for CPD with species × diet interaction were recorded for marker recovery and feed digestibility. This outcome of the study confirmed that titanium(IV)-oxide is a robust external marker which can be used in site and extent of digestion studies across different animal species as well as various diet types.

5.4. References

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Appendix Tables

Table 8: The composition of diets of sheep and cattle studies collected for the literature survey of the meta-analysis.

Diet type[a]	Chemical composition (g/kg DM)[b]				Source[c]
	Ash	NDF	ADF	CP	
Whole corn plant harvested at different stages of ear maturity and ensiled					1
Soft dent	—	—	—	80	
Medium-hard dough	—	—	—	77	
Early dent	—	—	—	78	
Glazed and forested	—	—	—	80	
Group 1					2
Diet A, L	75	589	309	192	
Diet A, P	90	590	292	188	
Diet B, L	74	646	347	165	
Diet B, P	82	610	329	167	
Diet C, L	58	580	239	151	
Diet C, P	64	543	221	155	
Group 2					
Diet A, L	75	589	309	192	
Diet A, P	90	590	292	188	
Diet B, L	74	646	347	165	
Diet B, P	82	610	329	167	
Diet C, L	58	580	239	151	
Diet C, P	64	543	221	155	
Group 3					
Diet A, L	75	589	309	192	
Diet A, P	90	590	292	188	
Diet B, L	74	646	347	165	
Diet B, P	82	610	329	167	
Diet C, L	58	580	239	151	
Diet C, P	64	543	221	155	
Experiment 1					3
Ration A	59	—	—	32	
Ration B	60	—	—	36	
Experiment 2					
Ration C	53	—	—	16	
Ration D	57	—	—	82	
Ration E	60	—	—	87	
Herbage (Manawa ryegrass and perennial ryegrass					4
Periods (for fecal collection)					
1	113	—	—	154	
2	91	—	—	120	
3	86	—	—	93	
4	79	—	—	86	
5	74	—	—	66	
Lucerne hay	—	423	316	153	5
Orchardgrass hay	—	475	304	151	

Table 8 (continued): The composition of diets of sheep and cattle studies collected for the literature survey of the meta-analysis.

Diet type[a]	Chemical composition (g/kg DM)[b]				Source[c]
	Ash	NDF	ADF	CP	
Pangola grass					6
6 weeks regrowth					
Leaf fraction	112	657	—	—	
Stem fraction	103	694	—	—	
12 weeks regrowth					
Leaf fraction	101	622	—	—	
Stem fraction	90	681	—	—	
Rhodes grass					
6 weeks regrowth					
Leaf fraction	115	700	—	—	
Stem fraction	86	721	—	—	
12 weeks regrowth					
Leaf fraction	107	730	—	—	
Stem fraction	71	768	—	—	
Rhodes grass					7
5 weeks regrowth	—	—	—	138	
10 weeks regrowth	—	—	—	44	
Kikuyu grass					
5 weeks regrowth	—	—	—	188	
10 weeks regrowth	—	—	—	38	
Pangola grass					
5 weeks regrowth	—	—	—	150	
10 weeks regrowth	—	—	—	38	
Lablab purpureus					8
Leaf fraction	120	425	—	—	
Stem fraction	76	542	—	—	
US	50	—	629	100	9
US + FM	59	—	593	131	
US + SBP	53	—	574	100	
US + FM + SBP	58	—	522	313	
AS	48	—	661	103	
AS + FM	53	—	624	141	
AS + SBP	52	—	598	106	
AS + FM + SBP	58	—	565	137	
Lucerne hay	183	406	—	—	10
Orchard grass	114	643	—	—	
Switch grass	78	734	—	—	

[a]Diet type, Diet A = Perennial ryegrass cut after 7 weeks of growth, Diet B = Perennial ryegrass cut after 12 weeks of growth, Diet C = 60% of grass B and 40% of milled and pelleted barley, L = long form grass without processing (baled), P = Pellets form, Ration A = 70% wheat straw, 6.66% lucerne chaff, 10% corn starch, 10% sucrose, 3% minerals and 0.33% sodium chloride, Ration B = All composition same as of ration A except addition of 0.40% sodium sulphate and having no sodium chloride, Ration C = 96.60% wheat straw, 3% minerals, 0.33% sodium chloride, Ration D = 94.60% wheat straw, 3% minerals, 2% urea and 0.33% sodium chloride, Ration E = Same as of ration D except addition of 0.40% sodium sulphate and without sodium chloride, US = Untreated barley straw , AS = Ammonia treated barley straw, FM =Fish meal (50 g/kg) SBP = Sugar beet pulp (150 g/kg). [b]Chemical composition, NDF = Neutral detergent fibre, ADF = Acid detergent fibre and CP = Crude protein. [c]Source: 1 = Colovos et al., 1970; 2 = Greenhalgh and Reid, 1973; 3 = Bird, 1974; 4 = Thomas and Campling, 1976; 5 = Kilmer et al., 1979; 6 = Poppi et al., 1980; 7 = Rees and Little, 1980; 8 = Hendricksen et al., 1981; 9 = Silva et al., 1989; and 10 = Reid et al., 1990.

Table 9: The composition of diets of sheep and goats studies collected for the literature survey of the meta-analysis.

Diet type[a]	Chemical composition (g/kg DM)[b]				Source[c]
	Ash	NDF	ADF	CP	
Experiment 1					1
Wilted lucerne silage	—	—	—	158	
Low DM corn silage	—	—	—	87	
High DM corn silage	—	—	—	79	
Experiment 2					
Wilted lucerne silage	—	—	—	178	
High DM corn silage	—	—	—	81	
Zambian natural grass hay	114	—	—	66	2
Lucerne chaff	84	—	—	184	3
Oaten chaff	58	—	—	57	
Barley straw	78	—	—	39	
Meadow Hay	49	—	—	44	4
Lucerne hay	75	—	—	149	
Desert grass (Hummra)	—	—	—	32	5
Yellow maize (YM) alone					6
(80%)	52	—	—	138	
YM:BDG (65:15)	48	—	—	161	
YM:BDG (50:30)	46	—	—	144	
YM:BDG (35:45)	50	—	—	149	
YM:BDG (20:60)	51	—	—	159	
YM:BDG (5:75)	51	—	—	166	
Barley hay (BH)	79	614	374	98	7
Sundax hay (SH)	115	619	408	94	
Lucerne hay (LH)	114	373	308	233	
Barley straw (BS)	94	757	533	51	
Acacia	82	347	319	144	
Conc. Mix. (C^2)	62	—	—	153	
WS 35	—	410	240	125	8
WS 50	—	520	320	122	
WS 65	—	620	400	115	
Sorghum hay	—	585		120	9
Lucerne hay	87	568	368	176	10
Bromegrass	75	704	393	136	
Experiment 1					11
LH	91	—	391	175	
Experiment 2					
ABS	52	—	567	106	
Experiment 3					
ABS	47	—	588	75	
Nettle	152	—	282	237	
E. stagnina	98	—	403	92	12
Experiment 1					13
Gorse (Leguminous shrub)	61	503	—	181	
Experiment 2					
Gorse (Leguminous shrub)	37	530	—	112	
Wheat straw (WS)	—	—	—	34	14
Sorghum hay (SH)	—	—	—	59	
Oat hay (OH)	—	—	—	38	

Table 9 (continued): The composition of diets of sheep and goats studies collected for the literature survey of the meta-analysis.

Diet type[a]	Chemical composition (g/kg DM)[b]				Source[c]
	Ash	NDF	ADF	CP	
Lucerne hay	89	392	—	195	15
Willow	86	415	—	132	
Guinea grass (GG)	—	764	436	108	16
GG:Leu (80:20)	—	721	384	139	
GG:Leu (60:40)	—	692	320	181	
GG:Leu (40:60)	—	665	249	227	
Lucerne hay	97	—	—	162	17
Prairie grass straw	—	637	—	96	18
Napier grass					19
Whole plant	93	—	—	84	
Leaf fraction	101	—	—	103	
Stem fraction	86	—	—	52	
UTM	109	725	425	156	20
Concentrate pellets	169	210	128	211	
SHM	98	470	391	189	
SLM	101	238	138	302	21
Sorghum S-29	64	739	449	31	
Leu	123	211	149	184	
Com	90	285	217	161	
C^3	155	229	94	267	
Lucerne hay (LH)	—	327	—	80	22
LH & C^4 (35: 65)	75	25	22	65	23
Stylosanthes	110	—	—	126	24
Copra cake	102	—	—	236	
Cassava peel	62	—	—	53	
Cassava pulp	37	—	—	25	
Barley diet	70	298	—	177	25
Cactus diet	77	134	—	422	

[a]Diet type, BDG = Brewers' dried grains, C^2 = Concentrate mixture (Crushed barley 461, crushed sorghum grain 307, soybean meal 164, wheat bran 50, dicalcium phosphate 5, limestone 10 and sodium chloride 3 g/kg), WS 35 = Wheat straw 35%, corn grain 37%, soybean oil meal 13%, molasses 9% and water 6%, WS 50 = Wheat straw 50%, corn grain 20%, soybean oil meal 15%, molasses 9% and water 6%, WS 65 = Wheat straw 65%, corn grain 4%, soybean oil meal 16%, molasses 9% and water 6%, ABS = Ammonia treated barley straw, *Echinochloa stagnina* = Perennial grass, PM = *Panicum maximum* (Guinea grass), UTM = Urea treated maize stover, SHM = Sunhemp hay meal, SLM = Subabul leaf meal, Leu = *Leuceana leucocephala*, Com = *Combretum aculaetum*, C^3 = Diet with concentrate (52.5% wheat bran, 25% cotton seed cake, 12.5% molasses, 5% fish meal, 5%NaCl), Leu 10 = Diet with 10% leaves of Leu, Leu 30 = Diet with 30% leaves of Leu, Com 30 = Diet with 30% leaves of Com, C^4 = Concentrate mixture (Ground corn 55%, soybean meal 3.5%, molasses 3%, dicalcium phosphate 0.72%, limestone 0.28%, vitamin premix 0.50%, trace mineralized salt 0.50%, ammonium chloride 0.50% & sodium sulphate 0.50%), *Stylosanthes guianensis* = A roughage, Barley diet = Hay *ad libitum* + (232.5 g barley + 60 g soybean meal + 7.5 g MVS (Mineral and vitamin supplement was composed of 53% $CaCo_3$, 21% NaCl, 16% dicalcium phosphate, 5% trace minerals and 5% vitamins), Cactus diet = Hay *ad libitum* + (350 g cactus + 60 g soybean meal + 7.5 g MVS + urea). [b]Chemical composition, NDF = Neutral detergent fibre, ADF = Acid detergent fibre and CP = Crude protein. [c]Source: 1 = Jones et al., 1972; 2 = Gihad, 1976; 3 = Boer et al., 1982; 4 = Alam et al., 1983; 5 = Mousa et al., 1983; 6 = Adebowale and Ademosun, 1985; 7 = Antoniou and Hadjipanayiotou, 1985; 8 = Brown and Johnson, 1985; 9 = Huston et al., 1986; 10 = Quick and Dehority, 1986; 11 = Wahed and Owen, 1986; 12 = Adebowale, E. A., 1988; 13 = Howe et al., 1988; 14 = Huston et al., 1988; 15 = McCabe and Barry, 1988; 16 = Adejumo and Ademosun, 1991; 17 = Domingue et al., 1991; 18 = Domingue et al., 1991a; 19 = Larbi et al.,1991; 20 = Chandrasekharaiah et al., 1996; 21 = Bosma and Bicaba, 1997; 22 = Burns et al., 2005; 23 = Animut et al., 2006; 24 = Baiden et al., 2007; and 25 = Abidi et al., 2009.

Table 10: The composition of diets of cattle and buffaloes studies collected for the literature survey of the meta-analysis.

Diet type[a]	Chemical composition (g/kg DM)[b]				Source[c]
	Ash	NDF	ADF	CP	
Berseem hay (Egyptian clover)	168	—	—	206	1
Dry grass	93	—	—	38	2
Sorghum stubble hay	106	—	—	52	3
RS	251	—	—	39	4
ARS	278	—	—	40	
Leucaena (L)	70	—	—	212	
EG	109	—	—	85	
Elephant grass (EG)	111	—	—	98	5
Rice bran (RB)	110	—	—	124	
Rhodes grass	—	—	—	20	6
Lucerne	—	—	—	139	
ARS	123	632	453	67	7
ARS 1	122	631	460	108	
ARS 2	122	627	448	129	
RS and molasses (70:30)	140	510	350	41	8
Experiment 1					9
RS	249	—	399	42	
Leu	80	—	179	213	
Experiment 2					
RS	200	—	408	36	
Experiment 1					10
RG	—	—	498	22	
Experiment 2					
SG	79	—	403	35	

[a]Diet type, Dry grass = A mixture of plant species of *Apluda aristata* & *Themada quadvivalvis*, RS = Rice straw, ARS = Alkali treated rice straw, ARS 1 = ARS + 14.5 g urea/kg, ARS 2 = ARS + 22 g urea/kg, Leu = Leucaena, Diet A = Rice straw + urea 206 g/ day, Diet B = Rice straw + sunflower meal 492 g/ day, rice grain 492 g/ day and urea 154 g/ day, RG = Rhodes grass, SG = Spear grass. [b]Chemical composition, NDF = Neutral detergent fibre, ADF = Acid detergent fibre and CP = Crude protein. [c]Source: 1 = Sharma and murdia, 1974; 2 = Sharma and Rajora, 1977; 3 = Moran et al., 1979; 4 = Moran et al., 1983; 5 = Moran, 1983; 6 = McSweeney et al., 1989; 7 = Pearson and Archibald, 1990; 8 = Abdullah et al., 1992; 9 = Kennedy et al., 1992; and 10 = Kennedy et al., 1992a.

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Publications

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