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NUTRITIONAL CONSTRAINTS TO LAMB
GROWTH AT PASTURE

A thesis
submitted in partial fulfilment
of the requirements for the degree
of
Doctor of Philosophy
in the
University of Canterbury

by

George John Cruickshank

Lincoln College
1986
To Mum, Dad, Jim, Ian, Doug and Dave.
Abstract of a thesis submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy.

NUTRITIONAL CONSTRAINTS TO LAMB GROWTH AT PASTURE

by

G. J. CRUICKSHANK

Intake and nutrient supply were measured in early weaned lambs grazing pure species swards of Rere lucerne (*Medicago sativa*, L), Huia white clover (*Trifolium repens*, C), Ruanui perennial ryegrass (*Lolium perenne*, R) and Matua prairie grass (*Bromus catharticus*, P). A study of the factors regulating intake was undertaken with these young lambs and this area was studied in greater detail with adult sheep, which permitted repeated measurement of rumen digesta content.

A preliminary experiment, conducted indoors, studied the effect of lamb age and cannulation on the development of rumen function in lambs weaned at 6 weeks of age and offered clover hay *ad libitum*. Cannulation did not affect intake (g.kg\(^{-1}\)W\(^{-1}\)), *in vivo* digestibility or marker retention time in the rumen. However, liveweight gain was 22% lower in cannulated lambs than in intact lambs, but this may have been due, at least partly, to differences in weaning weight, as liveweight gain per kg digestible organic matter intake was similar for both groups. Intake (g.kg\(^{-1}\)W\(^{-1}\)) increased rapidly from weaning until approximately 10 weeks of age and remained constant, at 36-38gDM.kg\(^{-1}\)W\(^{-1}\), thereafter. With increasing age there appeared to be a reduction in the proportion of apparently digestible organic matter intake (DOMI) and digestible neutral detergent fibre (NDF) intake apparently digested in the rumen, but this affect was largely explained by changes in the intake of cannulated lambs between the 4 periods of nutrient supply measurement.

In a later experiment lambs weaned at 6 weeks of age grazed single species swards. Growth rate, intake and nutrient supply were measured during the subsequent 6 week period. Liveweight gain was higher in lambs
grazing legumes (321 and 308 g.d\(^{-1}\) for C and L respectively) than for lambs grazing grasses (230 and 227 g.d\(^{-1}\) for P and R respectively). Nutrient supply was measured at 8 and 12 weeks of age. There was no difference in intake (g.kg\(^{W^{-1}}\)) or site of nutrient digestion between these periods. The higher growth rate of lambs grazing legumes was associated with a 36% higher DOMI (g.kg\(^{W^{-1}}\)) and a 33% higher NAN flow at the duodenum (g.kg\(^{W^{-1}}\)). The proportion of DOMI apparently digested in the rumen was similar for all pasture species (average, 0.56), although less digestible NDF was digested in the rumen of lambs grazing legumes (0.76) than in the rumen of lambs grazing grasses (0.88). Substantial losses of dietary nitrogen occurred across the rumen, particularly in lambs grazing legumes. The proportion of ingested nitrogen lost across the rumen was related to the nitrogen content of the diet.

Analysis of the present data and data from the literature suggested that growth rate was better related to the absorption of amino acid nitrogen (aaN) than to ME intake, although intake, which affected both amino acid and ME absorption, exerted the greatest influence. Estimated efficiency of utilisation of ME and aaN, above maintenance, i.e. for growth, appeared low (0.39 and 0.43, respectively) but were within the range commonly observed in animals consuming herbage diets.

The retention time of digesta in the rumen (RT) is an important aspect of intake regulation. Two techniques were identified as having potential for the estimation of RT in grazing animals, and these were evaluated in early weaned lambs and, more comprehensively, in adult sheep. Firstly, RT was estimated from the rate of disappearance of digesta from the rumen of fasted sheep. Secondly, RT was estimated from the average daily rumen fill and intake of grazing sheep. The latter technique appeared to give more reliable results and was recommended for general application. Legumes exhibited shorter RT of OM than grasses (average, 6.7 v 8.8h in adult sheep, 3.5 v 8.5h in early weaned lambs). Early weaned lambs displayed a shorter RT of legumes than adult sheep, but this was not apparent for grasses.

The pattern of rumen fill, in relation to grazing time, was examined in adult sheep. A consistent pattern was observed, with maximum rumen fill occurring around sunset and minimum fill occurring during the forenoon. The ability of sheep to alter the pattern of fill was studied by restricting the rumen capacity of sheep grazing P and L in spring.
This was effected by inserting water filled balloons into the rumen. The presence of balloons was associated with a reduction in OMI (23 and 9% for P and L respectively), although there was no apparent change in the pattern of rumen fill. The volume of digesta in the rumen was reduced in the presence of balloons, particularly in sheep grazing P (average 16 and 9% for P and L respectively), but the total volume of rumen contents (digesta + balloons) increased (7 and 17% for P and L respectively). Therefore, it appeared that intake could be markedly increased if sheep maintained rumen fill at the maximum observed value. This seriously challenged the concept of rumen capacity regulating intake and suggested the involvement of some other factor(s). A conceptual model was developed to study intake regulation. This was based on a combination of physical and metabolic mechanisms interacting in the overall regulation of intake. It provided a qualitative explanation of the response of sheep to restriction of rumen capacity. The model concept has wide potential and warrants further investigation.

In conclusion, it appears that the higher growth rate observed in lambs grazing legumes, compared to grasses, was mainly due to higher intake, although amino acid absorption appeared to be of greater importance than ME intake. The intake of high quality grazed herbage is complex and appears to be regulated by a combination of physical and metabolic mechanisms.
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### List of abbreviations

**Liveweight**
- \( W \) Liveweight
- \( LWG \) Liveweight gain

**Feeding value of forages**
- \( DM \) Dry matter
- \( DMI \) Dry matter intake
- \( OM \) Organic matter
- \( OMI \) Organic matter intake
- \( DOMI \) Digestible organic matter intake
- \( OMD \) Organic matter digestibility
- \( OMADR \) Organic matter apparently digested in the rumen
- \( DOMADR \) Proportion of apparently digestible organic matter apparently digested in the rumen
- \( NDF \) Neutral detergent fibre
- \( NDFI \) NDF intake
- \( NDFD \) NDF digestibility
- \( INDFDR \) Proportion of ingested NDF digested in the rumen
- \( PNDFDR \) Proportion of digested NDF digested in the rumen
- \( N \) Nitrogen
- \( NAN \) Non-ammonia nitrogen
- \( IADF \) Indigestible acid detergent fibre

**Retention time**
- \( RT \) Retention time of digesta in the rumen
- \( RT_{OM} \) Retention time of organic matter in the rumen
- \( k \) Fractional disappearance rate of digesta from the rumen
- \( k_{DM} \) Fractional disappearance rate of dry matter from the rumen
- \( k_{OM} \) Fractional disappearance rate of organic matter from the rumen
- \( k_{NDF} \) Fractional disappearance rate of NDF from the rumen
- \( k_p \) Fractional rate of passage from the rumen
- \( k_d \) Fractional rate of digestion in the rumen
CHAPTER 1

Introduction

Major advances in the development of effective pastoral livestock systems, for which New Zealand is renowned, have relied on maximising utilisation of herbage. As returns from further development of this approach diminish it is logical that research should concentrate on factors controlling nutrient intake, particularly in animals from which high performance, and therefore, high intake, is required. Early weaned lambs fall into this category.

Early weaning has the potential to increase the efficiency of pasture utilisation by diverting more highly digestible herbage to the lamb than to the ewe and, therefore, improving the efficiency of pasture utilisation (Jagusch et al., 1970; Rattray et al., 1976). Moreover, early weaning permits advancement of the lambing date, greatly increasing the potential to maximise lamb growth during the major period of pasture growth. However, early weaning has not been widely adopted in practical sheep production, despite experimental evidence that early weaned lambs can grow at similar rates to suckled lambs (Jagusch et al., 1970, 1971).

The growth rate of early weaned lambs depends on their ability to rapidly increase herbage intake following weaning. This may be limited by inadequate rumen development and this aspect is of critical importance in selecting weaning age. Secondly, early weaned lambs have a high potential nutrient requirement and growth rate will depend not only on herbage intake, but also on the nutrients derived from herbage digestion and their efficiency of utilisation for growth. These latter aspects are poorly understood and major advances in lamb growth could be achieved from a knowledge of the major limitations to growth and, subsequently, development and selection of plant species/cultivars to alleviate the limitations.

This review discusses the nutrient requirements of young lambs, both in terms of quantity and composition, and the factors limiting the ability of lambs to obtain these nutrients from fresh herbage. Particular emphasis is placed upon herbage composition, in relation to digestion characteristics, and the regulation of herbage intake. Finally the development of techniques to enable detailed studies of grazing animals is discussed.
CHAPTER 2

Review of Literature

2.1 NUTRITIONAL CONSTRAINTS TO LAMB GROWTH

The growth rate of grazing lambs is highly variable and depends upon the breed, sex and age of the lamb and the quantity and quality of the herbage on offer. A selection of high growth rates taken from the literature is shown in table 2.1.1. Grazing lambs tend to have growth rates considerably lower than housed lambs offered protein supplemented concentrate diets. There are also marked differences in growth rate between animals grazing different pastures, particularly between legumes and grasses. However, caution must be exerted in the interpretation of these data. The indoor data were obtained from studies in the U.K. and the grazing data from studies in New Zealand. It is possible that genetic differences in maximum growth rate may be, at least partly, responsible.

Attainment of the genetic potential for growth requires an adequate supply of nutrients which can be used with a high efficiency. Efficiency of utilisation is dependent on the supply of a range of absorbed nutrients, including energy, protein and minerals, in proportion to requirement. Suboptimal growth rate can occur because of low intake but also because of poor utilisation resulting from an imbalance of absorbed nutrients. The latter may be associated with adaptation in composition of the animal. For example, protein synthesis is dependent not only on the supply of amino acids, but also on energy supply. Energy is required for body maintenance and protein synthesis, with surplus being stored in adipose tissue. This is an oversimplification, but it serves to illustrate the difficulties in discussing requirement for any nutrient independently. Nutrient requirements for growth do, moreover, change with changing body composition, as the animal's tissue groups develop towards their mature relationships. It is important to understand compositional changes before discussing the problem of nutrient utilisation.

2.1.1 Body composition

Increases in body weight are mainly due to accretion of protein, (e.g. muscle), adipose and skeletal tissue. However, skeletal growth has not been considered in this review. The relative proportion of protein and adipose tissue in the body changes, in favour of adipose tissue, with
increasing bodyweight. The rate of change differs between breeds and sexes and may be slightly modified by diet (Mitchell & Jagusch, 1972; Ørskov et al, 1976). ARC (1980) calculated that the protein concentration in empty body gain (EBW; g.kg\(^{-1}\)) decreased from 159, between 10 and 11 kg EBW, to 138 between 40 and 41 kg EBW. The corresponding fat concentrations were 117 and 442. This emphasises the greater protein requirement of young lambs for growth. Although small variations in body composition occur at any given EBW, there is a surprising constancy of body composition in growing animals (Reid et al, 1968; Andrews & Ørskov, 1970).

2.1.2 Nutrient intake and liveweight gain.

Barry (1981) observed that infusion of casein into the abomasum of lambs consuming fresh herbage increased liveweight gain (LWG) and concluded that protein absorption appeared to be limiting lamb growth. If this conclusion was correct, the effect is likely to be more pronounced in younger lambs, due to their greater protein requirement for gain.

Data in the literature were used to assess the relative importance of energy and protein in the regulation of growth. Metabolisable energy (ME) intake and absorbed amino acid nitrogen (aaN) were calculated, and to account for differences in liveweight and level of intake, calculated maintenance requirement was deducted. Relationships were derived between LWG and utilisable amino acid nitrogen (aaN), i.e. absorbed aaN – maintenance N requirement, and between LWG and utilisable ME intake, i.e. ME intake – maintenance ME requirement. The references and details of assumptions used in the calculations are given in appendix 1. A paucity of data, particularly for young lambs, was revealed. All data were originally derived from predictive equations obtained with non-productive animals consuming similar diets and are shown in figure 2.1.1. There was a good correlation between LWG and utilisable ME intake (r\(^2\) = 0.69) and between LWG and utilisable aaN intake (r\(^2\) = 0.61). However, in the latter relationship, the data of Ørskov et al (1974) were unusual and their exclusion increased the correlation (r\(^2\) = 0.82). Multiple regression, using utilisable ME and aaN intake as independent variables, improved the correlation marginally (r\(^2\) = 0.84). Utilisable aaN was a significant component of the regression (P<0.01) and utilisable ME intake was non-significant (P>0.05). However, utilisable aaN and ME intake were correlated (r\(^2\) = 0.69), suggesting that intake, which influenced both aaN and energy supply, was a major cause of the differences in LWG. The particularly high LWG, relative to utilisable aaN, observed by
norov et al (1974) may reflect the fishmeal content of the diet. Microbial protein generally supplies the majority of utilisable aAn in animals consuming herbage diets but may supply insufficient methionine to sustain maximal growth rates (Storm & norov, 1984). Fishmeal, which contains a high proportion of sulphur amino acids (methionine and cysteine), a large proportion of which escapes degradation in the rumen (norov et al, 1974), could have improved the amino acid composition of absorbed aAn and, therefore, LWG.

In a limited study, MacRae (1976) adopted a similar approach to above, analysing data from Ulyatt (1971) and MacRae & Ulyatt (1974) for sheep consuming fresh herbage. He observed that LWG was highly correlated with rate of absorption of amino acids (r = 0.79) but not with the absorption of energy, estimated from energy absorbed as volatile fatty acids (VFA; r = 0.02). The low correlation observed in the latter relationship may have been influenced by the narrow range of intake observed in the study of Ulyatt (1971), compared to the present data set. Moreover, ME intake comprises a range of energy yielding substrates, including protein, and is therefore likely to differ from VFA-energy. Both the present study and that of MacRae (1976) suggest that protein absorption is a more important determinant of LWG than energy intake per se. However, absorption of glucogenic amino acids may increase the efficiency of utilisation of ME (Gill et al, 1984) and this may have been an important factor in the relationships between protein absorption and LWG observed above.

2.1.3 Nutrient utilisation and liveweight gain

The efficiency of utilisation of absorbed energy yielding nutrients, above maintenance, for deposition as body energy is an important determinant of nutrient requirement. The efficiency of utilisation of ME for gain (kg) is generally low in animals consuming roughage diets. For example, kg values of 0.26 for fresh pasture (Barry, 1981), 0.29 for fresh lucerne and pasture (Fennessy et al, 1972), 0.33 for fresh ryegrass (Rattray & Joyce, 1974), 0.38 for grazed ryegrass-white clover (Geenty, 1985), 0.28 for dried chopped lucerne (Thomson & Cammell, 1979) and 0.22 for meadow hay (Alam, 1985) have been observed. In part, these differences in kg reflect a complex interaction between the supply of energy and amino acids, and the efficiency of energy utilisation, possibly related to variations in the nature of the products of energy digestion and absorption. A general relationship, albeit for milk fed lambs, is shown in figure 2.1.2 (adapted from Black & Griffiths,
1975). This relationship suggests that nitrogen retention is related to both energy and protein intake, and may be used to analyse the relative importance of energy and protein in limiting growth. For example, the observation of Barry (1981), that abomasal infusion of casein increased N retention in sheep offered fresh herbage, suggested that N retention in non-infused sheep was limited by aaN supply. Conversely, Eskeland et al (1973; 1974) observed that infusion of various energy sources intravenously increased N retention in sheep offered a high protein diet, suggesting that energy supply was limiting N retention. The relationship also suggests that kg may be influenced by the relative supply of ME and protein. The optimum balance is illustrated in figure 2.1.2 as the intercept of the horizontal (energy limiting) and sloping (nitrogen limiting) lines. Deviation from this optimum balance may result in a decreased kg.

The low kg observed in roughage fed animals, including those consuming high quality fresh herbage, has long been recognised but never fully explained. Early studies by Armstrong & Blaxter (1957) and Armstrong et al (1958) observed an inverse relationship between kg and the proportion of acetic acid in the absorbed VFA. However, in later studies by Ørskov & Allen (1966a,b,c), Ørskov et al (1966) and Ørskov et al (1979) this relationship was not observed. Suggestions that the response was dependent on diet (Poole & Allen, 1970; Tyrell et al, 1979) strengthened the case for examination of herbage diets. A possible explanation may be obtained by studying the metabolism of acetic acid. Primarily, Armstrong et al (1958) and later, Ørskov (1975), MacRae & Lobley (1982) and Gill et al (1984) have drawn attention to the requirement for glucogenic precursors in the utilisation of acetic acid. As acetic acid is lipogenic, any surplus will be converted to fatty acids and stored in adipose tissue. However, lipogenesis requires a supply of nicotinamide-adenine dinucleotide phosphate (NADPH), which is mainly obtained from the pentose phosphate pathway. The major glucogenic precursors in forage fed animals are propionic acid and glucogenic amino acids. If these are limiting, the excess acetic acid may be wastefully catabolised in some form of futile cycle (Gill et al, 1984), inefficient utilisation of acetic acid will occur and low kg values will be observed. This may also cause inefficient utilisation of amino acids but glucogenic amino acids, surplus to the requirements for maintenance and protein deposition, could play an important role in energy utilisation.
It appears, therefore, that the ability of young lambs to obtain a sufficient supply of nutrients from herbage diets to express their genetic potential for growth may be limited by a deficiency of (an) essential amino acid(s) and an imbalance of absorbed energy yielding compounds, particularly a high proportion of acetic acid. If amino acid absorption exceeds the requirement for maintenance and deposition, the surplus glucogenic amino acids may play an important role in the utilisation of acetic acid and may, therefore, influence energy retention and LWG.
Table 2.1.1. The potential growth rate of lambs. A selection of high growth rates, illustrating the effect of diet on liveweight gain. Concentrates were offered indoors and lucerne (L), white clover (C), ryegrass (R) and mixed R/C pastures were grazed.

<table>
<thead>
<tr>
<th>Indoor</th>
<th>Grazing</th>
<th>Reference</th>
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<tbody>
<tr>
<td></td>
<td>L</td>
<td>C</td>
</tr>
<tr>
<td>377</td>
<td></td>
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<tr>
<td>360-409</td>
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<td>364</td>
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<tr>
<td>397</td>
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<tr>
<td>485 (compensatory growth)</td>
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<td>281</td>
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<td>330-350</td>
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<td>267</td>
<td></td>
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</tr>
</tbody>
</table>

Fraser & Ørskov (1974)
Frood & Owen (1974)
Ørskov et al (1976)
FIGURE 2.1.1 The relationships between liveweight gain (LWG, g.d⁻¹) and (a) ME intake less maintenance ME requirement, and (b) absorbed amino acid nitrogen (aaN, g.d⁻¹) less tissue N maintenance requirement.
Figure 2.1.2. Predicted relationship between nitrogen (N) balance and N intake for a milk fed lamb weighing 15kg, adapted from Black & Griffiths (1975)
2.2 THE NUTRITIVE VALUE OF FRESH HERBAGE

The major components of nutritive value are digestibility and the composition of absorbed nutrients. Differences in nutritive value are observed between (MacRae & Ulyatt, 1974; Ulyatt & MacRae, 1974; Moseley & Jones, 1979) and within plant species (Corbett et al, 1966; Blaxter et al, 1971) of similar digestibility. To understand the reason for these differences knowledge of the composition of plants and the products of digestion is important. The major chemical components of herbage are given in table 2.2.1. The quantity and relative proportions of these components are important determinants of the nutritive value of herbage. The digestion of feed components in the rumen is dependent upon several rate constants and the degradation characteristics of the components, as outlined in figure 2.2.1.

This section reviews the factors affecting nutritive value. Particular emphasis is placed upon energy and nitrogen constituents with brief reference to other nutrients where applicable.

2.2.1 Cell wall constituents

The plant cell wall is the structural part of the plant and contains the total fibre fraction. The major cell wall constituents (CWC) are cellulose, hemicellulose, lignin, cutin, elastin (fibre bound protein) and silica (Van Soest, 1985). The cell wall content of plant stems is higher than that of leaves (Laredo & Minson, 1975; Wilman & Altimimi, 1984). This difference becomes more pronounced as plants mature when cell wall content increases rapidly in stem but only slowly in leaf (Waite et al, 1964; Bailey et al, 1970). Legumes tend to have a lower cell wall content than grasses (Ulyatt & MacRae, 1974; Ulyatt et al, 1976; Norton, 1982; Campling, 1984; Thomson, 1984).

The digestion of CWC is entirely dependent upon the enzymes secreted by the microbiota in the reticulo-rumen and the caecum-proximal colon. Under the anaerobic conditions of the digestive tract carbohydrates are catabolised to yield volatile fatty acids (VFA), principally acetic, propionic and butyric, adenosine triphosphate (ATP), methane and water (Orskov, 1975). The microbes utilise the ATP for maintenance and growth, and VFAs are absorbed as the major source of energy for the host animal (Barcroft et al, 1944; Hungate, 1966). The extent of CWC digestion is influenced by the presence of a digestion lag,
the potential digestibility, the rate of digestion and the passage rate from the rumen (Mertens, 1977). The effect of digestion rate and passage rate on substrate digestion is shown in figure 2.2.2.

A lag time, when no or negligible digestion occurs, has been observed (Smith et al., 1971; Tauskey et al., 1974, Mertens, 1977) and is probably due to the time taken for colonisation of the CWC by the rumen microflora (Ulyatt et al., 1976).

A proportion of the CWC is indigestible (Wilkins, 1969; Bailey & Hironaka, 1970; Smith et al., 1971, 1972; Jacobs & Ellis, 1975). The potential digestibility is highly variable and decreases as plants mature (Waite et al., 1964), associated with the increased lignification (Van Soest, 1985). Lignin and silica are highly resistant to digestion (Van Soest, 1985) and their incorporation into the cell wall limits the microbial digestion of the associated cellulose and hemicellulose (Van Soest, 1967; Van Soest & Jones, 1968).

Digestion of the potentially digestible fraction, following the initial lag time, appears to exhibit first order kinetic behaviour (Gill et al., 1969; Smith et al., 1971; Tauskey et al., 1974).

The factors affecting digestion rate have not been well defined and may be related more to morphological structure than to chemical composition (Mertens, 1977). The rate of digestion may be reduced by dietary deficiencies of nitrogen (Campling et al., 1962; Coombe & Tribe, 1963; Weston, 1967; Kempton & Leng, 1979; Redman et al., 1980; Egan & Doyle, 1985) and certain minerals, e.g. sulphur (Rees & Minson, 1978), sodium (Joyce & Brunswick, 1975) and cobalt (McLean et al., 1962), due to reduced microbial growth rate.

The digestion of CWC also depends upon the time available for digestion and is therefore dependent upon outflow rate from the rumen. This subject is discussed in section 2.3.2.2.

Studies on the in vivo digestion of the CWC of fresh forage are limited. The rumen is the major site of CWC digestion. Thomson & Beever (1974) observed that over 90% of the whole tract digestion of the cellulose of long forages occurred in the rumen, irrespective of the digestibility of the forage which ranged from 58-88%. Ulyatt & Egan (1979), in studies of fresh herbage, observed that 87-97% of cellulose digestion occurred in the rumen when whole tract cellulose digestibility
ranged from 73-94%. The whole tract digestibility of hemicellulose tends to be lower than for cellulose and a smaller proportion of the digested hemicellulose is digested in the rumen (Beever et al, 1971, 1972; Thomson et al, 1972; Ulyatt & Egan, 1979).

2.2.2 Soluble carbohydrates

The major soluble carbohydrates are glucose, fructose, sucrose and the storage carbohydrates starch and fructosans (Norton, 1982). These accumulate in plant cells when photosynthetic rate exceeds respiration rate and growth requirements, and therefore content will depend upon plant species, climatic conditions and sward structure (Johns, 1955). The soluble carbohydrate content of plants increases in the early vegetative stages of growth and decreases slowly in stems, while remaining constant in leaves, as the plant matures (Bailey et al, 1970; Norton, 1982). Legumes and grasses tend to have a similar soluble carbohydrate content but legumes have a higher proportion of soluble:structural carbohydrate (Ulyatt, 1971; Ulyatt & MacRae, 1971, 1974; Ulyatt et al, 1976).

The soluble carbohydrates have a high rate of digestion and are, generally, completely digested in the digestive tract with over 90% of the digestion occurring in the rumen (Beever et al, 1971, 1972, 1978; Ulyatt & MacRae, 1974; Ulyatt & Egan, 1979) and the remainder being digested in the small intestine (Beever et al, 1972, 1978). When high starch diets, particularly maize, are offered, large quantities of starch may escape fermentation in the rumen (Ørskov et al, 1969, 1971). This is mostly digested in the small intestine but significant caecal fermentation may occur. This has been shown to increase nitrogen loss in faeces due to increased microbial synthesis in the caecum (Ørskov et al, 1970).

The ratio of CWC:soluble carbohydrate in the diet and the extent of CWC digestion is important in determining the composition of the absorbed energy. Increasing the proportion of digestible CWC present in the diet, relative to total digestible carbohydrate, leads to an increase in the production of acetic acid with a corresponding reduction in the production of propionic acid. Therefore, changes in plant composition will alter the relative production of acetate and propionate. Johns et al (1963) observed that the ratio of acetate:propionate in the rumen was lower in lambs grazing short-rotation ryegrass/white clover pasture (3.6:1) than in lambs grazing a perennial ryegrass pasture (2.4:1).
Similarly, McLean et al. (1967) reported a lower ratio of acetate:propionate in the rumen of lambs grazing lucerne (2.0:1) than in lambs grazing perennial ryegrass (2.7:1). Beever et al. (1978) observed that the production (moles.day\(^{-1}\)) of acetate, relative to propionate, was lower in sheep consuming spring harvested perennial ryegrass (2.5:1) compared to autumn harvested (3.1:1). Correspondingly, the ratio of CWC:total carbohydrate was 0.72:1 in spring harvested grass and 0.80:1 in autumn harvested grass.

The low efficiency of utilisation of absorbed energy for growth by animals consuming herbage diets may be due to the high proportion of acetate in the absorbed energy (see section 2.1.3), therefore the composition and digestion of fresh herbage may have important implications for energy utilisation.

### 2.2.3 Nitrogen

The nitrogen content of herbage can vary over a large range depending mainly upon plant species, plant maturity, the application rate of N fertilizer and climate (Hallock et al., 1965; Van Soest, 1985). Legumes have a relatively constant nitrogen content due to their ability to fix atmospheric nitrogen (Johns, 1955; Le Du et al., 1981; Losada et al., 1982). The nitrogen content of grasses tends to be lower than that of legumes, although the difference is not constant (Minson, 1976; Ulyatt et al., 1976; Thomson, 1984).

The classification of nitrogenous compounds is outlined in table 2.2.1. Protein may be divided into three major groups on the basis of chemical separation (Mangan, 1982). The approximate proportional distribution in leaf protein is shown in table 2.2.2 (from the data of Mangan, 1982).

Fraction 1 protein comprises around 50% of the chloroplast protein and is readily soluble.

Fraction II protein comprises a complex mixture of soluble proteins from chloroplasts and cytoplasm which are, generally, inseparable following ultracentrifugation (Mangan, 1982).

Chloroplast membrane proteins (CMP), mainly associated with chlorophyll, are insoluble in water and constitute about 40% of the chloroplast protein (Mangan, 1982).
Table 2.2.1. The major chemical components of herbage.

<table>
<thead>
<tr>
<th>Component</th>
<th>Cell wall</th>
<th>Cell contents</th>
<th>Protein</th>
<th>Non protein nitrogen</th>
<th>Minerals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>cellulose</td>
<td>fructosan</td>
<td>fraction I (ribulose-1,5-phosphatase carboxylase)</td>
<td>amino acids</td>
<td>calcium</td>
</tr>
<tr>
<td></td>
<td>hemicellulose</td>
<td>starch</td>
<td>fraction II</td>
<td>nucleic acids</td>
<td>phosphorous</td>
</tr>
<tr>
<td></td>
<td>lignin</td>
<td>glucose</td>
<td>chloroplast membrane protein</td>
<td>urea</td>
<td>magnesium</td>
</tr>
<tr>
<td></td>
<td>cutin</td>
<td>fructose</td>
<td></td>
<td>ammonia</td>
<td></td>
</tr>
<tr>
<td></td>
<td>silica</td>
<td>sucrose</td>
<td></td>
<td>nitrate</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>organic acids</td>
<td></td>
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</table>
Table 2.2.2. The composition and distribution of leaf proteins.

- Chloroplast -- fraction I: 35-40%
- Chloroplast membrane protein: 30%
- Leaf protein --- cytoplasm --- fraction II: 25%
- mitochondria: <5%
- nucleus --- DNA-associated: 1-2%
- cell wall --- extensin: 1-2%
Figure 2.2.1. Theoretical partition of feed constituents and their disappearance from the rumen.
Figure 2.2.2 The influence of rate of digestion ($k_d$) and rate of passage ($k_p$) on extent of digestion in the rumen.
Small quantities of protein associated with DNA, mitochondria and cell wall are also present (Lyttleton, 1973; Lamport & Northcote, 1960).

Non protein nitrogen is present in plants in variable quantities and is related to uptake in the roots and the intermediate steps in protein synthesis. The major constituents are shown in table 2.2.1. Nucleic acids are the most abundant form of non protein nitrogen and may represent 5.2 - 9.5% of the total nitrogen (Smith & McAllan, 1970; Coelho da Silva et al, 1972).

Absorption of amino acids only occurs in the small intestine. Therefore, nitrogen transactions in the rumen play an important role in determining the quantity and quality of absorbed amino acids. The major source of absorbed amino acids in sheep consuming fresh herbage is microbial protein, although dietary protein escaping degradation in the rumen is also important.

2.2.3.1 Ruminal degradation of herbage proteins

The ruminal digestion of protein can be examined as shown in figure 2.2.1 (Ørskov & McDonald, 1970). The potential digestibility of leaf proteins does not appear to have been studied although the quantity of indigestible protein is likely to be minimal (Thomson, 1982). However, several compounds react with proteins to render them indigestible in the rumen of which condensed tannins are of importance to the nutrition of grazing ruminants due to their natural occurrence in some plant species (Jones & Mangan, 1976; Barry & Manley, 1984).

The solubility of proteins has been proposed as an indirect measure of the rate of proteolysis (Wohlt et al, 1973) but the relationship is not precise and the rate of proteolysis varies between different soluble proteins (Mangan, 1972; Nugent & Mangan, 1981; Nugent et al, 1983).

Fraction 1 protein is readily released from plant cells during ingestive mastication and has been shown to degrade rapidly in the rumen leading Nugent & Mangan (1981) to conclude that only a small quantity was likely to escape rumen degradation.

The proteins of fraction II have not been studied but, as they are soluble, it is probable that they exhibit high rates of proteolysis. However, due to the variability of the rate of proteolysis between soluble proteins it is possible that some of the proteins pass undegraded from the rumen.
Chloroplast membrane proteins are insoluble and, although their digestion characteristics have not been studied, are therefore likely to have a slower rate of degradation than fraction 1 and fraction II protein (Mangan, 1982).

Similarly the behaviour of the minor proteins of the nucleus, mitochondria and the cell wall is unknown although cell wall proteins are likely to have a slow rate of degradation due to their association with structural carbohydrate.

The products of proteolysis are peptides and amino acids, which may be deaminated to yield ammonia and carbohydrate (Smith, 1975).

Nucleic acids are rapidly degraded in the rumen (Smith & McAllan, 1970; McAllan & Smith, 1973a) to purine and pyrimidine bases which may be converted to microbial nucleic acids (McAllan & Smith, 1973b). Nucleic acids leaving the rumen are absorbed from the small intestine with an efficiency of 70-80% (Smith, 1969) but are not utilized by the animal and are excreted in the urine as urea, allantoin and hippuric acid (Blaxter & Martin, 1962; Smith et al, 1969).

**2.2.3.2 Microbial protein synthesis**

The major source of nitrogen for microbial metabolism is ammonia (Hungate, 1966; Nolan & Leng, 1972; Bryant, 1973) although some bacteria and protozoa incorporate amino acids and peptides directly into cell protein (Nolan et al, 1976; Hespell & Bryant, 1979; Oldham, 1981). The energy source for microbial growth is ATP (Bauchop & Elsden, 1960; Hungate, 1966). Providing nitrogen is not limiting, microbial cell growth is dependent upon the energy obtained from organic matter degraded in the rumen and this forms the basis for the routine measurement of microbial protein synthesis and yield (Hume & Bird, 1970; Walker & Nader, 1970; Miller, 1973; Thomas, 1973; Roy et al, 1977, Czerkawski, 1978; ARC, 1980). ARC (1980) proposed a system based upon the degradability of dietary protein and the utilization of degraded nitrogen by the rumen microbiota. This system may be applied to grazing ruminants but the vast majority of data were obtained from animals housed indoors and offered diets of conserved forage, usually supplemented with cereal and/or protein concentrates. The factors influencing the accuracy of the ARC system which may differ in the grazing system are discussed below.
2.2.3.2.1 Organic matter digestion. The energy available for the synthesis of microbial organic matter is dependent upon the quantity of dietary organic matter degraded in the rumen and ARC (1980) has adopted a value of 30 grams microbial nitrogen yield per kg organic matter apparently digested in the rumen (OMADR). Relating microbial yield to fermented organic matter leads to higher variation than when related to total VFA production (Walker et al., 1975) but has the advantage of being more easily measured. The production of VFA in grazing animals may vary from housed animals offered cereal diets (Bath & Rook, 1965) and marked differences are observed due to plant species and plant maturity, as mentioned previously. Thus microbial yield may vary in relation to organic matter digestion in the rumen.

Similarly, the apparent digestion of organic matter was adopted by ARC (1980) as a measure of energy supply for microbial synthesis although it would be preferable to use organic matter truly digested, as bacteria can represent a significant proportion of the organic matter leaving the rumen and may bias the results. For example, Losada (1983, cited by Beever, 1984) observed that the proportion of the apparently digested organic matter (DOM) apparently digested in the rumen was higher for cattle grazing ryegrass (0.66) than for cattle grazing white clover (0.46) and that microbial protein synthesis (g microbial N per kg OMADR) averaged 45.5 on ryegrass and 83.0 on clover. Correcting for microbial organic matter flow from the rumen he calculated that the DOM truly digested in the rumen was 0.94 on ryegrass and 0.85 on clover. Microbial protein yield (g microbial N per kg organic matter truly digested in the rumen; OMTDR) then became 31.2 and 45.3 for ryegrass and clover respectively. Therefore, there is likely to be considerable variation in the measurement of microbial yield and caution is required in the interpretation of results.

2.2.3.2.2 Fractional outflow rate. Increasing the fractional outflow rate (FOR) of water from the rumen in vivo by infusing artificial saliva (Harrison et al., 1976, 1979), salt (Hemsley, 1975) or by exposure to cold (Kennedy et al., 1976; Kennedy & Milligan, 1978), has led to increases in microbial yield. In an in vitro experiment Isaacson et al. (1975) observed a similar effect. Robinson et al. (1985) suggested that the FOR of particulate matter also plays an important role in the efficiency of bacterial protein yield, due to the increased outflow rate of bacteria bound to particulate matter. The reasons for the increased
yield are not fully understood but may be due to a reduced autolysis of bacteria, reduced engulfment of bacteria by protozoa or a change in the microbial population (Kennedy & Milligan, 1978). Several studies have observed a decrease in protozoal numbers as FOR is increased (Hemsley, 1975; Harrison et al, 1979; Leng et al, 1984). In studies where protozoa were chemically eliminated from the rumen, efficiency of microbial growth (Knight et al, 1978; Demeyer & Van Nevel, 1979) and lamb growth rate (Bird et al, 1979; Bird & Leng, 1984) were increased. There is significant scope for increasing microbial yield as 30 - 50% of microbial protein is degraded in the rumen (Nolan & Leng, 1972; Smith & Smith, 1976; Nolan & Stachiw, 1979) and removal of protozoa may reduce this value. However, the effect of protozoa on microbial protein yield is equivocal and, despite the assertion by Leng (1984) that, "It now appears to be irrefutable that the presence of protozoa in the rumen decreases the quantity of digestible microbial protein potentially available in the intestines of ruminants", Rowe et al (1985) concluded that defaunation had a small effect on protein absorption and advantages were only likely to be obvious when dietary protein concentration was sub-optimal.

Grazing sheep tend to have a high FOR (Corbett et al, 1976b; Corbett & Pickering, 1983) and this may lead to grazing sheep having a higher microbial yield than the value adopted by the ARC (1980), as was observed by Losada (1983).

2.2.3.3 Relationship between nitrogen intake and nitrogen leaving the rumen

The complexity of the nitrogen transactions in the rumen lead to changes in the quantity of nitrogen and, more importantly, non ammonia nitrogen (NAN) leaving the rumen. Several studies have shown significant losses of nitrogen across the rumen (up to 50%) when fresh forages of high nitrogen content are eaten (Ulyatt & MacRae, 1971; Egan, 1974; MacRae & Ulyatt, 1974; Ulyatt & Egan, 1979; Moseley & Jones, 1979; Corbett et al, 1979; Verite et al, 1984; Beever et al, 1986a,b) with low nitrogen losses or gains when low nitrogen herbages are offered (Egan, 1974; Corbett et al, 1976b: Verite et al, 1984; Beever et al, 1986a,b). In general legumes, due to their higher nitrogen content, showed a higher proportional loss across the rumen than grasses.

Relationships between nitrogen intake, or dietary nitrogen concentration, and nitrogen leaving the rumen have been derived from in
vivo digestion studies on fresh herbage offered indoors, equation 2.2.1 (Ulyatt & Egan, 1979) or grazed, equation 2.2.2 (Beever et al., 1986a).

\[ Y = 1.188X - 0.11X^2 - 0.18 \quad \text{----eqn. 2.2.1} \]

where \( Y \) = Nitrogen entering the duodenum (g.d\(^{-1}\))
\( X \) = nitrogen intake (g.d\(^{-1}\))

\[ Y = 1.5074 - 0.01854X \quad \text{----eqn. 2.2.2} \]

where \( Y \) = NAN entering the duodenum (g.g N intake\(^{-1}\))
\( X \) = N(g).kg OM in diet\(^{-1}\)

Equations such as these are useful for prediction of nitrogen digestion but may have limitations in their application. If the ruminal digestion characteristics of nitrogen are altered, e.g. by freezing or drying herbage (Beever et al., 1976, MacRae, 1976) or due to the presence of condensed tannins (Barry & Manley, 1984) the relationships will alter and erroneous predictions of nitrogen flows from the rumen may be obtained.

2.2.4 Minerals

The mineral content of plants is highly variable, depending upon soil type, fertilizer application, stage of growth and plant species (Little, 1982; Norton, 1982; Van Soest, 1985). Given similar soil types and fertilizer application legumes tend to have a higher mineral content than grasses, particularly calcium, phosphorous and magnesium (Davies et al., 1966; Norton, 1982).

2.2.5 Conclusion

Nutritive value is influenced by plant composition and extent of digestion. Plant composition is highly variable, particularly between species and stage of maturity. The major difference occurs in cell wall content, particularly as plants mature. The potential digestibility and rate of digestion of CWC are important determinants of the total, and composition of, energy derived from the diet.

The digestion of nitrogen in the rumen is more complex. The flow of protein to the small intestine is dependent upon the microbial protein
yield and the amount of dietary protein escaping degradation in the rumen. Microbial protein yield is dependent upon the energy supplied from organic matter digestion and, to a lesser extent, to the fractional outflow rate of water and particulate matter from the rumen. The proportion of dietary protein passing undegraded from the rumen is dependent upon the rate of degradation in the rumen and the rate of passage from the rumen. Rate of digestion is likely to vary between different proteins. Significant quantities of nitrogen may be lost from the rumen when ammonia availability exceeds the capacity of the microflora for protein synthesis.
2.3 REGULATION OF HERBAGE INTAKE

The level of intake achieved is an important determinant of the feeding value of a diet. This section discusses the factors which limit the intake of grazed herbage.

The voluntary food consumption (VFC) of grazed herbage is determined by a wide range of factors including the ability of animal to process ingested herbage, physiological state of the animal, physical and chemical composition of the herbage and sward characteristics. Due to the difficulties in accurately measuring intake by grazing animals the vast majority of data have been obtained from indoor experiments with animals consuming conserved forages.

2.3.1 Digestibility

Early studies observed the relationship between the in vivo digestibility of the diet and VFC and the general relationship, as outlined by Conrad et al (1964) and Baumgardt (1970), is shown in figure 2.3.1. This suggested that when digestibility increased above a certain value, which depended on nutrient demand, VFC declined at a rate which maintained a relatively constant digestible energy intake. From this it was concluded that VFC was limited by the capacity of the digestive tract when feed digestibility was low (physical regulation) and by energy supply when digestibility was high (metabolic regulation). However, the digestibility of the diet was raised by increasing the proportion of cereal in the diet and this has been shown to alter rumen digestion characteristics (Ørskov & Fraser, 1975), possibly due to the effects of starch on fibre digestion (el Shazley et al, 1961).

Numerous studies have shown that the VFC of pure roughage diets increases linearly when digestibility increased up to 80-85% (Blaxter et al, 1961, 1966; Minson et al, 1964; Osbourn et al, 1966; Hodgson, 1968; Hogan et al, 1969; Troelson & Campbell, 1969; Thomson, 1971; Thornton & Minson, 1973; Hodgson et al, 1977; Freer & Jones, 1984). The digestibility of fresh temperate herbage tends to fall in the range 65-85% and the large differences in production observed as digestibility increases over this range could not occur if there was no increase in digestible energy intake.

The relationship between digestibility and VFC is not perfect and several anomalies occur where large differences in VFC of diets of
Figure 2.3.1 The relationship between feed and energy intake, and diet digestibility, adapted from Conrad et al (1964) and Baumgardt (1970).
similar digestibility have been observed between pasture species (Ulyatt, 1971; Demarquilly & Jarrige, 1974; Freer & Jones, 1984), plant components (Laredo & Minson, 1973; Poppi et al., 1981a), with particle size of diet (Heaney et al., 1963) and fertilizer application (Rees and Minson, 1976). Obviously a more detailed approach is required to fully understand the VFC of forages.

2.3.2 The evidence for physical regulation

The relationship between digestibility and VFC suggests a physical regulation to VFC but it does not provide direct evidence. Blaxter et al. (1956; 1961) observed that, over a range of forages, the quantity of dry matter present in the digestive tract, estimated from faecal output, marker excretion patterns and assumed digestion rate constants, remained constant despite variations in VFC. Subsequent studies suggested that cessation of eating occurred at similar rumen dry matter content, irrespective of digestibility or VFC (Campling et al., 1961; Freer & Campling, 1963; Ulyatt et al., 1967). This demonstrated the importance of rumen capacity in regulating VFC but it was only recently shown that the propulsive capacity of the intestines did not limit VFC (Grovum & Phillips, 1978).

Further studies on the role of rumen capacity have involved intraruminal addition or removal of inert materials or digesta, and although these tend to support the concept of physical regulation the results are often inconclusive. Restriction of rumen capacity with water filled balloons has been studied in several experiments with varying responses. Carr & Jacobson (1967) observed a small, non-significant decrease in VFC when balloons containing 10.3 and 17.3 g water.kgW\(^{-1}\) were placed in the rumen of cattle offered chopped lucerne hay over a 5 day period. Grovum (1979) also observed no change in intake when he placed balloons containing 9.75 g water.kgW\(^{-1}\) in the rumen of sheep offered ground and pelleted lucerne hay. However, as intake was measured over a 30 minute period following 339 minutes without food, the results relate to changes in the rate of intake and are not directly applicable to the physical regulation theory. Campling & Balch (1961) observed a linear decrease in VFC when balloons containing approximately 0, 45, 68 and 91 g water.kgW\(^{-1}\) were added to the rumen of cattle offered long hay over a 14 day period. A decrease in VFC of 45gDM.day\(^{-1}\) for every 1kg of water was calculated. Lloyd Davies (1962) observed a 27% reduction in VFC when balloons containing 2 litres of water were placed in the rumen of sheep.
of unknown weight, offered lucerne chaff. This represented a reduction of 125 gDM.day\(^{-1}\) per litre of water.

Studies on the effect of addition or removal of digesta do not provide direct evidence on the role of physical regulation due to the interaction with the release of end products of digestion.

The introduction of indigestible fibres into the rumen of cattle offered chopped lucerne hay (Welch, 1967) caused a marked reduction in VFC proportional to the quantity of fibres introduced, which gradually returned to previous levels as the fibres were passed from the rumen. Weston (1966) observed a marked reduction in VFC when sawdust was introduced into the rumen but only small decreases when finely ground polyvinyl chloride was introduced, suggesting the importance of particle size on VFC.

Although these studies implicate the rumen as the site of VFC regulation the results were equivocal and no attempts were made to examine the mode of action, in particular the effects on rumen fill and the retention time of digesta in the rumen.

2.3.2.1 Rumen fill

The physical capacity of the rumen plays a central role in the physical regulation theory but the exact nature of the limitation has not yet been described. Obviously an upper limit to rumen distension must exist and studies on the potential volume of the rumen \textit{in situ} (Murphy & Reid, 1984) and isolated (Johns \textit{et al}, 1963; Greenhalgh & Moir, 1974) have been conducted. More commonly rumen fill is referred to in terms of dry matter content (Campling \textit{et al}, 1961; Freer & Campling, 1963; Ulyatt \textit{et al}, 1967; Thornton & Minson, 1972) and water or digesta volume (Johns \textit{et al}, 1963; Ulyatt \textit{et al}, 1967).

The comparison of rumen fill in relation to liveweight is also confused. Rumen fill is generally related to bodyweight (Waldo \textit{et al}, 1965; Ingalls \textit{et al}, 1966) but may be related to empty, i.e. digesta free, bodyweight (Johns \textit{et al}, 1963), rumen digesta free bodyweight (Weston, 1984), fat free bodyweight (Egan & Doyle, 1982) or metabolic bodyweight (Robles \textit{et al}, 1981; Egan & Doyle, 1982).

During contractions of the rumen and reticulum the stretch receptors may respond to the consistency of the digesta, and preliminary
studies of this theory has been studied by Hidari (1979, 1981) and Welch (1982). The reticulum may play an important role in determining maximum rumen fill as it has a higher density of stretch receptors than the rumen (Leek & Harding, 1975) and is sensitive to distension (Grovum & Phillips, 1978).

There is some evidence to suggest that the water content of fresh herbage may restrict VFC. When sheep were offered fresh capeweed (Cryptostemma ssp.; Lloyd Davies, 1962) and white clover or ryegrass (Gibb & Treacher, 1983, 1984) organic matter intake increased with increasing dry matter content of the herbage. Adding water to the rumen did not affect VFC (Campling & Balch, 1961; Lloyd Davies, 1962) and it has been suggested that the association of the water with the plant cell contents is analogous to the insertion of water filled balloons into the rumen (Lloyd Davies, 1962).

The exact nature of the component of rumen fill which influences intake has not been identified and is possibly a combination of the quantity and consistency of the digesta present in the rumen. Moreover, there does not appear to be an accepted basis for comparison between animals, further complicating analysis.

2.3.2.2 Rumen retention time

If VFC is limited by the capacity of the rumen then the rate of disappearance, by digestion and passage of digesta from the rumen, and therefore retention time, will play an essential role in determining intake. The VFC of roughages has been shown to be highly correlated to apparent dry matter retention time in the rumen (MRT; Thornton & Minson, 1972, 1973). Rumen retention time is the inverse of fractional disappearance rate (k) and therefore has two components, fractional digestion rate (k_d) and fractional outflow rate (k_p). The results of model simulation (Mertens & Ely, 1979; Poppi et al, 1981c) and in vivo studies (Van Eys & Reid, 1983) suggest that passage rate and potential digestibility are the most important factors affecting VFC. The factors affecting k_d and potential digestibility have already been discussed (see section 2.2) and the factors affecting k_p are discussed below.

2.3.2.2.1 Particle size. The passage of digesta from the rumen is dependent upon the particle size and it is accepted that small particles leave the rumen more readily than large particles (Campling & Freer,
The importance of particle size reduction in the VFC of roughage diets has been demonstrated by the increased VFC following grinding of the diet (Minson, 1963; Campling & Milne, 1972; Greenhalgh & Wainman, 1972; Greenhalgh & Reid, 1974) and this has been associated with a reduced MRT (Blaxter et al., 1956; Campling & Freer, 1966). It is therefore expected that the rate of breakdown of herbage to small particles will play an important role in the regulation of VFC (Mertens & Ely, 1979; Ellis et al., 1979).

Reduction in particle size occurs by mastication during ingestion and rumination, by microbial fermentation in the rumen and physical detrition during rumen contractions. Microbial fermentation and rumen contractions play a minor role in particle size reduction (Murphy & Nicoletti, 1984) although microbial digestion weakens particles such that they are more easily fragmented during rumination (Evans et al., 1974).

The energy required to grind feed through a 1mm screen has been used to predict the VFC of roughages (Laredo & Minson, 1973; Minson & Cowper, 1974) although Ulyatt (1983) observed that feed was chewed until approximately 50% of the ingesta was reduced to a particle size of less than 1mm, irrespective of the amount of chewing required. The rapid initial reduction in particle size during ingestion will also influence \( k_d \) by exposing a larger surface area for microbial digestion (Poppi et al., 1981b; Ulyatt et al., 1982).

Inhibition of rumination activity was shown to decrease VFC (Pearce & Moir, 1964) but the treatment also reduced saliva secretion, which may also have been, at least partly, responsible for the reduction in VFC, due to the association between saliva secretion and the outflow rate of digesta from the rumen (see section 2.3.2.2.3)

The concept of particle size may be an over simplification as the shape of the particles may also affect passage from the rumen (Welch, 1982; Moseley & Jones, 1984).

2.3.2.2.2 Particle density. Ehle (1984) and Ehle et al. (1984) altered the fractional outflow rate of particles by mordanting with different quantities of chromium to obtain a variety of densities. A
quadratic response was observed with FOR increasing up to a particle density of 1.24-1.33, with little change or a decrease in FOR when density was increased further.

Campling & Freer (1962) introduced rubber particles of varying density into the rumen of cattle and observed a decrease in retention time as density increased from 1.02-1.21. There was a tendency for retention time to increase when particles with a density of 1.4 were introduced. They suggested that increased density would lead to a more rapid location of particles in the ventral rumen but that further increases would restrict particle movement between the ventral rumen and the reticulum. Particles with a high density (iron sand) were observed to have difficulty in leaving the reticulum (Reid, 1984) and Magee (1932) observed that dense material, e.g. nails and magnets, often remain on the floor of the rumen. The density of food particles has been observed to fall in the range 1.02-1.06 (Balch & Kelly, 1950) and 0.86-1.21 (Evans et al, 1973) and it is therefore unlikely that high density limits the passage of particles from the rumen. However, Balch & Kelly (1950) suggested that low particle density, caused by the association of gases formed during microbial fermentation, may lead to an increased retention time in the rumen, due to retention in the dorsal sac of the rumen.

2.3.2.2.3 Liquid outflow rate. Particulate matter leaves the rumen suspended in water and it has been suggested that the FOR of water may influence the FOR of particulate matter (Owens & Isaacson, 1977; Faichney et al, 1980). Direct evidence is scarce although it would be expected that the FOR of soluble DM and free floating bacteria would be the same as for water. However, difficulties in measuring the FOR of soluble DM (Dixon & Milligan, 1985) and the proportion of bacteria adherent to particulate matter (Merry & McAllan, 1983) have prevented accurate comparisons. The FOR of microbial N has been shown to be about 33-41% of the FOR of water (Faichney, 1980b; Egan & Doyle, 1985; Dixon & Milligan, 1985), indicating the high proportion of rumen microbes associated with the particulate fraction. The flow of saliva into the rumen appears to be the most important determinant of the FOR of water (Harrison et al, 1976; Thomson et al, 1975; Owens & Isaacson, 1977). Elevation of the FOR of water by inclusion of salivary salts to a ground diet has been shown to increase VFC (Thomson et al, 1978), although Pigott et al (1984) observed no difference in DMI or FOR of water when artificial saliva was infused into the rumen of sheep. Also, when sheep were exposed to low ambient
temperatures (Dixon & Milligan, 1985) water FOR was increased but the FOR of small particles was unchanged.

Saliva flow increases with increasing roughage content of the diet (Cole et al, 1976) and with increasing roughage intake (Doyle et al, 1982) due to the increased time spent eating and ruminating and may therefore be an important factor in the VFC of forages.

2.3.3 The evidence for metabolic regulation

It has long been known that VFC in monogastrics is regulated by the energy requirement of the animal and that glucose exerts the greatest influence on satiety (see Mayer, 1955). However, glucose infusion had no effect on VFC in ruminants (Simkins et al, 1965; Baile & Mayer, 1970). It was suggested by Conrad et al (1964) and Baumgardt (1970) that metabolic regulation of VFC was important when high quality diets were offered and several studies have been conducted on the importance and form of the regulation. The infusion of metabolites into the digestive tract or bloodstream has been important in understanding the subject. Infusion of acetate, particularly intraruminally (Thomas et al, 1961; Baile & Mayer, 1968), and propionate, particularly into the ruminal vein (Baile, 1971), have been shown to cause marked reductions in VFC. However the reduction in VFC only occurred when the concentration of acetate in the rumen or propionate in the bloodstream was raised above normal physiological levels. Anil & Forbes (1977) observed a reduction in VFC when propionate was infused into the hepatic portal vein and the reduction was increased when acetate and butyrate were included. Similarly Adams & Forbes (1981) observed a reduction in VFC when acetate was infused intraruminally and propionate was infused into the hepatic portal vein. When both infusions were concurrent the depression in VFC was additive and related to the level of infusion. Conversely, Bhattacharya & Warner (1968) observed that the addition of propionate to the rumen partly alleviated the depression of intake caused by the addition of acetate.

The post ruminal infusion of protein has been shown to increase VFC (Egan, 1965, 1972) and rumen fill (Egan, 1970). However, this response was limited to diets where protein supply to the small intestine may have been limiting as no increase in VFC occurred when the diet had a high protein content (Egan, 1966; Weston, 1973).

These results suggest that there is no single component responsible for the metabolic regulation of VFC and that the balance of absorbed nutrients may be important, as was suggested by Lepkovsky (1955).
Increases in VFC occur with increasing energy demand, as has been observed with lactation (Hutton, 1963; Hadjpieris & Holmes, 1966; Forbes, 1970; Foot & Russel, 1979; Owen et al., 1980), decreased fat content in the body (Bines et al., 1969; Foot, 1972; Bines & Morant, 1983), growth (see section 2.4) and cold exposure (Chai et al., 1985; Kennedy, 1985). These results suggest that VFC is influenced by the capacity of the animal to utilise nutrients and that metabolic regulation of VFC is a function of nutrient supply and utilisation.

Toutain et al. (1977) observed a 20% reduction in heat production in confined sheep between 1800 and 0900 hours. If this represents a reduced energy requirement it is possible that the importance of metabolic regulation may vary throughout the day and this would be important in the study of short term control of VFC.

2.3.4 The possibility of an interaction between physical and metabolic regulation

Weston (1973) showed that rumen fill could be increased by post ruminal infusion of protein and he suggested that the VFC of the chopped forages was not entirely regulated by rumen fill. Furthermore, Weston (1984) observed that rumen digesta fill was inversely related to VFC and ME intake in lambs offered a range of roughages ad libitum (OM digestibility, 0.517–0.765), suggesting that VFC was controlled by a combination of rumen fill and nutrient supply. Adams & Forbes (1981) observed an additive reduction in VFC when acetate was infused into the rumen and water filled balloons were placed in the rumen and concluded that VFC of the pelleted diet was regulated by a combination of physical and metabolic characteristics. However, caution must be exercised in the extension of data obtained from pelleted diets to herbage diets, due to the marked alteration of the structural characteristics of the diet. The possibility of an interaction between the mechanisms of physical and metabolic regulation was suggested by Jones (1972) and has been incorporated into models on the control of VFC (Forbes, 1980a,b).

Grasses tend to promote a higher rumen fill compared to legumes, despite lower intakes (McLean et al., 1962; 1965; Johns et al., 1963; Ulyatt, 1971; Thornton & Minson, 1972, 1973; Jagusch et al., 1976). The difference observed in the rumen fill of animals grazing, or offered indoors, different species of fresh herbage ad libitum may result from an interaction between different control mechanisms.
2.3.5 Grazing behaviour

The above data were mainly obtained from housed animals offered conserved forages and can only be extrapolated to the grazing animal with extreme caution. Furthermore, aspects of grazing behaviour may have important implications for grazing intake and these are briefly discussed below.

2.3.5.1 Animal characteristics

Hughes & Reid (1951) and Jamieson & Hodgson (1979b) observed that sheep spent more time grazing than cattle but Arnold (1981), summarising a range of data, concluded that there was no difference in the range of grazing time between sheep and cattle.

Hodgson & Jamieson (1981) observed that calves grazed for longer than adult cattle and also concluded that calves were more responsive to changes in sward characteristics. Conversely, Arnold (1981) observed that grazing time of sheep increased until approximately 3 years of age, remaining constant or declining slightly thereafter.

Grazing time of dry sheep was observed to be similar to sheep during late pregnancy but less than sheep during early lactation (Arnold & Dudzinski, 1967; Arnold, 1975). However, rate of intake increased during late pregnancy and early lactation, leading Arnold (1975) to conclude that intake could be increased during pregnancy by increasing rate of intake, but the additional intake during lactation could only be achieved by increasing rate of intake and grazing time. Similarly, thin sheep increased intake, relative to fat sheep, by increasing grazing time and, more markedly, rate of intake (Arnold & Birrell, 1978).

These results suggest that grazing behaviour may be influenced by animal species and physiological state and that changes in intake appear to be effected, primarily, by altering rate of intake.

2.3.5.2 Sward characteristics

Pasture species and sward structure influence grazing behaviour. Lancashire & Keogh (1966) observed that sheep grazed for longer and spent less time ruminating and idling on grass than on legumes. Stobbs (1974) noted that cattle grazed for longer on tropical pastures than on temperate pastures.
Greenhalgh et al (1966) and Gibb & Treacher (1976) observed that intake was curvilinearly related to herbage allowance, a result supported by the data of Jagusch et al (1979) studying the effect of herbage allowance on lamb growth rate.

Decreasing herbage mass is associated with a decrease in intake per bite (IB; Allden & Whittaker, 1970), an increase in the rate of biting (RB) and an increase in grazing time (GT; Arnold, 1975; Jamieson & Hodgson, 1979; Freer, 1981). The increase in RB and GT is seldom sufficient to compensate for the decreased IB (Allden & Whittaker, 1970; Hodgson, 1981). There appears to be an upper limit to GT of 12 -13 hours per day (Allden & Whittaker, 1970; Stobbs, 1970; Jamieson & Hodgson, 1979; Arnold, 1981).

2.3.5.3 Grazing pattern

Animals do not graze continuously throughout the day but display a distinct pattern of grazing intensity. This is characterised by intense periods of grazing following sunrise and preceding sunset, with less intense grazing periods around mid-day and mid-night (Hughes & Reid, 1951; Lancashire & Keogh, 1966; Arnold, 1981). During the middle of the day and at night the major activities tend to be resting and/or ruminating.

Climate influences the grazing pattern, in particular high ambient temperature tends to reduce grazing intensity (Arnold, 1981; Scott & Sutherland, 1981), although compensatory grazing may occur at periods of lower ambient temperature (Payne et al, 1951; Stobbs, 1970). Wind (Scott & Sutherland, 1981) and rain (Arnold, 1981) are less important in influencing the grazing pattern. Social interaction between sheep may lead to a group of sheep displaying a grazing pattern which may differ from other groups grazing similar pasture (Holder, 1962; Scott & Sutherland, 1981).

2.3.6 Conclusion

The regulation of herbage intake in grazing animals is highly complex. The simplest index of potential intake is digestibility, although this is an oversimplification and numerous anomalies are apparent. The physical capacity of the rumen appears to play a major role in the regulation of herbage intake, although the ability of the animal to adjust rumen fill,
particularly in response to changes in energy supply and demand, suggests an interaction between physical and metabolic regulation. The difficulty in accurately measuring intake in the grazing situation has limited the critical examination of grazing animals and research has tended to concentrate on the effects of sward characteristics rather than the capacity for intake when sward limitations are removed.

Despite the large volume of data obtained from housed animals the regulation of herbage intake in grazing animals is poorly understood.
2.4 EFFECT OF AGE ON INTAKE AND DIGESTION

There is a paucity of data relating to nutrient supply in young lambs, particularly when high quality herbages are offered. Extrapolation of data obtained from older lambs and adult sheep may introduce errors of unknown magnitude. Moreover, the interactions between liveweight and age, and between feed quality and age, complicate analysis of comparative data.

The nutrient requirements of young lambs is high, particularly for protein, and if young lambs have the ability to alter intake and/or digestion characteristics this may have important implications for their ability to obtain sufficient nutrients.

This section studies the possible effects of age on intake and digestion, as these will have important implications for nutrient supply in young lambs.

2.4.1 Scaling factors

The effect of age on intake is confounded by changes in liveweight and no satisfactory method has been found to remove this source of variation. Conrad et al (1964) and Penning & Gibb (1979) observed that between animal variation in VFC was minimised when related to liveweight (W) in lactating cattle and lambs, respectively. Similarly, Freer & Dennis (1973) observed a linear relationship between VFC and liveweight in lambs offered lucerne and phalaris from 2 - 12 months of age, although lambs consistently ate 200gDM/day more lucerne than phalaris. Rumen digesta content is linearly related to liveweight in calves and lambs (Kesler et al, 1951; Preston et al, 1957; Wardrop & Coombe, 1961). Therefore, if VFC is restricted by rumen capacity, intake would also be related to liveweight. However, if VFC is restricted by energy demand, e.g. at maturity, some other exponent of liveweight would best describe VFC. It is probable that the exponent of liveweight which best explains VFC varies with age (Freer, 1981), thus complicating comparisons.

2.4.2 Intake

Intake of solid food by suckling lambs starts at 2-3 weeks of age and increases rapidly throughout lactation (Wardrop & Coombe, 1961; Joyce & Rattray, 1970; Geenty & Sykes, 1981). Related to bodyweight VFC was observed to increase until 8 weeks of age and remain constant thereafter.
(Wardrop & Coombe, 1961). Intake increases in response to decreased milk consumption (Spedding et al., 1963; Joyce & Rattray, 1970; Penning & Gibb, 1979) and weaning (Langlands & Donald, 1975; Gibb et al., 1981; Geenty & Sykes, 1981). This is associated with an increase in rumen capacity which reaches a constant proportion of liveweight by 8 weeks of age (Wardrop & Coombe, 1960, 1961). Development of the rumen microflora is rapid; Joyce & Rattray (1970) observed that the ability of rumen microflora to digest herbage in vitro reached adult status by 3 weeks of age.

Allden (1968) observed that intake (DMI.day⁻¹) of a pelleted diet increased until animals were 30–40% of their mature liveweight, after which VFC remained constant or declined slightly. Graham & Searle (1972) observed that the VFC of a pelleted diet (DMI.day⁻¹) increased from weaning until 4 months of age and remained constant until 2 years of age. Related to liveweight or metabolic liveweight VFC declined after 4 months of age. Langlands (1968) and Langlands & Hamilton (1969) observed that the intake of grazing sheep increased until approximately 3 years of age and declined thereafter. Related to liveweight intake decreased between 8 and 32 months of age.

Diet quality may influence intake and young ruminants may be disadvantaged when low quality roughages are offered. Leibholz (1984) observed that the VFC of calves offered lucerne was similar to adult cattle (32 v 30 gDM.kg⁻¹W) but was markedly less when straw was offered (12.7 v 19.3 gDM/kgW⁻¹). Similarly, Egan & Doyle (1982) observed that lambs consumed more chopped subterranean clover hay than adult sheep (34.4 v 26.7 gOM.kg fat free liveweight⁻¹) but similar quantities of chopped ryegrass hay (21.3 v 20.4 gOM.kg fat free liveweight⁻¹). These results suggest that young ruminants are more sensitive to changing feed quality than older ruminants, and that the mechanisms regulating VFC may alter with age.

2.4.3 Digestion

Weston & Margan (1979) studied the effect of age on digestion of dried subterranean clover, with intake held constant at 61–68 gOM/kgW⁻⁰.⁷⁵. No differences were observed between 15 and 24 weeks of age in in vivo OM and NDF digestibility, the proportion of digestible OM and NDF apparently digested in the rumen, NAN flow at the abomasum (related to N intake) or retention time of Cr-EDTA in the rumen. However, at 40 weeks of age in vivo OM and NDF digestibility was significantly reduced,
although the proportion of digestible NDF digested in the rumen increased, and NAN flow past the abomasum increased, relative to N intake. The concentration of ammonia in rumen liquor and ammonia leaving the rumen, related to N intake, were also reduced at 40 weeks of age. Similarly, Egan & Doyle (1982) observed no difference in in vivo OM and NDF digestibility between lambs, aged 19-24 weeks, and adult sheep offered subterranean clover hay, chopped ryegrass (full bloom) or chopped ryegrass-subterranean clover (senescent) hay ad libitum. The OM digestibilities were, respectively, 0.71, 0.59 and 0.45. The retention time of Ru-P in the rumen tended to be shorter for lambs when subterranean clover was offered (13.9 v 17.1 hrs; N.S.) but was longer when ryegrass (22.5 v 18.9 hrs; N.S.) and ryegrass-clover (22.4 v 18.9 hrs; P < 0.05) were offered. These results suggest a feed x age interaction but the exact nature of the changes has not been elucidated.

Increased level of feeding tends to reduce in vivo digestibility (Grovum & Williams, 1977) and the proportion digested in the rumen (Robinson et al 1985). There is indirect evidence to suggest that, when high quality diets are offered at high allowances, this phenomenon may be more pronounced in young ruminants (Jagusch et al 1976; Graham, 1980; Margan et al, 1982).

These results suggest that digestion characteristics may differ between lambs and adult sheep when offered high quality roughages, although this may possibly be a function of increased intake. However, these data obtained from lambs have tended to concentrate on conventionally weaned lambs following complete adaptation to fully functional ruminants. No attempt has been made to study early weaned lambs, particularly during the crucial post-weaning period when the rumen is not fully developed.

2.4.4 Conclusion

The effect of age on intake and digestion is confused by changes in liveweight. Related to liveweight intake increases until 8 - 10 weeks of age, tends to remain constant during growth and decreases as animals approach maturity. Lambs appear to be able to increase VFC, compared to adults, as herbage quality increases. Small changes in digestibility and site of digestion may occur, particularly with respect to nitrogen digestion. There appear to be no data on the effect of early weaning on
the site of digestion but indirect evidence suggests that, where high quality diets are offered, young lambs may exhibit reduced digestion in the rumen, relative to the hindgut.
2.5 TECHNIQUES

The major reason for the paucity of data pertaining to intake and nutrient supply in grazing animals has been the absence of techniques suitable for application in the grazing system. The measurement of herbage intake has long been a perplexing problem, whereas the measurement of nutrient supply is a more recent challenge. Several techniques have been developed for indoor, controlled experiments and their application to grazing studies is often based on assumptions which have not been fully validated under field conditions.

The search for new, improved techniques must recognise the assumptions made in the preliminary development and strive for improved accuracy.

2.5.1 Measurement of herbage intake

The starting point of any nutritional study involves the measurement of intake. In the grazing situation it is not possible to measure the individual animal intake directly, although an estimate of the average intake for a group of animals may be obtained from pre and post grazing herbage mass. This has several disadvantages in that herbage growth rate must be assumed, herbage mass may not be measured accurately and no account is taken of between animal variation in intake.

Individual intakes can be estimated from a knowledge of faecal output and the digestibility of the ingested herbage from the following equation:

\[ I = 0/(1 - D) \quad \text{eqn.2.5.1} \]

where

- I = organic matter intake (g.d\(^{-1}\))
- 0 = faecal organic matter output (g.d\(^{-1}\))
- D = \textit{in vivo} digestibility

2.5.1.1 Estimation of faecal output

Faecal output may be estimated directly by collecting all faeces in bags attached to the animal by a harness (e.g. Sears & Goodall, 1942; Lesperance & Bohman, 1961). This method has several disadvantages in that collection may be incomplete, urine contamination may occur with female animals and animal behaviour and performance may be adversely affected, especially if the quantity of faeces produced is high or the harness badly adjusted or designed (Corbett, 1978).
Indirect estimation of faecal output may be obtained following frequent administration of a known quantity of an external marker. Provided the marker is not absorbed from the gastro-intestinal tract faecal output may be estimated using the following equation:

\[ O = \frac{D}{F} \quad \text{eqn.2.5.2} \]

where

- \( O \) = faecal organic matter output (g.d\(^{-1} \))
- \( D \) = marker dose (quantity.d\(^{-1} \))
- \( F \) = marker concentration in faecal organic matter (quantity.g\(^{-1} \))

Chromium sesquioxide (Cr\(_2\)O\(_3\)) is commonly administered twice daily in a gelatin capsule as an external marker (Corbett \textit{et al}, 1960). Pulse dosing in this manner results in a diurnal fluctuation in marker concentration in faeces, therefore spot samples of faeces may show a considerable bias in marker concentration. This must be corrected by obtaining complete faecal collections and spot samples from a proportion of the animals being dosed. Comparison of marker concentration in spot samples and bulked daily samples allows correction of marker concentration in spot samples. To overcome the problems of pulse dosing it would be more satisfactory to administer markers continuously and this may be done by portable peristaltic pumps (Corbett \textit{et al} 1976a; Evans \textit{et al}, 1981a) or controlled release devices (CRD) inserted into the rumen (Ellis, K.J. \textit{et al}, 1981). The use of portable pumps is expensive and therefore impractical for a large number of animals and the CRD, although an attractive alternative, has not been fully evaluated at present. Continuous marker administration minimises the diurnal pattern of marker concentration in faeces (Corbett & Pickering, 1983), therefore spot sampling may be used to obtain an accurate estimate of faecal output.

2.5.1.2 Estimation of \textit{in vivo} digestibility

The accurate estimation of \textit{in vivo} digestibility is of paramount importance in the calculation of herbage intake. With high quality fresh herbage, where digestibility is generally within the range 0.7-0.8, a small proportional error in measuring digestibility will lead to a greater proportional error in estimated intake. Considerable emphasis has therefore been placed on finding techniques to estimate digestibility as accurately as possible. Emphasis must also be placed upon the importance of estimating digestibility values from ingested herbage as grazing ruminants tend to select a diet of higher digestibility than the herbage
on offer (Hamilton et al, 1973; Hodgson, 1975). This is best accomplished by the use of animals fistulated in the oesophagus (see McManus, 1981). The major approaches to estimating in vivo digestibility are discussed below.

2.5.1.2.1 In vitro digestibility. In vitro digestibility can be estimated by the two-stage technique of Tilley & Terry (1963). This technique has the advantage of being simple, cheap and requiring small quantities of ingesta. However it is dependent upon previously derived relationships between the in vitro procedure and in vivo standards, usually obtained from animals fed at maintenance. It also makes the assumption that there is a unique digestibility for a particular feed. This assumption is false as digestibility varies between animals (Raymond et al, 1953), with level of feed intake (Grovum & Williams, 1977; Margan et al, 1982), physiological state (Weston, 1979; Gonzalez et al, 1985), ambient temperature (Kennedy et al, 1976; Kennedy, 1985) and physical form of the diet (Beever et al, 1972; Greenhalgh & Wainman, 1972).

2.5.1.2.2 Faecal nitrogen. The use of faecal nitrogen concentration is unique in that its validity is based upon endogenous losses from the animal. Initial development of the technique was based upon the linear relationship between organic matter intake and faecal nitrogen output (Gallup & Briggs, 1948; Lancaster, 1949). Thus in vivo digestibility was assumed to be directly related to faecal nitrogen concentration. However the technique has limited value as variations occur due to animal species, physiological state, internal parasitism, level of feeding, plant species, season of growth, variation in nitrogen content of plants at a given digestibility and nitrogen fertilizer application (Corbett, 1978).

2.5.1.2.3 Internal markers. An internal marker is defined as a feed component which is neither digested, absorbed from or excreted into the digestive tract, such that the quantity eaten will equal the quantity excreted in the faeces. Organic matter digestibility can then be calculated from the following equation (Penning & Johnson, 1983a).

\[
\text{OMD} = \frac{A_i}{A_f} \quad \text{eqn. 2.5.3}
\]

where OMD = organic matter digestibility

\[
A_i = \text{concentration of internal marker in feed}
\]

\[
A_f = \text{concentration of internal marker in faeces}
\]
A variety of substances have been suggested as internal markers including lignin, chromogens (plant pigments), silica, n-alkanes, potentially indigestible cellulose (PIC), acid insoluble ash (AlA) and indigestible acid detergent fibre (IADF). Lignin, although often used, does not fulfill the requirements of an internal marker as some digestion occurs in the digestive tract. Silica may be partly absorbed and soil contamination may occur (Kotb & Luckey, 1972). There are reports of faecal chromogen recoveries varying markedly from 100% (e.g. Greenhalgh & Corbett, 1960). Recently, Grace & Body (1981) and Mayes & Lamb (1984) have observed the potential of n-alkanes as internal markers although further study is required on their suitability. Penning & Johnson (1983a) studied PIC and AlA, and Penning & Johnson (1983b) studied IADF. They concluded that AlA could not be recommended as an internal marker and that IADF appeared preferable to PIC. Internal markers have significant potential as they are not dependant upon standard digestibilities and allow comparisons to be made between animals, or groups of animals, grazing the same pasture.

2.5.2 Measurement of digesta flow

The ability to measure nutrient supply in grazing ruminants has been limited by the development of suitable techniques and apparatus. Practical studies were initiated by Phillipson (1948, 1952) who collected all the digesta leaving the abomasum from two T-shaped cannulae inserted in the duodenum. A third cannula, inserted in the distal portion of the duodenum, was used to return digesta following weighing and sampling. Subsequent development of a re-entrant cannula (Hogan & Phillipson, 1960) improved the measurement procedure but doubts remained about the normality of digesta flow during sampling periods. Harris & Phillipson (1962) suggested that samples of digesta obtained prior to the measurement period be used to replace digesta removed during the sampling procedure and that an inert reference marker be introduced to correct flows, which may be reduced during sampling (Topps et al, 1968; MacRae & Armstrong, 1969). The development of automatic sampling devices (Axford et al, 1971; Taylor et al, 1971) facilitated the application of re-entrant cannulae. However queries about the effect of cannulation on the metabolism of experimental animals (MacRae & Wilson, 1977; MacRae et al, 1982) and the high maintenance requirement of cannulated animals (Hogan, 1981) have limited the acceptance of re-entrant cannulation. They are also impractical for grazing studies.
An alternative method of measuring digesta flow involves the use of a single T-shaped cannula from which spot samples of digesta are obtained. Digesta flow is estimated from the dilution of inert reference markers infused continuously into the rumen (Hyden, 1961). This technique was used by Hogan (1964) to study digesta flow in grazing sheep. A soluble marker was injected at 3-hourly intervals into the rumen of grazing sheep, to simulate continuous infusion, and samples of digesta collected from a cannula placed in the duodenum.

The inability to obtain samples of digesta which were representative of the digesta flowing past the cannula led Hogan & Weston (1967) to propose a system incorporating two markers, lignin and Cr-EDTA, to estimate particulate and solute flow, respectively. However the lack of suitable markers limited the application of this technique. The observation of Tan et al (1971) that the phenanthroline complex of ruthenium bound readily to particulate matter led to the development of mathematical techniques to correct for non-representative sampling (Faichney, 1975; 1980a). This improved the accuracy of digesta flow measurements but it was not until portable infusion apparatus was developed (Corbett et al, 1976a; Evans et al, 1981a) that routine measurements could be obtained with grazing animals.

Measurement of digesta flow requires that marker equilibrium is achieved, i.e. marker infused into the rumen = marker leaving the rumen, and this is usually obtained by continuously infusing markers into the rumen for a period of 4 days (Faichney, 1975). Similarly the mathematical interpretation of marker concentration requires that the flow of digesta through the digestive tract should also be in equilibrium (Faichney, 1975), although this problem may be overcome by frequent sampling such that bulked digesta samples are representative of a complete feeding cycle (Faichney, 1980a). Grazing sheep do not exhibit steady-state conditions (Corbett & Pickering, 1983) and representative samples of digesta can only be obtained by frequent sampling or by the development of portable sampling equipment, as has been developed for use with cattle (Evans et al, 1981b).

2.5.3 The use of markers in the study of digesta flow and retention time

Selective retention of solute and particulate digesta phases occurs in parts of the digestive tract, most notably in the rumen, and markers have been advanced to differentiate between these two phases.
2.5.3.1 Solute markers

One of the first solute markers used was polyethylene glycol (PEG; Hyden, 1961). However the flow of PEG may deviate from the flow of water due to adsorption onto particulate marker (Clarke et al, 1972) and exclusion from the water absorbed by the digesta (Czerkawski & Breckenridge, 1969). Teeter & Owens (1983) did not consider these to be serious limitations although they noted that precipitation by tannins could seriously alter the characteristics of PEG.

The ethylene-diamine tetraacetic acid (EDTA) complex of chromium (Cr; Downes & McDonald, 1964) is the most commonly used solute marker. Recently, EDTA complexes of cobalt (Co; Uden et al, 1980), ytterbium (Yb) and iron (Fe; Teeter & Owens, 1983) have been shown to behave in a similar fashion to Cr-EDTA. Intestinal absorption of 1-5% of EDTA complexes occurs (Downes & McDonald, 1964; Weston & Hogan, 1967; Teeter & Owens, 1983) but correction leads to insignificant loss of accuracy (Faichney, 1975). The use of radio-isotopes, e.g. $^{51}$Cr, $^{169}$Yb, facilitates analysis.

2.5.3.2 Particulate markers

A wide range of heavy metals have been shown to bind to particulate matter (Ellis, 1968; Ellis & Huston, 1968; Tan et al, 1971; Hartnell & Satter, 1979; Teeter et al, 1984). Internal markers, such as lignin have also been used (e.g. Hogan & Weston, 1967; Egan & Doyle, 1984). Despite the large number of proposed markers their non-ideal behaviour places restrictions on their accuracy.

Migration is a major problem in the use of digesta markers and precludes the extension of marker retention times to the retention time of particulate matter (Ellis et al, 1979; Dixon & Milligan, 1985), but it does not influence the estimation of digesta flow (Faichney, 1975).

Migration between particles has been observed to occur readily in the rumen with ruthenium phenanthroline (Ru-P; Faichney & Griffiths, 1978; Dixon et al, 1983; Dixon & Milligan, 1985) and Yb (Teeter et al, 1984). Combs et al (1984) observed that Yb and cerium (Ce) migrated readily from marked hay \textit{in vitro} and adhered mainly to bacteria at pH 6.5 or were displaced into solution at pH 2.2. Migration may be minimised by mordanting heavy metals to the feed constituent being studied (Ellis et al, 1979; Uden et al, 1980; Eliman & Ørskov, 1984). However, mordanting increases the density (Ehle, 1984; Ehle et al, 1984) and reduces \textit{in vivo}
digestibility (Van Soest et al., 1983; Eliman & Ørskov, 1984) of treated feed, therefore altering digestion and passage characteristics.

The distribution of particulate markers between particles of different sizes also precludes the extension of marker retention time to the retention time of digesta (Dixon & Milligan, 1985) and may also lead to bias in estimating digesta flow (Egan & Doyle, 1984). The concentration of Ru-P has been observed to increase as particle size decreases (Dixon & Milligan, 1985; Egan & Doyle, 1984), the highest concentration occurring on microbes (Dixon & Milligan, 1985). This was shown to influence estimation of DM flow past the abomasum due to the high proportion of large particles obtained in abomasal samples, relative to large particles passing the abomasum (Egan & Doyle, 1984). Conversely, the concentration of lignin decreased as particle size decreased (Egan & Doyle, 1984). Pienaar et al. (1980) and Redman et al. (1980) also observed discrepancies in the use of Ru-P as a particulate marker when digesta flow was estimated from abomasal digesta. Erroneous estimation of marker concentration in DM may be caused by non-representative sampling of the particles passing the abomasum. More accurate estimates of marker concentration could be obtained by analysing digesta samples from the duodenum or by the discovery of an internal marker which was evenly distributed.

2.5.4 Measurement of the retention time of digesta in the rumen

The effects of retention time in the rumen on intake and digestion have been discussed in section 2.2.2 and 2.3.2.2. However the difficulties involved in direct measurement have led to a paucity of data and hence to incomplete understanding of the controlling factors.

Two direct methods of estimating rumen retention time have been developed and these will be referred to as the serial sampling and rumen fill methods. Furthermore, reference to digesta markers is commonly used to estimate digesta retention time.

It is important in any study of retention time to have an understanding of the definitions of the various terms used. These are described below, prior to a discussion of the techniques employed for the estimation of retention time.
2.4.5.1 Definition of terms

The passage of markers and digesta from the rumen may be described by a number of terms which have biological application and may therefore be readily interchanged. The following definitions and relationships were obtained from Grovum & Phillips (1973) and Faichney (1980b).

1. Retention time (RT; hours): the average residence time in the rumen; the inverse of k.
2. Fractional disappearance rate (k; hour\(^{-1}\)): the proportion of the rumen pool disappearing from the rumen per unit time.
3. Fractional outflow rate (k\(p\); hour\(^{-1}\)): the proportion of the rumen pool leaving via the reticulo-omasal orifice per unit time.
4. Fractional digestion rate (k\(d\); hour\(^{-1}\)): the proportion of the rumen pool removed by digestion per unit time.
5. Half-time (T\(_{1/2}\); hours): the time taken for half of the rumen pool to disappear.

The basic assumption in the measurement of retention time is that disappearance of rumen digesta displays first order kinetics and may, therefore, be described by the following equation:

\[
C_t = C_0 e^{-kt} \quad \text{eqn.2.5.4}
\]

where

- \(C_t\) = rumen digesta content at time \(t\)
- \(C_0\) = rumen content at time 0
- \(t\) = time

From this equation the relationship between \(k\) and \(T_{1/2}\) may be determined, as \(T_{1/2}\) refers to the time when \(C_t:C_0 = 0.5\). Therefore \(0.5 = e^{-kt}\) and \(k = 0.693/T_{1/2}\).

Under steady state conditions, i.e. constant rumen fill, the quantity of food consumed per unit time is equal to the quantity leaving the rumen. Also, the quantity leaving the rumen per unit time can be described by the following equation.

\[
Q = k.C \quad \text{eqn.2.5.5}
\]

where

- \(Q\) = quantity of digesta leaving rumen = intake (g.hr\(^{-1}\))
- \(C\) = rumen content (g)

Therefore, \(k\) can be calculated during steady state conditions or from the rate of disappearance with zero intake.
2.4.5.2 Serial sampling method

Campling et al. (1961) measured the rate of disappearance of digesta during feeding and between meals in cattle fed once daily by manually emptying the rumen before and after feeding. This technique was modified by Reid (1965) who observed that, following an initial lag period, DM disappearance from the rumen of cows fed once daily could be described by equation 2.5.4.

This technique may be applied to grazing sheep by measuring the rate of disappearance of digesta during a period of fasting, either by slaughtering animals, or by manually emptying the rumen through a large cannula, at discrete time intervals. Slaughter of animals leads to inaccuracies due to between animal variation and does not permit repeated measurements on the same animals. Manual rumen emptying may bias results by adversely affecting rumen function (Reid, 1965).

2.5.4.3 Rumen fill method

Minson (1966) described a technique for measuring apparent rumen retention time from a knowledge of intake and rumen digesta content.

\[
RT (h) = \frac{\text{weight of component in the rumen (g)}}{\text{weight of component eaten (g.hr}^{-1})} \quad \text{-- eqn. 2.5.6}
\]

This technique requires steady state conditions in the rumen and therefore continuous feeding is necessary to obtain accurate estimates. It has the advantage of requiring only one emptying per animal thus reducing the labour requirement and avoiding the potential inaccuracies involved with repeated sampling. Ulyatt (1971) used the rumen fill technique to obtain estimates of retention time for grazed herbages but he concluded that, due to the absence of steady state conditions in the rumen, the measurements were only crude estimates of retention time.

2.5.4.4 Marker techniques

Digesta markers are frequently used for comparative studies of digesta retention time. Early studies involved the introduction of stained feed particles into the rumen and analysis of the faecal excretion curve (Balch, 1950; Blaxter et al, 1956; Castle, 1956). Grovum & Williams (1973a,b; 1977) subsequently studied the excretion curves of solute and particulate markers and concluded that fractional outflow rate from the rumen \(k_1\) could be measured from the rate of decline of marker concentration in rumen digesta and in faeces by applying eqn.2.5.4.
Faecal sampling has the advantage of negating any requirement for surgical modification of the gastro-intestinal tract (GIT). However, there are at least three mixing compartments in the GIT, namely the rumen, abomasum and caecum-proximal colon (hereafter referred to as the caecum) and these markedly alter the excretion curve between the rumen and faeces. The descending portion of the rumen and faecal curves have, however, been observed to give similar estimates of $k_1$ (Grovum & Williams, 1973b; Eliman & Ørskov, 1984). Conversely, Mira & MacRae (1982) and Mudgal et al (1982) obtained lower estimates of $k_1$ from the faecal excretion curve, suggesting that the mixing pools distal to the rumen may alter interpretation of the descending portion of the faecal excretion curve.

Compartmental analysis may be used to analyse faecal excretion curves (Faichney & Boston, 1983; Pond et al, 1984; Dhanoa et al, 1985) but these have the disadvantage of requiring complex computation.

The fractional outflow rate of digesta markers from the rumen is useful in comparative studies but, due to the problems mentioned in section 2.5.3, the values cannot be related directly to digesta kinetics.

2.5.5 Conclusion

Recent developments have increased the range and accuracy of measurements in nutritional studies of grazing animals. Reliable estimates of intake can be made following the continuous administration of external markers and advances in the study of internal markers have increased the accuracy of estimating \textit{in vivo} digestibility. The development of portable infusion pumps permits measurement of digesta flow, although the non-ideal behaviour of external markers and the diurnal variation in marker concentration in digesta suggest that extreme caution must be exercised to obtain accurate estimates. These aspects require stringent evaluation to ensure that the resultant data measure what they purport to.

No method exists for the accurate measurement of the retention time of digesta in the rumen of grazing animals, due to the lack of steady-state conditions. This area is critical to understanding the role of the physical regulation theory in the control of herbage intake and the supply of nutrients from ingested herbage.
2.6 GENERAL CONCLUSIONS

The growth of grazing lambs depends upon the digestible nutrients obtained from ingested herbage, the composition of absorbed nutrients, and the level of intake. Therefore, ruminal digestion is of critical importance. Potential digestibility, the rate of digestion of the potentially digestible fraction in the rumen and the rate of passage of digesta from the rumen are the most important components of nutrient digestion and, possibly, intake.

Apparent organic matter digestion is closely related to energy absorption but the apparent digestibility of nitrogen is not an accurate indicator of protein absorption. The rapid degradation of ingested protein to yield ammonia in the rumen may lead to substantial nitrogen losses across the rumen. Amino acid absorption is closely related to protein flow from the rumen and is therefore determined by the microbial protein yield and the quantity of dietary protein passing undegraded from the rumen. Microbial protein yield is related to organic matter digestion in the rumen and the outflow rate of digesta from the rumen and the quantity of undegraded dietary protein is related to protein intake, rate of proteolysis and the outflow rate from the rumen.

The potential for growth in grazing lambs may be limited by energy intake, protein absorption or a combination of both. It is therefore important to study both digestible organic matter intake and the supply of protein to the small intestine in any attempt to analyse the importance of these factors in limiting lamb growth rate.

The concept of physical regulation of intake, where intake is related to the rate of removal of digesta from the rumen, by digestion and passage, has not been examined critically in the grazing animal. It is possible that metabolic regulation is also an important determinant of intake.

The techniques required to study these aspects in grazing animals depend upon indirect measurement of intake, digesta flow and the fractional outflow rate of digesta from the rumen, and place heavy reliance on the use of markers. The validity of using marker techniques in grazing animals has not been fully evaluated. In any study of grazing animals it is important to give full cognisance to the limitations of the techniques employed.
In conclusion, the most important limitations to the growth rate of grazing lambs are likely to be associated with the intake of digestible organic matter and amino acid absorption from the small intestine.
CHAPTER 3

General materials and methods used in experiments

3.1 Introduction

This section describes the general materials and methods, which were of fundamental importance in the studies which are reported in this thesis. Where materials and methods were specific to individual experiments these are described in the relevant section.

3.2 Animals

Nutrient supply was estimated in lambs weaned at 6 weeks of age. The advantage of using young lambs is twofold. Firstly, they have a high growth potential, and therefore high nutrient demand, in particular a high protein requirement. Secondly, rumen development may not be complete in these young lambs, therefore digestion and passage characteristics may be altered with a resultant change in nutrient supply. Study of the regulation of herbage intake was limited in young lambs by the necessity to sacrifice lambs to measure rumen fill. Therefore, older sheep (1-2 years) were used for the majority of this study. These were fitted with a large rumen cannula (ID = 8.5cm) to enable manual rumen emptying.

3.3 Pasture

Two 0.8ha paddocks of Huia white clover (*Trifolium repens*), Rere lucerne (*Medicago sativa*), Ruanui ryegrass (*Lolium perenne*) and Matua prairie grass (*Bromus catharticus*) were maintained as pure species swards. During experimental periods herbage masses of 2000-2500 kgDM.ha\(^{-1}\) (grass) and 2000-3000kgDM.ha\(^{-1}\) (legume) were planned, with herbage in the vegetative state and containing low quantities of dead material. This was achieved by subdividing paddocks into 3 or 4 areas and grazing individual areas to a low residual herbage mass (400-600kgDM.ha\(^{-1}\)) at 1-2 week intervals from 0-6 weeks prior to the start of the experiment. The exact timing of the pre-experimental grazing depended on the time required for regrowth. Visual assessment proved to be the most satisfactory method of ensuring desirable sward characteristics as pasture growth rate varied substantially between pastures and experiments.
3.3.2 Grazing management

During experimental periods pasture was strip grazed on 2 day shifts, unless otherwise stated. Herbage allowance was liberal, in order to maximise intake and growth rate. The data of Gibb & Treacher (1976) and Jagusch et al (1979) suggested that herbage allowances of 6 and 3.5 kgDM.lambd\(^{-1}\), for ryegrass and white clover respectively, were sufficient to allow maximum herbage intakes. Making allowance for the higher content of stem in lucerne, relative to white clover, the following herbage allowances were selected as minima.

- ryegrass, 6kgDM.d\(^{-1}\)
- prairie grass, 6kgDM.d\(^{-1}\)
- white clover, 3.5kgDM.d\(^{-1}\)
- lucerne, 4.5kgDM.d\(^{-1}\)

Fresh water and salt licks were freely available at all times.

3.4 Experimental techniques

The study of grazing animals requires the application of several techniques which differ from indoor studies. The major techniques used in this thesis were for the measurement of digesta flow, faecal output and grazing behaviour.

3.4.1 Digesta flow

Digesta flow was estimated by the double marker technique of Faichney (1975, 1980a). Portable infusion pumps ('Siropump', Everest Electronics, South Australia) were used to continuously infuse, daily, 10μCi \(^{103}\)Ruthenium phenanthroline \((^{103}\text{Ru-P})\) and 50μCi \(^{51}\)Chromium ethylene diamine tetraacetic acid \((^{51}\text{Cr-EDTA})\) in 150ml water, into the rumen. Plastic containers (Vaxipac, 200ml, ICI Tasman) were used as infusate reservoirs.

To minimise surgery, temporary catheters were preferred to rumen cannulae. This was inserted 3-4 days prior to the start of infusion. Four days of continuous infusion were allowed for marker equilibration and samples of duodenal digesta were collected twice daily for the next 4 days, such that 8 samples were obtained at 3h intervals on a theoretical 24h day.
3.4.2 Faecal output

Faecal output was estimated from marker dilution in faeces. The techniques adopted for collection of faeces depended upon the method of marker administration and experimental requirements.

3.4.2.1 \( \text{Cr}_2\text{O}_3 \) dosing. Gelatin capsules containing 1g Cr as \( \text{Cr}_2\text{O}_3 \) were administered orally to intact lambs, twice daily at approximately 08.00 and 16.00h, for 10 days. During the last 5 days samples of faeces (standardised to 10ml in a modified syringe) were obtained, per rectum, at the time of dosing. These were bulked within lambs. To correct for diurnal variation in marker concentration in faeces, total faecal collection was carried out on 4 lambs per treatment and faecal samples were also obtained per rectum, as above. Following experimentation with a variety of techniques for faecal collection pantyhose was used exclusively, being effective, lightweight, cheap and adaptable. The hind legs of lambs were inserted through 2 holes, 5-8cm below the waistband. The waistband then fitted around the pelvic region. One leg of the pantyhose was drawn over the lamb’s back and tied to a girth strap around the thorax. The other leg was cut and tied to collect the faeces. The marker concentration in total faecal collections and in grab samples were compared and marker concentration in grab samples from all lambs on the same treatment corrected for diurnal variation in marker concentration.

3.4.2.2 Continuous infusion. Continuous marker infusion removes the diurnal variation in faecal marker concentration (Corbett et al., 1982). Therefore, the sampling methods are less critical. When radio-isotopes were infused, total faecal collections were carried out and samples taken for analysis. When non-radioactive markers were infused, grab samples were obtained at various times throughout the day and bulked for analysis.

3.4.3 Grazing behaviour.

Automatic grazing recorders were used to record the duration and pattern of grazing behaviour. These are described in appendix 5.
3.5 Analytical techniques

3.5.1 Radio-isotopes
Radioactivity of $^{51}$Cr and $^{103}$Ru-P was measured in an auto gamma scintillation spectrometer (Packard, USA). Dual channels measured both isotopes simultaneously with appropriate crossover corrections. Window settings for each isotope were adjusted such that less than 15% crossover of $^{103}$Ru-P radioactivity was recorded in the $^{51}$Cr channel whilst less than 1% $^{51}$Cr radioactivity was recorded in the $^{103}$Ru-P channel.

3.5.2 Nitrogen
Total N content of all samples was determined in 0.5gDM using a kjeltic digestion system (Tecator, Hoganas, Sweden) with a 19:1 K$_2$SO$_4$:CuSO$_4$ catalyst, and an automated filtration unit (Multi-Dosimat E415, Metrohm, Herison, Switzerland). NH$_3$-N concentration in rumen fluid and digesta was determined using sodium tetraborate to increase the pH, distilling into boric acid and titrating with hydrochloric acid.

3.5.3 Fibre
Ash free neutral detergent fibre (NDF) was analysed as described by Van Soest & Wine (1967). Indigestible acid detergent fibre (IADF) was analysed as described by Penning & Johnson (1983b), using a 7 day incubation with cellulase ('Onozuka' FA, Yakult, Japan).

3.5.4 Ytterbium and Chromium
Yb and Cr were analysed by atomic absorption spectrophotometry (Model 351, Instrument Laboratories, USA). Chromic oxide concentration in faeces was analysed by the technique of Williams et al (1962) and Yb by the technique of Ellis, W.C. et al (1981).
Figure 3.1 Two views of a lamb during a grazing experiment, showing the infusion apparatus, duodenal sampling and faecal collection.
CHAPTER 4

Nutrient supply and lamb growth

Two investigations are reported in this chapter. These relate to intake and nutrient supply in early weaned lambs, in relation to liveweight gain. Section 4.1 describes the effects of cannulation on intake, digestibility and marker retention time in the rumen, in an indoor experiment. Section 4.2 describes the intake and digestion of fresh herbage by grazing lambs and draws conclusions on the major limitations to lamb growth.
4.1 THE EFFECT OF AGE, ABOMASAL CANNULATION AND RUMEN CATHETERISATION ON INTAKE AND DIGESTION BY EARLY WEANED LAMBS

4.1.1 INTRODUCTION

There are few data on which to evaluate the effect of age on intake and digestion in young lambs. Similarly, although MacRae & Wilson (1977) and MacRae et al (1982) have studied adult sheep, the effect of cannulation in early weaned lambs have not been previously evaluated. As a prelude to studies of the intake and digestion of pasture by early weaned lambs it was important to study the effects of age and cannulation on digestion so that, if necessary, these may be allowed for in the design of experiments to measure differences in digestion characteristics of grazed herbage. This experiment examined the intake and digestion of a clover hay through the probable period of rumen development, by lambs weaned at 6 weeks of age.
4.1.2 MATERIALS AND METHODS

4.1.2.1 Animals

Twelve Polled Dorset lambs were obtained from a synchronised lambing. Six lambs were weaned at 38 days of age (average weight, 14.9 kg), at which time they were fitted with a simple T-shaped cannula in the abomasum (hereafter referred to as CAN lambs). A further 6 lambs were weaned at 44 days of age (average weight, 16.2 kg) and remained intact (hereafter referred to as INT lambs). All lambs were placed in individual metabolism crates for the duration of the experiment. A continuous lighting regime was adopted to eliminate possible effects of changing daylength.

4.1.2.2 Diet and feeding

Chaffed clover hay (73% clover; N = 40 g.kg\textsuperscript{DM}\textsuperscript{-1}, NDF = 384 g.kg\textsuperscript{DM}\textsuperscript{-1}) was offered ad libitum, i.e. previous days intake + 25%. Feed was delivered at 2-hourly intervals from an automatic feeder. Fresh water was available at all times.

4.1.2.3 Measurements

Food consumption was recorded daily and liveweight weekly. In vivo digestibility, abomasal flow and marker retention time in the rumen (MRT) were measured as indicated in table 4.1.1.

Abomasal digesta flow was measured by the technique of Faichney (1975, 1980a). Samples of abomasal digesta (approximately 50g) were collected at 8h intervals over the last 4 days of infusion. Of this a 20g sample of whole digesta (WD) was retained. The remainder was strained through pantyhose and a 20g sample of the filtrate (FIL) retained. Samples of WD and FIL were separately bulked during the first and last 2 days of the sampling period for analysis of digesta flow.

Following the cessation of infusion MRT was estimated in CAN lambs from the rate of decline of marker concentration in abomasal digesta and faeces. A single injection of marker solution into the rumen of INT lambs allowed MRT to be estimated from marker disappearance in faeces.

4.1.2.4 Statistical analysis

The data were analysed by analysis of variance and student's t test.
Table 4.1.1. Timetable for measurement of digestibility (DIG) abomasal digesta flow (ABflow) and marker retention time in the rumen (MRT).

<table>
<thead>
<tr>
<th>AGE (weeks)</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
<th>19</th>
<th>20</th>
<th>21</th>
<th>22</th>
<th>23</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIG(^a)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>ABflow(^b)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>MRT(^a)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

\(^a\); measured in all lambs

\(^b\); measured in cannulated lambs only
4.1.3 RESULTS

4.1.3.1 Intake

Dry matter intake (DMI; g.d\(^{-1}\)) increased throughout the experiment. However, as a proportion of liveweight, DMI increased rapidly initially and remained constant, at approximately 36-38gDM.kg\(^{-1}\)W, after about 4 weeks post weaning (figure 4.1.1). There was no difference between CAN and INT lambs in DMI.kg\(^{-1}\)W.

4.1.3.2 Digestibility

Data relating to \textit{in vivo} digestibility are presented in table 4.1.2. The organic matter (OM) and neutral detergent fibre (NDF) digestibility averaged 0.69 over the experiment. There were some individual differences but no trend was apparent and the observed differences probably reflected slight fluctuations in feed quality. Cannulation had no effect on digestibility.

4.1.3.3 Site of OM and NDF digestion

There was a decrease in the proportion of apparently digested OM apparently digested in the rumen (DOMADR) with advancing age (table 4.1.3) and this was particularly pronounced between 12 and 16 weeks of age (0.62 - 0.53; P<0.05). The proportion of digested NDF which was digested in the rumen was similar at 8, 12 and 16 weeks of age (0.93, 0.96 and 0.92, respectively), but was lower at 24 weeks of age (0.86) than at 8 and 12 weeks of age (P<0.05; table 4.1.4).

4.1.3.4 Nitrogen digestion

Nitrogen (N) intake and flow of non-ammonia nitrogen (NAN) at the abomasum are presented in table 4.1.5. The intake of N (g.kg\(^{-1}\)W) was higher at 24 weeks of age (1.39) than at 8, 12 or 16 weeks of age (0.95, 1.11 and 1.11 respectively; P<0.05). Related to N intake, the abomasal flow of N and NAN was higher at 16 weeks of age (1.08 and 1.03 g.g\(^{-1}\) respectively) than at 12 weeks of age 0.84 and 0.80 g.g\(^{-1}\) respectively; P<0.05) and were intermediate at 8 and 24 weeks of age (0.91 and 0.87 g.g\(^{-1}\) respectively for both 8 and 24 weeks of age). On average, 6% of ingested N disappeared prior to the abomasum and 5% of the total N flow past the abomasum was as ammonia-N. Abomasal NAN flow increased with age in relation to liveweight (0.83, 0.88, 1.12 and 1.21 gNAN.kg\(^{-1}\)W at 8, 12, 16 and 24 weeks of age respectively) and OMADR (84.5, 85.0, 107.8 and
124.4 gNAN.kgOMADR\(^{-1}\) at 8, 12, 16 and 24 weeks of age respectively), but remained constant in relation to DOMI (average, 55.1 gNAN.kgDOMI\(^{-1}\)).

4.1.3.5 Marker retention time

The rumen retention times of \(^{103}\)Ru-P and \(^{51}\)Cr-EDTA are presented in table 4.1.6. There was no difference in MRT between CAN and INT lambs, estimated from faeces. Estimated from abomasal digesta MRT was shorter for \(^{103}\)Ru-P at 24 weeks of age (7.7h) than at 8 weeks of age (10.1h, \(P<0.05\)), but there was no difference for \(^{51}\)Cr-EDTA (5.4-7.7h). In CAN lambs MRT was significantly lower when estimated from abomasal digesta than when estimated from faeces (\(P<0.05\)). This observation is discussed in detail in appendix 3.

4.1.3.6 Liveweight gain

Live weight change over the first week was omitted from the analysis due to possible changes in gut contents. The liveweight gain of CAN lambs was lower than INT lambs (109 and 139 g.d\(^{-1}\), respectively; \(P<0.05\)).
Table 4.1.1 The average daily dry matter intake (g/kgW⁻¹) of cannulated and intact lambs from 6 to 24 weeks of age.

LSD = least significant difference
Table 4.1.2. *In vivo* digestibility of organic matter (OMD) and NDF (NDFD) in cannulated (CAN) and intact (INT) lambs.

<table>
<thead>
<tr>
<th>AGE (weeks)</th>
<th>7</th>
<th>9</th>
<th>11</th>
<th>13</th>
<th>15</th>
<th>17</th>
<th>23</th>
</tr>
</thead>
<tbody>
<tr>
<td>OMD</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- CAN</td>
<td>0.71±0.005</td>
<td>0.66±0.008</td>
<td>0.70±0.004</td>
<td>0.69±0.008</td>
<td>0.69±0.003</td>
<td>0.69±0.006</td>
<td>0.68±0.004</td>
</tr>
<tr>
<td>- INT</td>
<td>0.73±0.011</td>
<td>0.67±0.008</td>
<td>0.69±0.004</td>
<td>0.69±0.009</td>
<td>0.70±0.007</td>
<td>0.69±0.006</td>
<td>0.70±0.010</td>
</tr>
<tr>
<td>NDFD</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- CAN</td>
<td>0.70±0.011</td>
<td>0.68±0.009</td>
<td>0.68±0.007</td>
<td>0.66±0.010</td>
<td>0.69±0.004</td>
<td>0.67±0.006</td>
<td>0.70±0.003</td>
</tr>
<tr>
<td>- INT</td>
<td>0.71±0.015</td>
<td>0.69±0.008</td>
<td>0.69±0.009</td>
<td>0.65±0.011</td>
<td>0.71±0.007</td>
<td>0.66±0.008</td>
<td>0.72±0.016</td>
</tr>
</tbody>
</table>

¶ = SEM
Table 4.1.3. The intake and digestion of organic matter (OM) by lambs weaned at 6 weeks of age and offered clover hay *ad libitum*. The proportion of apparently digested OM apparently digested in the rumen (DOMADR) is compared with the value predicted from Ulyatt & Egan (1979).

<table>
<thead>
<tr>
<th>Age (weeks)</th>
<th>8</th>
<th>12</th>
<th>16</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td>OMI</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- g.d⁻¹</td>
<td>343</td>
<td>404</td>
<td>518</td>
<td>815</td>
</tr>
<tr>
<td>- g.kgW⁻¹</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>22.8±1.32ᵃ</td>
<td>24.7±3.60ᵇ</td>
<td>27.2±2.79ᵇ</td>
<td>30.1±1.06ᵇ</td>
</tr>
<tr>
<td>Abomasal OM flow (g.d⁻¹)</td>
<td>195</td>
<td>231</td>
<td>330</td>
<td>546</td>
</tr>
<tr>
<td>Faecal OM output (g.d⁻¹)</td>
<td>102</td>
<td>123</td>
<td>160</td>
<td>241</td>
</tr>
<tr>
<td>DOMI (g.kgW⁻¹)</td>
<td>16.1</td>
<td>17.1</td>
<td>18.8</td>
<td>21.2</td>
</tr>
<tr>
<td>DOMADR (g.g⁻¹)</td>
<td>0.63±0.046ᵃ</td>
<td>0.62±0.018ᵃ</td>
<td>0.53±0.024ᵇ</td>
<td>0.47±0.032ᵇ</td>
</tr>
</tbody>
</table>

DOMADR
Predicted from 0.61
Ulyatt & Egan (1979)

<p>| |</p>
<table>
<thead>
<tr>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>¶ = SEM</td>
</tr>
</tbody>
</table>

*SEM = Standard Error of the Mean"
Table 4.1.4. The intake and digestion of NDF by lambs weaned at 6 weeks of age and offered clover hay *ad libitum*.

<table>
<thead>
<tr>
<th>Age (weeks)</th>
<th>8</th>
<th>12</th>
<th>16</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDFI (g.d⁻¹)</td>
<td>139</td>
<td>172</td>
<td>246</td>
<td>369</td>
</tr>
<tr>
<td>Abomasal flow (g.d⁻¹)</td>
<td>48</td>
<td>60</td>
<td>83</td>
<td>141</td>
</tr>
<tr>
<td>Faecal output (g.d⁻¹)</td>
<td>44</td>
<td>55</td>
<td>68</td>
<td>104</td>
</tr>
<tr>
<td>Proportion of <em>in vivo</em> NDF digestion occurring in the rumen</td>
<td>0.93±0.022&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.96±0.024&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.92±0.024&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.86±0.020&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Table 4.1.5. Nitrogen intake (NI), abomasal non-ammonia nitrogen flow (NAN\textsubscript{A}) and the proportion of NI passing the abomasum as NAN\textsubscript{A} and total N (N\textsubscript{A}).

<table>
<thead>
<tr>
<th>Age (weeks)</th>
<th>8</th>
<th>12</th>
<th>16</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td>NI - g.d\textsuperscript{-1}</td>
<td>14.2</td>
<td>18.2</td>
<td>21.0</td>
<td>37.6</td>
</tr>
<tr>
<td>- g.kg\textsuperscript{-1}</td>
<td>0.95±0.055\textsuperscript{a}</td>
<td>1.11±0.114\textsuperscript{a}</td>
<td>1.11±0.113\textsuperscript{a}</td>
<td>1.39±0.059\textsuperscript{b}</td>
</tr>
<tr>
<td>NAN\textsubscript{A} (g.d\textsuperscript{-1})</td>
<td>12.5</td>
<td>14.6</td>
<td>21.5</td>
<td>32.6</td>
</tr>
<tr>
<td>NAN\textsubscript{A} (g.kg\textsuperscript{-1})</td>
<td>0.83±0.107\textsuperscript{a}</td>
<td>0.88±0.094\textsuperscript{a}</td>
<td>1.12±0.084\textsuperscript{b}</td>
<td>1.21±0.092\textsuperscript{b}</td>
</tr>
<tr>
<td>NAN\textsubscript{A} (g.kgDOMI\textsuperscript{-1})</td>
<td>51.2±3.7</td>
<td>52.1±2.2</td>
<td>60.1±2.9</td>
<td>57.2±4.8</td>
</tr>
<tr>
<td>NAN\textsubscript{A} (g.kgOMADR\textsuperscript{-1})</td>
<td>84.5±7.98\textsuperscript{ab}</td>
<td>85.0±5.72\textsuperscript{a}</td>
<td>107.8±7.44\textsuperscript{bc}</td>
<td>124.4±5.00\textsuperscript{c}</td>
</tr>
<tr>
<td>NAN\textsubscript{A} :NI</td>
<td>0.87±0.078</td>
<td>0.80±0.072</td>
<td>1.03±0.055</td>
<td>0.87±0.056</td>
</tr>
<tr>
<td>N\textsubscript{A} :NI</td>
<td>0.91±0.076</td>
<td>0.84±0.076</td>
<td>1.08±0.053</td>
<td>0.91±0.059</td>
</tr>
</tbody>
</table>

Predicted from Ulyatt & Egan (1979)

| NAN\textsubscript{A} (g.d\textsuperscript{-1}) | 15.7 | 19.2 | 21.6 | 36.1 |

\( \dagger = \text{SEM} \)
Table 4.1.6. The retention time (h) of digesta markers ($^{103}$Ru-P and $^{51}$Cr-EDTA) in the rumen of cannulated (CAN) and intact (INT) lambs, estimated from marker disappearance in abomasal digesta and faeces.

<table>
<thead>
<tr>
<th>Age (weeks)</th>
<th>8</th>
<th>12</th>
<th>16</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abomasal digesta</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$^{103}$Ru-P</td>
<td>10.1±0.8</td>
<td>7.9±1.3</td>
<td>9.0±0.5</td>
<td>7.7±0.8</td>
</tr>
<tr>
<td>$^{51}$Cr-EDTA</td>
<td>5.6±0.6</td>
<td>6.9±1.2</td>
<td>7.1±0.7</td>
<td>5.4±0.6</td>
</tr>
<tr>
<td>Faeces</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$^{103}$Ru-P</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-INT</td>
<td>16.4±1.99</td>
<td>10.9±0.77</td>
<td>11.7±0.66</td>
<td>11.1±0.50</td>
</tr>
<tr>
<td>-CAN</td>
<td>12.3±1.36</td>
<td>11.0±1.13</td>
<td>13.1±0.89</td>
<td>10.0±0.59</td>
</tr>
<tr>
<td>$^{51}$Cr-EDTA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-INT</td>
<td>11.4±1.26</td>
<td>8.9±0.54</td>
<td>8.8±0.82</td>
<td>7.8±0.55</td>
</tr>
<tr>
<td>-CAN</td>
<td>9.2±1.23</td>
<td>9.5±1.25</td>
<td>10.2±0.50</td>
<td>8.5±0.20</td>
</tr>
</tbody>
</table>

\* = SEM
Abomasal cannulation had no affect on DMI (g.kg\(^{-1}\)) and marker retention time in the rumen, estimated from faecal excretion curves. These findings in young lambs are in agreement with previous studies on the effects of cannulation on adult sheep (MacRae & Wilson, 1977; MacRae et al., 1982). Insertion of a temporary rumen catheter was observed to decrease DMI on the day of insertion but intake returned to normal within 1-2 days. The lower LWG of CAN lambs may reflect a higher ME requirement for maintenance. However, the different weaning age of CAN and INT lambs may have been of importance. Whereas INT lambs would be expected to grow at approximately 250 g.d\(^{-1}\) during the week preceding weaning the CAN lambs, which were weaned earlier, to allow sufficient time for post-operative recovery, suffered a check in LWG. Related to average liveweight during the experiment LWG (5.5 and 6.0 g.kg\(^{\text{LWG}}\)\(^{-1}\) for CAN and INT lambs, respectively) and DOMI (19.6 and 19.7 g.kg\(^{\text{DOMI}}\)\(^{-1}\)) were not significantly different. Also, when related to DOMI, LWG was similar for both groups (0.28 and 0.30 g.lWG.gDOMI\(^{-1}\) for CAN and INT lambs respectively). Therefore, there appeared to be no change in the gross efficiency of energy utilisation.

The hay was of lower quality than expected, given the high clover content (OM digestibility, 0.69). This was unfortunate, as the effects of age on intake and digestion appear to be more pronounced with high quality diets (see section 2.4) and fresh herbage tends to be of considerably higher quality.

Intake increased rapidly during the first 4 weeks post-weaning and remained constant, relative to liveweight thereafter. This pattern was similar to the pattern observed by Wardrop & Coombe (1961) who offered lucerne hay to lambs weaned at 6 weeks of age.

The site of OM and NDF digestion tended to change towards increased hindgut fermentation, most noticeably between 12 and 16 weeks of age. These changes suggested that a reduction in rumen retention time occurred, but this was not reflected in the marker retention times. This may, at least partly, have been due to daily fluctuations in DMI and the inherent inaccuracies involved in using markers to estimate retention time of digesta in the rumen. The daily fluctuations in DMI may have resulted in changes in retention time between the measurement of digesta flow and retention time.
Between the measurement periods OM intake increased (23, 25, 27 and 30g.kgW\(^{-1}\) at 8, 12, 16 and 24 weeks of age respectively, table 4.1.3). No explanation can be suggested for this increase but it may have been partly responsible for the changes in site of OM and NDF digestion. The proportion of DOMI which was apparently digested in the rumen (DOMADR) was significantly related to DOMI (g.kgW\(^{-1}\); P<0.01) by eqn. 4.1.1, which accounted for 65.5% of the variation in DOMADR.

\[\text{DOMADR} = 0.845 - 0.016\text{DOMI} \quad \text{eqn. 4.1.1}\]

This suggested that the change in site of digestion was influenced by the level of intake and may not reflect an age effect per se.

There appear to be no data on site of digestion in lambs younger than 15 weeks of age with which to compare this observation. In the study of Weston & Margan (1979), where intake of dried subterranean clover was held constant at 61-68 gOM/kgW\(^{0.75}\), the proportion of DOMADR was similar at 15, 24 and 40 weeks of age (0.61 - 0.63) despite a reduction in \textit{in vivo} OM digestibility at 40 weeks of age. The proportion of digestible CWC digested in the rumen was 0.85, 0.84 and 0.90 at 15, 24 and 40 weeks of age respectively, similar to those observed at 16 and 24 weeks of age in the present experiment.

The DOMADR observed in the present experiment was lower at 16 and 24 weeks of age than has generally been observed. However, similar values of 0.51 and 0.50 have been recorded by Margan \textit{et al} (1982) in lambs consuming a ground and pelleted diet at 74 and 75 gOM.kgW\(^{0.75}\)d\(^{-1}\), respectively, 0.50 by Gonzalez \textit{et al} (1985) in pregnant sheep consuming a hay + concentrate diet and 0.45-0.58 (average 0.53) by Beever \textit{et al} (1986b) in cattle consuming 17-25 gDM.kgWd\(^{-1}\) of fresh white clover indoors.

Abomasal NAN flow (gNAN.kgWd\(^{-1}\)) was higher at 16 and 24 weeks of age than at 8 and 12 weeks of age. There was no difference in abomasal NAN flow, related to DOMI, but flow increased with age, in relation to OMADR. Comparison of NAN flows with those predicted from Ulyatt & Egan (1979) for dried herbage diets did not give good agreement. Predicted and actual flows were similar at 16 weeks of age but the former were 25, 32 and 11% higher at 8, 12 and 24 weeks of age. This may reflect differences in intake as the predictive equation relies upon nitrogen intake and
takes no account of OM digestion in the rumen, which would affect microbial protein synthesis and, therefore, protein supply to the small intestine. The vast majority of data analysed by Ulyatt & Egan (1979) were obtained from older sheep and may not be applicable to young lambs without modifications to the predictive equations. However, there are insufficient data which relate to digestion by young lambs to allow this modification.

If one assumes that half of the abomasal NAN was of microbial origin (from the data of Walker et al, 1975, for clover, lucerne and wheaten hays), that amino acid N (aaN) comprises 0.81 of microbial NAN (ARC, 1980), that absorption and utilisation of amino acid N were 0.7 and 0.75 respectively (ARC, 1980), that maintenance N requirement was 0.2 gN/kgW0.75 (Black et al, 1973) and that DOMI contains 15.83 MJME.kg⁻¹ (Beever et al, 1986a) it can be calculated that N retention per MJME intake ranged from 1.44-1.69. These values are more than sufficient to maintain LWG at 350 g.d⁻¹ (Ørskov, 1977), provided that energy intake was high enough. The average ME intake of 0.35 MJ.kgW⁻¹ is close to the requirement given in ARC (1980) for lambs growing at 200 g.d⁻¹ (0.38 and 0.35 MJ.kgW⁻¹ for lambs weighing 20 and 30 kg, respectively). Therefore, it appears that the efficiency of utilisation of ME and amino acid N were lower than usually observed but, as mentioned in section 2.1, this is often the case in forage fed animals.

In conclusion, cannulation appeared to have no affect on intake, digestibility or marker retention time in the rumen. However, problems in comparison may arise from the different weaning age of CAN and INT lambs, which was adopted in this experiment to allow for recovery after cannulation. Intake (g.kg⁻¹) increased rapidly until approximately 10 weeks of age and remained constant thereafter. However, there was a continual increase in intake by CAN lambs between periods of digesta flow measurement, which could not be explained. Therefore, it was not possible to conclude whether the change in the site of digestion of OM and NDF and increased NAN flow past the abomasum were caused by increasing age or by increasing intake. The supply of energy and protein appeared adequate to maintain considerably higher growth rates than were achieved and this suggested inefficient utilisation of absorbed nutrients.
4.2 THE INTAKE AND DIGESTION OF GRAZED HERBAGE BY EARLY WEANED LAMBS

4.2.1 INTRODUCTION

The high growth potential and, therefore, high nutrient requirement of young lambs make them sensitive to diet quality and nutrient supply. The growth rate of grazing lambs is dependent upon herbage intake, the nutrients absorbed during digestion and the efficiency of utilisation of absorbed nutrients. However, the majority of studies on the digestion of fresh herbage have used housed animals (MacRae & Ulyatt, 1974; Ulyatt & MacRae, 1974; Ulyatt & Egan, 1979, Beever et al, 1986b), due to the problems associated with grazing studies. Recently, grazing studies involving sheep (Corbett et al, 1982; Corbett & Pickering, 1983) and cattle (Beever et al, 1986a) have been conducted, but young, rapidly growing lambs do not appear to have been examined.

This section studies the intake, nutrient supply and growth rate of early weaned lambs grazing 4 pasture species at high allowances.
4.2.2 MATERIALS AND METHODS

4.2.2.1 Animals

Ninety four South Suffolk x Coopworth ram lambs were weaned at 6 weeks of age. Twenty four lambs were fitted with a T-shaped cannula in the duodenum (CAN lambs) and 6 lambs with an oesophageal fistula (OF lambs) 4-7 days before weaning. Lambs were removed from their dam for 4-6 hours before surgery, following which they were promptly returned and continued to suckle vigorously. This removed the potential trauma associated with simultaneous surgery and weaning, and also permitted, subsequently, simultaneous weaning of CAN and intact lambs.

Sixteen intact lambs (INT lambs) and 6 CAN lambs grazed each pasture. The 6 OF lambs were rotated around pastures as required.

4.2.2.2 Pasture

Pure species swards of lucerne (L), white clover (C), ryegrass (R) and prairie grass (P) were strip-grazed on 2 day shifts for the 6 weeks of the experiment. When lambs were 8 and 12 weeks old the herbage mass (kgDM.ha\(^{-1}\)) was, respectively, 2790 and 3230, L; 2460 and 2020, C; 1900 and 1740, R, and 1660 and 1965, P. Actual DM allowances (kgDM.lamb\(^{-1}\)) were, at 8 and 12 weeks of age respectively, 5.4 and 5.1, L; 4.1 and 4.7, C; 6.8 and 6.1, R, and 6.2 and 6.0, P.

4.2.2.3 Measurements

4.2.2.3.1 Timing. The experiment was carried out between 29:9:83 and 25:11:83. The difficulties involved in simultaneously sampling lambs on all 4 pasture species was overcome by staggering the weaning dates such that the study of lambs grazing L and P commenced 14 days before C and R. This was facilitated by colour coding lambs at birth, so they could be easily and accurately aged without handling. This also aided removal of ewes and lambs when surgery was to be performed. The surgery, weaning and sampling dates are given in table 4.2.1.

4.2.2.3.2 Intake. Intake was estimated by the techniques described in section 2.5 when lambs were 8 and 12 weeks old. Faecal output was estimated by reference to Cr\(_2\)O\(_3\) dilution in INT lambs and \(^{103}\)Ru-P dilution in CAN lambs. In vivo digestibility was estimated by reference to IADF.
4.2.2.3.3 Digesta flow. Duodenal digesta flow was estimated in CAN lambs at 8 and 12 weeks of age by the technique described by Faichney (1975, 1980a). Samples of duodenal digesta were obtained over the last 4 days, according to the schedule given in table 4.2.2. Approximately 100g of digesta were obtained at each sampling, from which 30g of whole digesta and 30g of filtrate (strained through pantyhose), were retained. Digesta was bulked for the first and last 2 day period and frozen at -20°C until analysis.

4.2.2.3.4 Rumen ammonia concentration. At 8 and 12 weeks of age, 8 INT lambs from each pasture species were slaughtered at various times throughout the day, as detailed in section 4.2. Samples of mixed rumen liquor were removed for analysis of ammonia concentration.

4.2.2.3.5 Fractional outflow rate of markers from the rumen. The fractional outflow rate from the rumen of the digesta markers was estimated in CAN lambs, following the cessation of continuous infusion, from the rate of decline of marker concentration in duodenal digesta and faeces. A single pulse of marker infusate (equivalent to 40% of the daily infusion rate) was introduced into the rumen of 4 INT lambs on each pasture species and the fractional outflow rate from the rumen was estimated from the rate of decline of marker concentration in faeces.

4.2.2.3.6 Live weight gain. Lambs were weighed once weekly and prior to slaughter. Live weight gain (LWG) was estimated by regressing liveweight (kg) against time (days).
Table 4.2.1. Dates of surgery, weaning and measurements, at 8 (T1) and 12 (T2) weeks of age, for lambs grazing prairie grass and lucerne (P + L), and ryegrass and white clover (R + C).

<table>
<thead>
<tr>
<th></th>
<th>P + L</th>
<th>R + C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surgery</td>
<td>21 and 23:9:83</td>
<td>6 and 7:10:83</td>
</tr>
<tr>
<td>Measurements</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(T1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marker retention time</td>
<td>15-17:10:83</td>
<td>28-30:10:83</td>
</tr>
<tr>
<td>Rumen fill</td>
<td>14:10:83</td>
<td>29:10:83</td>
</tr>
<tr>
<td>(T2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digesta flow</td>
<td>8-12:11:83</td>
<td>22-26:11:83</td>
</tr>
<tr>
<td>Intake</td>
<td>8-11:11:83</td>
<td>21-24:11:83</td>
</tr>
<tr>
<td>Marker retention time</td>
<td>11-13:11:83</td>
<td>24-26:11:83</td>
</tr>
<tr>
<td>Rumen fill</td>
<td>10:11:83</td>
<td>25:11:83</td>
</tr>
</tbody>
</table>
Table 4.2.2. Sampling times for estimation of duodenal digesta flow, corrected to New Zealand standard time. Prairie grass (P), ryegrass (R), white clover (C) and lucerne (L), measured at 8 (1) and 12 (2) weeks of age.

<table>
<thead>
<tr>
<th></th>
<th>P1, C1, R2, L2</th>
<th>P2, C2, R1, L1</th>
</tr>
</thead>
<tbody>
<tr>
<td>day 1</td>
<td>14.00</td>
<td>20.00</td>
</tr>
<tr>
<td>day 2</td>
<td>05.00, 17.00</td>
<td>11.00, 23.00</td>
</tr>
<tr>
<td>day 3</td>
<td>02.00, 23.00</td>
<td>08.00, 17.00</td>
</tr>
<tr>
<td>day 4</td>
<td>11.00, 20.00</td>
<td>02.00, 14.00</td>
</tr>
<tr>
<td>day 5</td>
<td>08.00</td>
<td>05.00</td>
</tr>
</tbody>
</table>
4.2.3 RESULTS

4.2.3.1 Composition of OF extrusa

The composition of OF extrusa and OM and NDF digestibility are given in table 4.2.3. The composition and digestibility of L and C remained constant at 8 and 12 weeks of age (average NDF, 191 g.kgDM\(^{-1}\); average OMD, 0.84), apart from L NDF digestibility (0.80 and 0.72 at 8 and 12 weeks of age). Grasses tended to increase in NDF content (P, 361 and 469; R, 312 and 375 k.kgDM\(^{-1}\) at 8 and 12 weeks of age respectively) and decrease in N content (P, 33 and 28; R, 45 and 36 g.kgDM\(^{-1}\) at 8 and 12 weeks of age respectively). Digestibility was similar at 8 and 12 weeks of age for R (OMD, 0.80; NDFD, 0.81), but was higher at 8 weeks of age than at 12 weeks of age for P (OMD, 0.84 and 0.80; NDFD, 0.86 and 0.80, respectively).

4.2.3.2 Liveweight gain

Liveweight gain of INT lambs was 230±8, 227±9, 308±25 and 321±18 g.d\(^{-1}\) for P, R, L and C respectively (table 4.2.4). Liveweight gain was significantly lower for CAN lambs (33%; P<0.05) on all pasture species. However, LWG per kg DOMI was similar within each pasture species.

4.2.3.3 Intake and digestibility

There appeared to be significant diurnal variation in faecal Cr\(_2\)O\(_3\) concentration, as reflected by the differences between spot and bulked samples. Bulked samples had higher Cr concentration than spot samples for all pasture species (13, 17, 27 and 44% for P, R, C and L respectively).

With the exception of P, intake (g.kgW\(^{-1}\)) was similar at 8 and 12 weeks of age and, therefore, results were grouped within pasture species. The OM intake and OM digestibility of CAN and INT lambs are given in table 4.2.4. There was no difference in OM digestibility between CAN and INT lambs. However, OMI (g.kgW\(^{-1}\)) was consistently lower for CAN lambs (16, 18, 26 and 27% for P, R, L and C respectively; P<0.05). For both CAN and INT lambs OMI was higher on legumes (29 and 46% for CAN and INT respectively; P<0.05), although no difference was observed between P and R, or between L and C.
4.2.3.4 Sites of nutrient digestion

The proportion of apparently digested organic matter (DOMI) apparently digested in the rumen (DOMADR) was similar for all pasture species (0.52-0.58; P>0.1; table 4.2.5). A higher proportion of digested NDF was digested in the rumen of lambs grazing grasses than for lambs grazing legumes (0.88, 0.87, 0.78 and 0.73 for P, R, L and C respectively; table 4.2.6).

Nitrogen intake was significantly different for all pasture species (P<R<C<L; P<0.05; table 4.2.7), caused by differences in intake and herbage N content. However, duodenal NAN flow was similar for P and R, and for L and C, due to variable N losses across the rumen. Duodenal NAN flow was higher in lambs grazing legumes (1.24 and 1.20gNAN.kgWd\(^{-1}\) for L and C respectively) than in lambs grazing grasses (0.87 and 0.96gNAN.kgWd\(^{-1}\) for P and R respectively). Related to DOMI, duodenal NAN flow tended to be higher for legumes than for grasses (average, 45 and 41 gNAN.kgDOMI\(^{-1}\) for legumes and grasses respectively; N.S.). Related to the quantity of organic matter apparently digested in the rumen (OMADR), there was no difference between pasture species (average, 80 gNAN.kgOMADR\(^{-1}\)).

4.2.3.5 Rumen ammonia concentration

The concentration of ammonia is shown in table 4.2.8. There was, in general, an increase in concentration throughout the day, which resulted in the concentration in the afternoon being, on average, 60% higher than in the morning. Legumes tended to promote higher concentrations than grasses, although R (8 weeks of age) displayed a similar average concentration to L (8 weeks of age) and C (12 weeks of age).

4.2.3.6 Marker outflow rate

The fractional outflow rate (FOR) of digesta markers, estimated from duodenal digesta and faeces, is shown in table 4.2.9. The concentration of \(^{51}\text{Cr-EDTA}\) in duodenal digesta declined rapidly, with the result that insufficient samples were obtained from several lambs, particularly on C. Estimated from duodenal digesta, lambs grazing legumes tended to display higher FOR of \(^{103}\text{Ru-P}\) than lambs grazing grasses (0.120, 0.109, 0.068 and 0.092 for L, C, R and P respectively), although the difference between P and C was not significant (P>0.05). There was no significant difference between plant species in the FOR of \(^{51}\text{Cr-EDTA}\),
although L displayed a higher value (0.177) than P and R (0.142 and 0.123 respectively). However, the missing values may have influenced this result. Estimated from faeces, the trends remained similar, although the level of significance altered. There was no difference between CAN and INT lambs in the FOR of $^{103}$Ru-P (0.084 and 0.091 for CAN and INT respectively) and $^{51}$Cr-EDTA (0.116 and 0.119 for CAN and INT respectively).
Table 4.2.3. The organic matter (OM), NDF and nitrogen (N) content of oesophageal extrusa (g.kgDM\(^{-1}\)) and the digestibility of organic matter (OMD) and NDF (NDFD) by lambs aged 8 (T1) and 12 (T2) weeks of age.

<table>
<thead>
<tr>
<th></th>
<th>OM</th>
<th>NDF</th>
<th>N</th>
<th>OMD</th>
<th>NDFD</th>
</tr>
</thead>
<tbody>
<tr>
<td>P T1</td>
<td>858</td>
<td>361</td>
<td>33</td>
<td>0.84±0.003(^{¶})</td>
<td>0.86±0.005</td>
</tr>
<tr>
<td>T2</td>
<td>848</td>
<td>496</td>
<td>28</td>
<td>0.80±0.010</td>
<td>0.80±0.006</td>
</tr>
<tr>
<td>R T1</td>
<td>842</td>
<td>312</td>
<td>45</td>
<td>0.80±0.007</td>
<td>0.81±0.008</td>
</tr>
<tr>
<td>T2</td>
<td>866</td>
<td>375</td>
<td>36</td>
<td>0.80±0.006</td>
<td>0.81±0.006</td>
</tr>
<tr>
<td>C T1</td>
<td>871</td>
<td>187</td>
<td>49</td>
<td>0.84±0.003</td>
<td>0.73±0.011</td>
</tr>
<tr>
<td>T2</td>
<td>865</td>
<td>200</td>
<td>44</td>
<td>0.82±0.005</td>
<td>0.72±0.011</td>
</tr>
<tr>
<td>L T1</td>
<td>854</td>
<td>198</td>
<td>49</td>
<td>0.86±0.003</td>
<td>0.80±0.003</td>
</tr>
<tr>
<td>T2</td>
<td>864</td>
<td>180</td>
<td>52</td>
<td>0.83±0.005</td>
<td>0.72±0.006</td>
</tr>
</tbody>
</table>

¶ = SEM
Table 4.2.4. Liveweight gain (LWG, g.d\(^{-1}\)), organic matter intake (OMI, g.kg\(W^{-1}\)), OM digestibility (OMD) and LWG per kg digestible OMI (DOMI) of cannulated (CAN) and intact (INT) lambs grazing prairie grass (P), ryegrass (R), white clover (C) and lucerne (L).

<table>
<thead>
<tr>
<th></th>
<th>LWG</th>
<th>OMI</th>
<th>OMD</th>
<th>LWG/DOMI</th>
</tr>
</thead>
<tbody>
<tr>
<td>P CAN</td>
<td>156±18.4†</td>
<td>25.1±1.61</td>
<td>0.81±0.012</td>
<td>396±47.3</td>
</tr>
<tr>
<td>INT</td>
<td>230±8.1</td>
<td>30.0±1.44</td>
<td>0.80±0.014</td>
<td>425±16.3</td>
</tr>
<tr>
<td>R CAN</td>
<td>153±20.0</td>
<td>28.8±1.82</td>
<td>0.81±0.006</td>
<td>335±26.9</td>
</tr>
<tr>
<td>INT</td>
<td>227±8.8</td>
<td>35.3±1.82</td>
<td>0.80±0.006</td>
<td>351±13.5</td>
</tr>
<tr>
<td>C CAN</td>
<td>202±21.4</td>
<td>33.4±1.11</td>
<td>0.84±0.004</td>
<td>316±20.2</td>
</tr>
<tr>
<td>INT</td>
<td>321±18.3</td>
<td>46.0±2.99</td>
<td>0.83±0.005</td>
<td>341±30.7</td>
</tr>
<tr>
<td>L CAN</td>
<td>211±10.5</td>
<td>36.5±1.74</td>
<td>0.85±0.007</td>
<td>320±12.6</td>
</tr>
<tr>
<td>INT</td>
<td>308±24.8</td>
<td>49.2±1.86</td>
<td>0.84±0.005</td>
<td>297±13.3</td>
</tr>
</tbody>
</table>

† = SEM
Table 4.2.5. Site of organic matter (OM) digestion. Organic matter intake (OMI), digestible OM (DOMI), duodenal OM flow (DFOM), faecal OM output (OMO) (all units g.kg\(^{-1}\)) and site of DOM digestion in lambs grazing prairie grass (P), rye grass (R), white clover (C) and lucerne (L).

<table>
<thead>
<tr>
<th></th>
<th>P</th>
<th>R</th>
<th>C</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>OMI</td>
<td>25.1±1.61a</td>
<td>28.8±1.82a</td>
<td>33.4±1.11b</td>
<td>36.5±1.74b</td>
</tr>
<tr>
<td>DFOM</td>
<td>14.4±0.91a</td>
<td>15.2±1.03ab</td>
<td>17.4±1.74ab</td>
<td>18.6±0.92b</td>
</tr>
<tr>
<td>OMO</td>
<td>4.8±0.39</td>
<td>5.3±0.37</td>
<td>5.5±0.56</td>
<td>5.3±0.28</td>
</tr>
<tr>
<td>DOMI</td>
<td>20.4±1.41a</td>
<td>23.1±1.3a</td>
<td>27.9±1.1b</td>
<td>31.2±1.6b</td>
</tr>
</tbody>
</table>

Proportion of DOM apparently digested in:-

<table>
<thead>
<tr>
<th></th>
<th>rumen</th>
<th>post ruminal</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td>0.52±0.025</td>
<td>0.48</td>
</tr>
<tr>
<td>R</td>
<td>0.58±0.030</td>
<td>0.42</td>
</tr>
<tr>
<td>C</td>
<td>0.58±0.024</td>
<td>0.42</td>
</tr>
<tr>
<td>L</td>
<td>0.57±0.033</td>
<td>0.43</td>
</tr>
</tbody>
</table>

\(\dagger\) = SEM
Table 4.2.6. Site of NDF digestion. The intake (NDFI), duodenal flow (DFNDF), faecal output (NDFO) (all units g.kgW\(^{-1}\)) and site of NDF digestion in lambs grazing prairie grass (P), ryegrass (R), white clover (C) and lucerne (L).

<table>
<thead>
<tr>
<th></th>
<th>P</th>
<th>R</th>
<th>C</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDFI</td>
<td>12.5±0.86(^a)</td>
<td>11.9±0.88(^a)</td>
<td>7.5±0.85(^b)</td>
<td>7.9±0.40(^b)</td>
</tr>
<tr>
<td>DFNDF</td>
<td>3.5±0.55</td>
<td>3.5±0.55</td>
<td>3.5±0.53</td>
<td>3.4±0.23</td>
</tr>
<tr>
<td>NDFO</td>
<td>2.2±0.24</td>
<td>2.2±0.18</td>
<td>2.1±0.27</td>
<td>1.9±0.27</td>
</tr>
</tbody>
</table>

Proportion of digested NDF digested in:

<table>
<thead>
<tr>
<th></th>
<th>rumen</th>
<th>post ruminal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.88±0.029(^a)</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>0.87±0.016(^a)</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>0.73±0.053(^b)</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.78±0.032</td>
</tr>
</tbody>
</table>

\(^a\) = SEM
Table 4.2.7. Nitrogen digestion. Nitrogen intake (NI; g.kg\(^{-1}\)W), duodenal non-ammonia nitrogen (NAN) flow, related to liveweight (g.kg\(^{-1}\)), digestible organic matter intake (g.kgDOMI\(^{-1}\)) and apparently digested organic matter in the rumen (g.kgOMADR\(^{-1}\)), and duodenal N and NAN flow, as a proportion of NI (N:NI and NAN:NI respectively).

<table>
<thead>
<tr>
<th></th>
<th>P</th>
<th>R</th>
<th>C</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>NI</td>
<td>0.9±0.07(^a)</td>
<td>1.2±0.05(^b)</td>
<td>1.7±0.15(^c)</td>
<td>2.1±0.11(^d)</td>
</tr>
<tr>
<td>Duodenal NAN flow:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>g.kg(^{-1})W</td>
<td>0.87±0.07(^a)</td>
<td>0.96±0.06(^a)</td>
<td>1.20±0.09(^b)</td>
<td>1.24±0.11(^b)</td>
</tr>
<tr>
<td>g.kgDOMI(^{-1})</td>
<td>42.8±1.7</td>
<td>39.2±2.2</td>
<td>45.0±2.3</td>
<td>44.9±2.1</td>
</tr>
<tr>
<td>g.kgOMADR(^{-1})</td>
<td>85.3±6.82</td>
<td>73.7±7.34</td>
<td>80.8±10.47</td>
<td>80.9±11.79</td>
</tr>
<tr>
<td>N:NI</td>
<td>1.02±0.039(^a)</td>
<td>0.83±0.052(^b)</td>
<td>0.72±0.051(^b)</td>
<td>0.67±0.056(^b)</td>
</tr>
<tr>
<td>NAN:NI</td>
<td>0.97±0.038(^a)</td>
<td>0.78±0.050(^b)</td>
<td>0.69±0.047(^b)</td>
<td>0.61±0.053(^b)</td>
</tr>
</tbody>
</table>

\(\dagger\) = SEM
Table 4.2.8. The concentration of ammonia in rumen liquor
\((\text{mg} \cdot \text{l}^{-1})\) of lambs aged 8 (T1) and 12 (T2) weeks
of age. Measurements were made at the start
(PRE) and end (POST) of the morning (AM) and
afternoon (PM) grazing periods in lambs grazing
prairie grass (P), ryegrass (R), white clover
(C) and lucerne (L).

<table>
<thead>
<tr>
<th></th>
<th>PRE-AM</th>
<th>POST-AM</th>
<th>PRE-PM</th>
<th>POST-PM</th>
<th>Average</th>
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<td>P</td>
<td>156</td>
<td>162</td>
<td>183</td>
<td>274</td>
<td>194</td>
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<tr>
<td>R</td>
<td>180</td>
<td>486</td>
<td>702</td>
<td>640</td>
<td>502</td>
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<tr>
<td>C</td>
<td>822</td>
<td>687</td>
<td>828</td>
<td>536</td>
<td>478</td>
</tr>
<tr>
<td>L</td>
<td>354</td>
<td>474</td>
<td>546</td>
<td>816</td>
<td>788</td>
</tr>
<tr>
<td>T2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>47</td>
<td>67</td>
<td>401</td>
<td>400</td>
<td>229</td>
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<tr>
<td>R</td>
<td>210</td>
<td>236</td>
<td>400</td>
<td>492</td>
<td>335</td>
</tr>
<tr>
<td>C</td>
<td>295</td>
<td>289</td>
<td>546</td>
<td>744</td>
<td>469</td>
</tr>
<tr>
<td>L</td>
<td>546</td>
<td>621</td>
<td>688</td>
<td>846</td>
<td>675</td>
</tr>
</tbody>
</table>
Table 4.2.9. The fractional outflow rate of the digesta markers $^{103}\text{Ru-P}$ and $^{51}\text{Cr-EDTA}$ from the rumen of cannulated (CAN) and intact (INT) lambs grazing prairie grass (P), ryegrass (R), white clover (C) and lucerne (L), estimated from the rate of decline of marker concentration in duodenal digesta (Duod) and faeces, and the number of observations per plant species (n).

<table>
<thead>
<tr>
<th></th>
<th>$^{103}\text{Ru-P}$ (n)</th>
<th>$^{51}\text{Cr-EDTA}$ (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CAN Duod</td>
<td>0.092±0.0059 (12)</td>
<td>0.142±0.0100 (10)</td>
</tr>
<tr>
<td>CAN Faeces</td>
<td>0.081±0.0038 (12)</td>
<td>0.106±0.0067 (12)</td>
</tr>
<tr>
<td>INT Faeces</td>
<td>0.076±0.0035 (8)</td>
<td>0.108±0.0100 (8)</td>
</tr>
<tr>
<td>R</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CAN Duod</td>
<td>0.068±0.0047 (10)</td>
<td>0.123±0.0262 (7)</td>
</tr>
<tr>
<td>CAN Faeces</td>
<td>0.066±0.0033 (10)</td>
<td>0.098±0.0039 (10)</td>
</tr>
<tr>
<td>INT Faeces</td>
<td>0.078±0.0043 (8)</td>
<td>0.105±0.0049 (8)</td>
</tr>
<tr>
<td>C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CAN Duod</td>
<td>0.109±0.0077 (9)</td>
<td>N.S. (0)</td>
</tr>
<tr>
<td>CAN Faeces</td>
<td>0.096±0.0045 (10)</td>
<td>0.132±0.0086 (10)</td>
</tr>
<tr>
<td>INT Faeces</td>
<td>0.105±0.0057 (8)</td>
<td>0.130±0.0216 (8)</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CAN Duod</td>
<td>0.120±0.0058 (10)</td>
<td>0.177±0.0194 (5)</td>
</tr>
<tr>
<td>CAN Faeces</td>
<td>0.092±0.0057 (10)</td>
<td>0.129±0.0122 (10)</td>
</tr>
<tr>
<td>INT Faeces</td>
<td>0.106±0.0056 (8)</td>
<td>0.135±0.0096 (8)</td>
</tr>
</tbody>
</table>

¶ = SEM
4.2.4 DISCUSSION

4.2.4.1 Liveweight gain

The liveweight gain of intact lambs was high, and was similar to the high growth rates observed by McLean et al (1965) and Jagusch et al (1971) for early weaned lambs grazing pure species swards of white clover, lucerne and perennial ryegrass. Growth rates were similar for lambs grazing legumes and for lambs grazing grasses. The similarity between P and R was surprising, considering the higher NDF and lower N content of P. However, the digestibility of P was higher than that of R at 8 weeks of age. The decline in quality of P over the experiment was unfortunate and was probably related to its growing season, which is considerably earlier than the other pasture species. Therefore, had P been studied earlier in its growing season the performance of lambs may have been better.

The low growth rate and intake of CAN lambs cannot be readily explained. The lambs quickly became accustomed to the regular handling and continued to graze or ruminate during sampling and routine handling. However, leakage of digesta around the cannula attracted large numbers of flies and, although regular treatment prevented the establishment of fly strike, the continual presence of flies may have caused some distress, with a subsequent reduction in intake.

The greater growth rate of lambs grazing legumes was associated with greater intake and duodenal NAN flows. The ratio of NAN flow:DOMI was 10% higher in lambs grazing legumes but it was unlikely that this increase could have caused the 38% increase in growth rate. The higher DOMI (36%, g.kgW⁻¹) and duodenal NAN flow (33%, g.kgW⁻¹) were the major differences. The relationships between utilisable amino acid N (aaN) absorption (total aaN absorbed - maintenance N requirement), and between growth rate and utilisable ME absorption (ME absorbed - maintenance ME requirement), as derived in section 2.1 for data from the literature, are shown in figure 4.2.1. The calculated values from this experiment (see table 4.2.10) have been superimposed. Several assumptions were made to enable these calculations and these are outlined below.

1. DOMI contained 15.83 MJME.kg⁻¹ (Beever et al, 1986a).
2. Maintenance ME requirement was 0.5MJME/kgW⁰.75 (MAFF, 1975).
3. Duodenal NAN flow per kg DOMI was similar in CAN and INT lambs.
4. Microbial NAN comprised 0.76 and 0.68 of the duodenal NAN, for grass and legume respectively (Beever et al, 1986b).
5. Duodenal aaN was absorbed from the small intestine with an efficiency of 0.7 (ARC, 1980).

6. Maintenance N requirement was $0.2gN/kgW^{0.75}$ (Black et al., 1973).

The results from the present study appear to agree with the general relationship for forage fed animals, despite the high growth rates (figure 4.2.1). It was hoped that the diverse plant species used in the present experiment would lead to differences in the relative supply of energy and protein, thereby permitting analysis of the relative importance of energy and protein to promote liveweight gain. However, it was not possible to determine the relative importance of energy and protein as a growth limiting nutrient, due to the close relationship between energy and protein supply, and this suggested that infusion of energy and/or protein would be required to alter the balance of absorbed nutrients and to enable this analysis.

Further analysis of the results permits a tentative estimate of the efficiency of utilisation of ME and absorbed aaN for growth. The composition and energy content of the empty body gain was calculated from the relationships given in ARC (1980). Empty body gain was calculated by assuming that the increase in gut contents between 8 and 12 weeks of age reflected the rate of change over the 6 weeks of the experiment. This was unlikely to be an accurate estimate, as gut contents would be expected to increase rapidly in the immediate post weaning period. Therefore, this assumption would lead to a slight overestimation of empty body gain and, therefore, overestimation of efficiency of nutrient utilisation. The results of the calculation are shown in table 4.2.10. The predicted efficiencies of utilisation were considerably lower than the values recommended by ARC (1980). However, the predicted $k_g$ (0.34-0.42) was within the range commonly observed in forage fed animals (Fennessy et al., 1972; Rattray & Joyce, 1974; Thomson & Cammell, 1979; Barry, 1981; Alam, 1985; Geenty, 1985). The efficiency of utilisation of absorbed aaN has not been widely studied and ARC (1980) admitted to having insufficient data to make an accurate estimate. The present estimates appear low (0.39-0.48) but are similar to the value of 0.45 observed by Alam (1985) for forage fed lambs. They are also similar to values calculated from the data of Corbett et al. (1979) for lambs grazing phalaris (0.31, 0.38, 0.49 and 0.57) and lucerne (0.43 and 0.49). These were calculated by assuming that microbial aaN comprised 0.73 (lucerne) and 0.83 (phalaris) of duodenal NAN (Pickering et al., 1982), that aaN was absorbed from the
small intestine with a similar efficiency to NAN and that maintenance N requirement was $0.2\text{gN/kgW}^{0.75}$ (Black et al., 1973).

4.2.4.2 Site of nutrient digestion

4.2.4.2.1 Organic matter. The proportion of apparently digested OM apparently digested in the rumen (DOMADR) was similar on all pasture species (0.52–0.58). There have been conflicting reports on the affect of plant species on the site of OM digestion. Ulyatt & MacRae (1974) observed DOMADR to be 0.55 for short-rotation ryegrass and 0.64 and 0.65 for perennial ryegrass and white clover respectively. Similarly, Beever et al. (1986b) observed higher values of DOMADR in cattle offered perennial ryegrass indoors (0.68–0.74) than in cattle offered white clover indoors (0.51–0.56). However, Thomson & Beever (1980), analysing a range of data, could find no evidence for species differences and estimated a mean value of 0.6. Beever et al. (1986a) observed similar values of 0.69 and 0.71 in cattle grazing perennial ryegrass and white clover respectively. Correcting for duodenal OM of microbial origin they calculated that 0.97 of the OM apparently digested in the digestive tract was truly digested in the rumen. Although this value would overestimate the proportion of OM truly digested in the digestive tract which was digested in the rumen, it nevertheless emphasised the extensive degradation of dietary OM which occurred in the rumen. This suggests that changes in the fractional outflow rate of digesta from the rumen ($k$), which tend to be high in animals consuming fresh herbage, are unlikely to markedly alter the true digestion of dietary OM. However, the possibility of increased microbial OM flow with increased $k$ (Owens & Isaacson, 1977) may have important implications for DOMADR and the composition of nutrients passing from the rumen.

The values of DOMADR observed in the present experiment tended to fall in the lower limit of reported data for animals consuming fresh herbage, as illustrated in figure 4.2.2. However, the DOMI ($\text{g.kgW}^{-1}$) observed in the present experiment tended to be higher than data from the literature so direct comparison of the data may not be valid, as the low values of DOMADR may have been caused by the high intakes (see section 4.1).
4.2.4.2.2 Neutral detergent fibre. The higher concentration of NDF in grasses led to lambs consuming 58% more NDF (g·kg\(^{-1}\)) on grasses than on legumes (P<0.05). However, this difference was removed by digestion in the rumen, and duodenal flow and faecal output were similar for all pasture species. This was due to the higher digestibility of NDF (0.82 and 0.74, for grasses and legumes respectively) and the higher proportion of digestible NDF digested in the rumen of lambs grazing grasses, compared to lambs grazing legumes (0.88 and 0.76 for grasses and legumes respectively).

The partitioning of NDF digestion between the rumen and hindgut has been poorly studied in sheep consuming fresh herbage. However, the site of cellulose and hemicellulose digestion appears to be similar for fresh and conserved forage (Ulyatt & MacRae, 1974). In general, the proportion of digestible NDF digested in the rumen lies in the range 0.85-0.95 (Hogan, 1973; Weston & Margan, 1979; Alam, 1985; Kennedy, 1985). Lower values of 0.59-0.73 (average, 0.67) have been observed in lambs consuming a ground and pelleted roughage/concentrate diet (Margan et al, 1982). The values observed in the present experiment appear low, particularly for legumes and this is probably due to high fractional outflow rate of digesta from the rumen, as reflected by the high outflow rate of markers from the rumen (table 4.2.9).

Further analysis of the data, incorporating the fractional disappearance rate of NDF from the rumen, which is estimated in section 4.2, permits the estimation of fractional digestion rate (\(k_d\)) and fractional outflow rate (\(k_p\)) of NDF. Assuming that all the ingested NDF is potentially digestible the proportion of ingested NDF digested in the rumen (PNDFDR) can be related to \(k_d\) and \(k_p\) by the following equation.

\[ PNDFDR = k_d \cdot (k_d + k_p)^{-1} \] ——eqn.4.2.1

Fractional disappearance rate (k) is the sum of \(k_d\) and \(k_p\), therefore \(k_d = k \times PNDFDR\) and \(k_p = k - k_d\). The results of this calculation are shown in table 4.2.11. Although there was, undoubtedly, error associated with the assumption that all NDF was potentially digestible, the calculation provided a useful approximation. It can be seen that \(k_d\) was similar for P, R and C (0.061-0.068), although a higher value of 0.109 was calculated for L. However, C exhibited a higher \(k_p\) (0.054) than P and R (0.025), and L again exhibited the highest value.
(0.075). Therefore, it appears that the lower proportion of digested NDF digested in the rumen of lambs grazing legumes was due mainly to increased $k_p$.

4.2.4.2.3 Nitrogen. The nitrogen concentration was, on average, 37% higher in legumes than in grasses. Combined with the higher OM intake, lambs grazing legumes had a considerably higher N intake than lambs grazing grasses (1.9 and 1.1 gN.kg$^{-1}$ respectively). However, nitrogen transactions in the rumen considerably altered the quantity of N flowing past the duodenum. As a result lambs grazing P gained 2% across the rumen while lambs grazing R, C and L lost 17, 28 and 33% respectively. Duodenal $\text{NAN} \text{flow}$ was lower than N intake for all plant species (0.97, 0.78, 0.69 and 0.61 gNAN.gN intake$^{-1}$ for P, R, C and L respectively). Increased N loss was associated with increased rumen NH$_3$ concentration (average, 211, 418, 629 and 576 mg.l$^{-1}$ for P, R, C and L respectively).

Ammonia-N represented 5-7% of total N flow past the duodenum with no difference being attributable to plant species. The resultant $\text{NAN} \text{flow}$ was similar for both grass species (0.87 and 0.96 g.kg$^{-1}$ for P and R respectively) and for both legume species (1.20 and 1.24 g.kg$^{-1}$ for C and L respectively). However, the increased flow observed in lambs grazing legumes was associated with increased DOMI (36%) and a 41% increase in OM digestion in the rumen (OMADR; gOM.kg$^{-1}$) with the result that duodenal $\text{NAN} \text{flow}$ was only 10% (per kg DOMI) and 2% (per kg OMADR) higher in lambs grazing legumes.

Initial comparison of the results from the present experiment with data in the literature is confused by the generally higher intakes observed in the present experiment and the high N content of the diets. However, it is important to recognise that digestion is a dynamic process and comparison of individual values may be misleading. Therefore, the results obtained in the present experiment have been compared with published data in the form of general relationships, using relevant data from published studies on the digestion of fresh herbage conducted with sheep (indoor studies, MacRae & Ulyatt, 1974; Ulyatt & MacRae, 1974; Ulyatt & Egan, 1979: grazing studies, Ulyatt, 1971; Corbett et al, 1976, 1982) and cattle (indoors, Beever et al, 1980, 1986b: grazing, Ulyatt et al, 1980; Beever et al, 1986a).
The generally high NH₃ concentration in rumen liquor agrees with published data, when related to N concentration in dietary OM (figure 4.2.3).

Increasing rumen NH₃ concentration was associated with increasing N losses across the rumen, as reflected by the ratios of duodenal N and NAN flow:N intake (table 4.2.7). Nitrogen losses across the rumen have been related to N intake (MacRae & Ulyatt, 1974; Ulyatt & Egan, 1979) or to N concentration in the diet (Beever et al., 1986a). The relationship between duodenal NAN flow, as a proportion of N intake, and nitrogen content of the diet (gN.kgOM⁻¹), which was only derived from sheep data from the literature, is shown in figure 4.2.4, along with the results of the present experiment. The linear regression, excluding the present results, explains 47% of the variation and is given in eqn. 4.2.2.

\[ y = 1.445 - 0.0141x \]  
\[ x = \text{dietary N content (gN.kgOM}^{-1}) \]

This equation is similar to the corresponding relationship (eqn.2.2.2) derived from cattle data by Beever et al. (1986a) and to eqn.4.2.3, derived solely from the present experiment.

\[ y = 1.392 - 0.0132x \text{ (n = 8, } r^2 = 0.74) \]  

Equality between N intake and duodenal NAN flow was predicted to occur when dietary N concentration was 27.4, 31.6 and 29.8 gN.kgOM⁻¹ from eqns. 2.2.2, 4.2.2 and 4.2.3 respectively. These relationships reflect the ability of rumen microbes to capture dietary N and suggests that nitrogen transactions in the rumen are similar in early weaned lambs, older sheep and cattle. This also explains why the large differences in N intake observed in this experiment were largely removed by transactions in the rumen and further emphasises the importance of the rumen in modifying the nutrients available for absorption.

In the present experiment duodenal NAN flow was closely related to DOMI (average, 43gNAN.kgDOMI⁻¹) and to the quantity of OM apparently digested in the rumen (average, 80gNAN.kgOMADR⁻¹). These results are comparable with a range of data in the literature, relating to animals consuming fresh herbage (table 4.2.12), although low values were observed
by Beever et al (1986a,b). Apart from the study of Beever et al (1986b) there was no difference in NAN flow (g.kgDOMI$^{-1}$) between grasses and legumes. There was more variation in NAN flows when related to OMADR, but there was no consistent difference between grasses and legumes.

Individual treatment data from the literature and the results from the present experiment, relating NAN flow to the small intestine, N intake, DOMI and OMADR (all g.kg$^{-1}$), were analysed by regression analysis to determine which factor(s) were most closely related to NAN flow to the small intestine. The resulting regression equations are shown in table 4.2.13. Surprisingly, the correlation between NAN flow to the small intestine and OMADR was very low ($r^2=0.350$) and was markedly higher for DOMI ($r^2=0.679$), a cruder estimate of energy available for microbial synthesis. This suggested that OMADR was a poor indicator of energy availability in the rumen, as was also suggested by Losada (1983; cited by Beever, 1984) who related microbial NAN yield to OMADR and OM truly digested in the rumen. Nitrogen intake provided the highest correlation with NAN flow to the small intestine ($r^2=0.764$) and this was only marginally improved by including DOMI ($R^2=0.786$) or OMADR ($r^2=0.766$) in the regression. Ulyatt & Egan (1979) observed that duodenal N flow was best explained by N intake, although large variation was observed between individual experiments. Similarly, Beever et al (1986b) observed highly significant relationships between N intake and duodenal NAN flow within treatments, but the relationships altered markedly between treatments. Therefore, derived relationships between N intake and NAN flow to the small intestine may yield erroneous predictions if applied to individual sets of experimental data. These data also highlight the large variation which exists between NAN flow to the small intestine and OMADR, suggesting that the system derived by ARC (1980) to predict NAN flow to the small intestine may not be applicable to animals consuming fresh herbage.

4.2.5 CONCLUSIONS

Lambs grazing legumes grew significantly faster than lambs grazing grasses, although there was a marked similarity between the two legume species and between the two grass species. The higher growth rates observed in lambs grazing legumes were associated with higher levels of intake and increased flow of NAN to the small intestine, but it was not
possible to differentiate between the relative importance of energy and protein. Related to DOMI the duodenal flow of NAN was slightly higher in lambs grazing legumes, but the major difference appeared to be in the total quantity of nutrients supplied.

The efficiency of utilisation of ME and absorbed aaN appeared low, but were within the range of values commonly observed in animals consuming herbage diets. There did not appear to be any marked difference between plant species.

Compared to published data, the proportion of digested OM and NDF digested in the rumen appeared low. This was attributed to the high intake achieved in the present experiment and the high fractional outflow rate of digesta from the rumen, which was reflected in the present experiment by the high fractional outflow rate of markers from the rumen. Digestion in the rumen significantly altered the quantity of N flowing to the small intestine, particularly for legumes, where significant losses of dietary N across the rumen were observed. These losses were associated with high N content of ingesta and high rumen ammonia concentrations, suggesting that N supply was in excess of the synthetic capacity of rumen microbes. This suggested that NAN flow to the small intestine was related to the energy available in the rumen for microbial synthesis, but OMADR was poorly correlated with NAN flow to the small intestine. Nitrogen intake was highly correlated with NAN flow to the small intestine and the correlation was only marginally improved by including DOMI or OMADR in the analysis.

Therefore, the major cause of the difference in growth rate between lambs grazing legumes and grasses appeared to be the level of intake achieved, which affected both energy and protein absorption.
Figure 4.2.1 The relationships between liveweight gain (LWG, g.d\(^{-1}\)) and (a) ME intake less maintenance ME requirement and (b) absorbed amino acid nitrogen (aaN, g.d\(^{-1}\)) less maintenance tissue N requirement.
Figure 4.2.2 The relationship between organic matter apparently digested in the rumen (OMADR; g.kgW$^{-1}$) and digestible organic matter intake (DOMI; g.kgW$^{-1}$).
Figure 4.2.3 The relationship between rumen ammonia concentration (mg.l$^{-1}$) and dietary nitrogen concentration (g.kgOM$^{-1}$).
Figure 4.2.4 The relationship between non-ammonia nitrogen flow to the small intestine (NAN), as a proportion of nitrogen intake (NI), and dietary nitrogen concentration (g.kgOM\(^{-1}\)).
Table 4.2.10. Predicted absorption and efficiency of utilisation of metabolisable energy (ME) and amino acid nitrogen (aaN) in lambs grazing prairie grass (P), ryegrass (R), white clover (C) and lucerne (L).

<table>
<thead>
<tr>
<th></th>
<th>P</th>
<th>R</th>
<th>C</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>Supply</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ME intake (MJ.d⁻¹)</td>
<td>9.3</td>
<td>10.1</td>
<td>15.3</td>
<td>16.0</td>
</tr>
<tr>
<td>Absorbed aaN (gN.d⁻¹)</td>
<td>14.9</td>
<td>14.7</td>
<td>24.4</td>
<td>26.1</td>
</tr>
<tr>
<td>Growth (g.d⁻¹)</td>
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<td></td>
</tr>
<tr>
<td>Fat</td>
<td>29.8</td>
<td>35.2</td>
<td>43.9</td>
<td>39.9</td>
</tr>
<tr>
<td>Nitrogen</td>
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<tr>
<td>wool</td>
<td>0.8</td>
<td>0.9</td>
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<td>1.5</td>
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<td>3.4</td>
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<td>7.0</td>
<td>6.4</td>
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<tr>
<td>Energy retained (MJ.d⁻¹)</td>
<td>1.69</td>
<td>1.97</td>
<td>3.89</td>
<td>3.54</td>
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<td>Maintenance (.d⁻¹)</td>
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</tr>
<tr>
<td>ME (MJ)</td>
<td>5.3</td>
<td>5.4</td>
<td>5.4</td>
<td>5.6</td>
</tr>
<tr>
<td>aaN (g)</td>
<td>2.1</td>
<td>2.2</td>
<td>2.2</td>
<td>2.2</td>
</tr>
<tr>
<td>Efficiency of utilisation for gain</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>ME</td>
<td>0.42</td>
<td>0.42</td>
<td>0.39</td>
<td>0.34</td>
</tr>
<tr>
<td>ARC (1980)</td>
<td>0.51</td>
<td>0.52</td>
<td>0.55</td>
<td>0.56</td>
</tr>
<tr>
<td>aaN</td>
<td>0.42</td>
<td>0.48</td>
<td>0.44</td>
<td>0.39</td>
</tr>
<tr>
<td>ARC (1980)</td>
<td>0.75</td>
<td>0.75</td>
<td>0.75</td>
<td>0.75</td>
</tr>
</tbody>
</table>
Table 4.2.11. Estimation of the fractional digestion rate \( (k_d) \) and fractional outflow rate \( (k_p) \) of NDF from the rumen. Results were calculated from eqn. 4.2.1, using the values for fractional disappearance rate from section 5.2 and the proportion of ingested NDF digested in the rumen \( (\text{INDFDR}) \) from the present experiment. Lambs grazed prairie grass \( (P) \), ryegrass \( (R) \), white clover \( (C) \) and lucerne \( (L) \).

<table>
<thead>
<tr>
<th></th>
<th>P</th>
<th>R</th>
<th>C</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>( k(\text{NDF}) )</td>
<td>0.093</td>
<td>0.088</td>
<td>0.115</td>
<td>0.184</td>
</tr>
<tr>
<td>( \text{INDFDR} )</td>
<td>0.73</td>
<td>0.71</td>
<td>0.53</td>
<td>0.59</td>
</tr>
<tr>
<td>( k_p )</td>
<td>0.025</td>
<td>0.025</td>
<td>0.054</td>
<td>0.075</td>
</tr>
<tr>
<td>( k_d )</td>
<td>0.068</td>
<td>0.063</td>
<td>0.061</td>
<td>0.109</td>
</tr>
</tbody>
</table>
Table 4.2.12. The flow on NAN into the small intestine, in relation to digestible OM intake (DOMI) and the quantity of OM apparently digested in the rumen (OMADR), in animals consuming fresh herbage.

<table>
<thead>
<tr>
<th>Reference</th>
<th>gNAN.kgDOMI(^{-1})</th>
<th>gNAN.kgOMADR(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>MacRae &amp; Ulyatt (1974)</td>
<td>grass 42.5</td>
<td>72.8</td>
</tr>
<tr>
<td></td>
<td>legume 39.2</td>
<td>59.8</td>
</tr>
<tr>
<td>Corbett et al (1976)</td>
<td>grass 53.5</td>
<td>89.0</td>
</tr>
<tr>
<td></td>
<td>legume 47.2</td>
<td>71.5</td>
</tr>
<tr>
<td>Ulyatt &amp; Egan (1979)</td>
<td>grass 43.9</td>
<td>77.6</td>
</tr>
<tr>
<td></td>
<td>legume 46.4</td>
<td>83.7</td>
</tr>
<tr>
<td>Corbett et al (1982)</td>
<td>grass 47.1</td>
<td>76.1</td>
</tr>
<tr>
<td></td>
<td>legume 45.9</td>
<td>77.6</td>
</tr>
<tr>
<td>Beever et al (1986a)</td>
<td>grass 36.2</td>
<td>52.6</td>
</tr>
<tr>
<td></td>
<td>legume 37.0</td>
<td>52.4</td>
</tr>
<tr>
<td>Beever et al (1986b)</td>
<td>grass 31.6</td>
<td>44.8</td>
</tr>
<tr>
<td></td>
<td>legume 45.0</td>
<td>85.5</td>
</tr>
<tr>
<td>Present results</td>
<td>grass 41.0</td>
<td>79.6</td>
</tr>
<tr>
<td></td>
<td>legume 45.0</td>
<td>80.8</td>
</tr>
</tbody>
</table>
Table 4.2.13. Regressions relating NAN flow to the small intestine (NAN$_{si}$, g.kg$^{-1}$) to nitrogen intake (NI, g.kg$^{-1}$), DOMI (g.kg$^{-1}$) and OM apparently digested in the rumen (OMADR, g.kg$^{-1}$). Data were obtained from the literature for animals consuming fresh herbage and include the present study (n = 85).

<table>
<thead>
<tr>
<th>Regressions</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{NAN}_{si} = 0.480^{<em><strong>} \text{NI} + 0.275^{</strong></em>}$</td>
<td>0.764</td>
</tr>
<tr>
<td>$\text{NAN}_{si} = 0.0348^{**<em>} \text{DOMI} + 0.105^{</em>}$</td>
<td>0.679</td>
</tr>
<tr>
<td>$\text{NAN}_{si} = 0.0343^{<em><strong>} \text{OMADR} + 0.318^{</strong></em>}$</td>
<td>0.350</td>
</tr>
<tr>
<td>$\text{NAN}_{si} = 0.346^{*<strong>} \text{NI} + 0.0121^{</strong>} \text{DOMI} + 0.188^{**}$</td>
<td>0.786</td>
</tr>
<tr>
<td>$\text{NAN}_{si} = 0.501^{<em><strong>} \text{NI} - 0.00316^{N.S.} \text{OMADR} + 0.291^{</strong></em>}$</td>
<td>0.766</td>
</tr>
</tbody>
</table>

***; $P<0.001$

**; $P<0.01$

*; $P<0.05$

N.S.; non-significant
Regulation of intake in grazing sheep

In the previous chapter it was concluded that intake was an important determinant of lamb growth rate and, therefore, this area requires stringent examination. This chapter describes a series of experiments designed to examine the role of physical regulation of intake in the control of VFC. The major components of the physical regulation theory are rumen digesta content and the retention time of digesta in the rumen, and these areas are described for grazing sheep in sections 5.1 and 5.2, respectively. The response of sheep to restriction of rumen capacity is reported in section 5.3 and the results are used to form a conceptual model of intake regulation (section 5.4).
5.1 PATTERN OF RUMEN FILL IN GRAZING SHEEP

5.1.1 INTRODUCTION

Diurnal patterns of grazing behaviour have been well documented, but the relationship between grazing pattern and rumen fill does not appear to have been studied. This aspect has important implications for the regulation of herbage intake. For example, if grazing intake is regulated by the physical capacity of the rumen the grazing pattern would be expected to closely relate to changes in rumen fill. Therefore, grazing would cease at a similar, high, rumen fill and, possibly, commence at a similar, low, rumen fill.

This series of experiments examined the diurnal pattern of rumen fill, in relation to the grazing pattern, in sheep grazing prairie grass during summer, winter and spring, and lucerne during spring.

The development of models to predict VFC (e.g. Forbes, 1980a,b) require the prediction of changes in rumen fill and this does not appear to have been studied. A predictive equation, derived in appendix 4, was applied to some of the experimental data to assess the accuracy of prediction and, also, to suggest some possible explanations for anomalies in the actual changes in rumen fill.
5.1.2 MATERIALS AND METHODS

5.1.2.1 Animals and management

Expt.1. Four 1-2 year old wethers (average liveweight, 67.5±2.2kg), each fitted with a permanent rumen cannula (I.D.=8.5cm), and 3 oesophageal fistulated (OF) sheep grazed a prairie grass sward (summer PG) from 20:3:84 until 6:4:84. They were set stocked on a 2 acre (0.8 ha) paddock with an initial herbage mass of 2100 kgDM.ha\(^{-1}\). Herbage allowance was therefore liberal at 14.1 kg DM.sheep\(^{-1}\). The pattern of rumen fill was studied over the last 8 days of the grazing period.

Expt.2. The same sheep (average liveweight, 62.5±2.24) grazed a prairie grass pasture (winter PG), along with 3 OF sheep, from 11:7:84 until 26:7:84. Animals were set stocked at a herbage allowance of 14.2 kgDM.sheep\(^{-1}\) (1860 kgDM.ha\(^{-1}\)). The pattern of rumen fill was studied over the last 9 days of the grazing period.

Expts.3 and 4. Animals, pasture and experimental design are described in section 5.3. The data reported in this section are from the same four sheep used in the above experiments, but were derived when they operated as controls, during grazing of prairie grass in spring (expt.3; spring PG) and lucerne in spring (expt.4; spring L).

Subsequent to the preliminary experiment (summer PG) the sheep were placed on restricted intake prior to experimental periods to reduce body energy reserves and therefore minimise the possibility of sheep eating to maintenance levels.

5.1.2.2 Sampling times

Grazing patterns were monitored for at least 7 days, using automatic grazing recorders (see appendix 5), to determine grazing pattern. Sampling times for estimation of rumen fill were selected to correspond, where possible, to the beginning (PRE) and end (POST) of the morning (AM) and afternoon (PM) grazing periods. Two additional measurements were made (ODD-A and ODD-B) at intermediate times such that the 6 measurements were made at approximately 4h intervals of a theoretical 24h day. Grazing times were monitored throughout the measurement period although these did not influence the sampling times.
Rumen digesta content was measured twice daily, with a minimum 8h interval for each animal, during 6-9 days, such that, within animals, each sampling time was replicated at least twice. The sampling times for each experiment, which changed in relation to the grazing pattern, and the number of replicates for each sampling time is given in table 5.1.1.

5.1.2.3 Measurement of rumen content

Sheep were removed from pasture and taken immediately to an adjacent laboratory site which was prepared for sampling. Digesta was manually removed through the rumen cannula and stored, in a tared bucket, in a water bath at 39-40°C. Volume and fresh weight of digesta were recorded and subsamples of 60-120g were taken for DM, OM, and NDF analysis. The remaining digesta was replaced in the rumen and the sheep returned to pasture. The whole operation took approximately 10min for each sheep and the sheep were off pasture for approximately 45-50min.

5.1.2.4 Intake

A solution containing Ytterbium chloride was continuously infused into the rumen for 10-13 days. Grab samples of faeces were obtained at each measurement period and bulked over 3 day intervals. Digestibility was estimated by reference to IADF (see section 2.5.1.3).

The intake of metabolisable energy (ME) was calculated assuming 1kg of DOMI contained 15.83 MJME (Beever et al, 1986a) and maintenance ME requirement ($M_m$) was estimated from the following equation (MAFF, 1975),

$$M_m = 0.5W^{0.75}$$

5.1.2.5 Statistical analysis

The results were analysed by analysis of variance, student's t test and paired t test, where applicable.
Table 5.1.1. Sampling times, corrected to New Zealand standard time, and number of replicates (n) for each experiment.

<table>
<thead>
<tr>
<th></th>
<th>Summer PG</th>
<th>Winter PG</th>
<th>Spring PG</th>
<th>Spring L</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>time</td>
<td>time</td>
<td>time</td>
<td>time</td>
</tr>
<tr>
<td>ODD-A</td>
<td>01.00</td>
<td>04.00</td>
<td>02.30/03.30</td>
<td>23.30/24.00</td>
</tr>
<tr>
<td>PRE-AM</td>
<td>05.00</td>
<td>07.00</td>
<td>05.30/06.30</td>
<td>04.00</td>
</tr>
<tr>
<td>POST-AM</td>
<td>09.00</td>
<td>10.30</td>
<td>09.30/10.30</td>
<td>08.00</td>
</tr>
<tr>
<td>PRE-PM</td>
<td>13.00</td>
<td>14.30</td>
<td>14.30</td>
<td>11.30/12.00</td>
</tr>
<tr>
<td>ODD-B</td>
<td>17.00</td>
<td>22.00</td>
<td>22.30</td>
<td>15.30/16.00</td>
</tr>
<tr>
<td>POST-PM</td>
<td>21.00</td>
<td>18.00</td>
<td>1900/1930</td>
<td>19.30/20.00</td>
</tr>
</tbody>
</table>

‡ Two sampling times were used in the study of spring PG and spring L, as these data were obtained from the 2x2 crossover experiment described in section 5.3.
5.1.3 RESULTS

5.1.3.1 Grazing pattern

There was no difference in the grazing time or pattern between premeasurement and measurement periods and the average patterns are shown in figures 5.1.1 and 5.1.2. Grazing intensity, expressed as the proportion of each hour spent grazing, tended to increase steadily between sunrise and sunset, with an additional grazing period during the night. The average grazing times were 8.9±0.82, 9.6±0.53, 7.7±0.60 and 6.9±1.00 h.d⁻¹ for summer PG, winter PG, spring PG and spring L, respectively.

5.1.3.2 Intake and composition of ingesta

The composition of OF extrusa and OM digestibility are given in table 5.1.2. No intake data were obtained from one sheep on summer PG due to problems in maintaining continuous marker infusion. Intakes of OM, DOM, NDF and ME are given in table 5.1.3, along with maintenance ME requirements. In absolute terms (g.d⁻¹), organic matter intake was similar for summer PG and winter PG but, in relation to liveweight (g.kg⁻¹W), OMI, DOMI and NDFI were higher (P<0.05) for winter PG than for summer PG. Intake of OM and NDF was higher (P<0.05) for spring PG and spring L than for summer PG and winter PG. The low NDF content of spring L resulted in a low NDFI, which was similar to summer PG.

5.1.3.3 Rumen fill

There was a marked diurnal fluctuation in rumen fill, measured as volume of digesta, weight of digesta and rumen DM, OM and NDF content (tables 5.1.4 and 5.1.5; figures 5.1.3 and 5.1.4), and in digesta composition, particularly DM% (table 5.1.6; figures 5.1.3 and 5.1.4). Rumen DM, OM and NDF content reached a maximum around sunset and tended to remain low throughout the rest of the day. Volume, weight and DM% of rumen digesta tended to follow a similar pattern although the variation was less consistent. In the study of summer PG the cessation of the afternoon grazing period occurred between two sampling times and, therefore, no accurate estimate of maximum rumen fill was obtained and the rate of increase of rumen fill appeared low prior to the POST-PM sample.
Figure 5.1.1 The grazing pattern of sheep grazing prairie grass in summer and winter.
Figure 5.1.2 The grazing pattern of sheep grazing prairie grass and lucerne in spring.
Figure 5.1.3 Diurnal pattern of rumen digesta volume (ml.kg\(^{-1}\)), rumen organic matter content (g.kg\(^{-1}\)) and dry matter content of rumen digesta (k.kg\(^{-1}\)) in sheep grazing prairie grass in summer and winter.
Figure 5.1.4 Diurnal pattern of rumen digesta volume (ml.kg$^{-1}$), rumen organic matter content (g.kg$^{-1}$) and dry matter content of rumen digesta (k.kg$^{-1}$) in sheep grazing prairie grass and lucerne in spring.
Table 5.1.2. The organic matter (OM) and NDF content (g.kgDM\(^{-1}\)), and OM digestibility (OMD) of OF extrusa.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>OM</th>
<th>NDF</th>
<th>OMD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer PG</td>
<td>854</td>
<td>324</td>
<td>0.78±0.012(a)</td>
</tr>
<tr>
<td>Winter PG</td>
<td>820</td>
<td>345</td>
<td>0.82±0.004(b)</td>
</tr>
<tr>
<td>Spring PG</td>
<td>827</td>
<td>376</td>
<td>0.78±0.023(ab)</td>
</tr>
<tr>
<td>Lucerne</td>
<td>848</td>
<td>234</td>
<td>0.83±0.010(b)</td>
</tr>
</tbody>
</table>

\(\dagger\) = SEM
Table 5.1.3. The intake of organic matter (OMI), digestible OM (DOMI), NDF (NDFI) and metabolisable energy (MEI), and calculated maintenance ME requirements ($M_m$).

<table>
<thead>
<tr>
<th>Experiment</th>
<th>OMI</th>
<th>DOMI</th>
<th>NDFI</th>
<th>MEI</th>
<th>$M_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g.d$^{-1}$</td>
<td>g.kg$\cdot$</td>
<td>g.kg$\cdot$</td>
<td>MJ.d$^{-1}$</td>
<td>MJ.d$^{-1}$</td>
</tr>
<tr>
<td>Summer PG</td>
<td>1204±78.1$^a$</td>
<td>17.7±1.32$^a$</td>
<td>14.7±2.22$^a$</td>
<td>6.6±0.44$^a$</td>
<td>14.8</td>
</tr>
<tr>
<td>Winter PG</td>
<td>1244±103.9$^a$</td>
<td>19.8±0.98$^b$</td>
<td>16.3±0.82$^b$</td>
<td>8.3±0.40$^b$</td>
<td>16.2</td>
</tr>
<tr>
<td>Spring PG</td>
<td>1672±188.8$^b$</td>
<td>24.8±2.05$^c$</td>
<td>19.6±1.81$^c$</td>
<td>11.3±1.53$^c$</td>
<td>20.9</td>
</tr>
<tr>
<td>Spring L</td>
<td>1709±109.1$^b$</td>
<td>24.8±2.11$^c$</td>
<td>20.8±1.94$^c$</td>
<td>6.8±0.44$^a$</td>
<td>22.5</td>
</tr>
</tbody>
</table>

$^a$ = SEM
Table 5.1.4. The weight (Wt; g.kg$^{-1}$) and volume (Vol; ml.kg$^{-1}$) of rumen digesta and the weight of dry matter (DM; g.kg$^{-1}$) and NDF (g.kg$^{-1}$) in the rumen of sheep grazing summer PG (expt.1) and winter PG (expt.2).

<table>
<thead>
<tr>
<th></th>
<th>ODDA</th>
<th>PREAM</th>
<th>POSTAM</th>
<th>PREPM</th>
<th>ODD-B</th>
<th>POSTPM</th>
<th>ODD-B</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Summer PG</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wt</td>
<td>$83\pm5.7$</td>
<td>$77\pm5.3$</td>
<td>$62\pm5.9$</td>
<td>$77\pm7.1$</td>
<td>$97\pm5.9$</td>
<td>$93\pm6.3$</td>
<td></td>
<td>$81\pm5.9$</td>
</tr>
<tr>
<td>Vol</td>
<td>$100\pm7.4$</td>
<td>$91\pm5.5$</td>
<td>$74\pm6.5$</td>
<td>$89\pm8.2$</td>
<td>$111\pm5.9$</td>
<td>$102\pm7.7$</td>
<td></td>
<td>$94\pm6.7$</td>
</tr>
<tr>
<td>DM</td>
<td>$8.4\pm0.64$</td>
<td>$7.5\pm0.65$</td>
<td>$5.2\pm0.58$</td>
<td>$7.4\pm0.82$</td>
<td>$9.0\pm0.77$</td>
<td>$9.7\pm0.94$</td>
<td></td>
<td>$7.8\pm0.73$</td>
</tr>
<tr>
<td>NDF</td>
<td>$4.2\pm0.35$</td>
<td>$3.8\pm0.41$</td>
<td>$2.5\pm0.30$</td>
<td>$3.8\pm0.47$</td>
<td>$4.6\pm0.46$</td>
<td>$5.1\pm0.58$</td>
<td></td>
<td>$4.0\pm0.41$</td>
</tr>
<tr>
<td><strong>Winter PG</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wt</td>
<td>$89\pm6.6$</td>
<td>$78\pm5.6$</td>
<td>$76\pm8.0$</td>
<td>$89\pm9.6$</td>
<td>$117\pm11.5$</td>
<td></td>
<td>$94\pm5.0$</td>
<td>$91\pm7.6$</td>
</tr>
<tr>
<td>Vol</td>
<td>$101\pm6.7$</td>
<td>$88\pm6.6$</td>
<td>$89\pm8.9$</td>
<td>$102\pm11.0$</td>
<td>$128\pm12.0$</td>
<td></td>
<td>$105\pm5.5$</td>
<td>$105\pm8.5$</td>
</tr>
<tr>
<td>DM</td>
<td>$7.7\pm0.50$</td>
<td>$5.4\pm0.44$</td>
<td>$5.6\pm0.62$</td>
<td>$7.7\pm0.94$</td>
<td>$11.9\pm1.18$</td>
<td></td>
<td>$8.3\pm0.50$</td>
<td>$7.8\pm0.67$</td>
</tr>
<tr>
<td>NDF</td>
<td>$3.8\pm0.22$</td>
<td>$2.5\pm0.15$</td>
<td>$2.6\pm0.28$</td>
<td>$3.9\pm0.44$</td>
<td>$6.2\pm0.54$</td>
<td></td>
<td>$4.1\pm0.22$</td>
<td>$3.8\pm0.26$</td>
</tr>
</tbody>
</table>

$\dagger$ = SEM
Table 5.1.5. The weight (Wt; g.kg$^{-1}$) and volume (Vol; ml.kg$^{-1}$) of rumen digesta the weight of dry matter (DM; g.kg$^{-1}$) and NDF (g.kg$^{-1}$) in the rumen of sheep grazing spring PG (expt.3) and lucerne (expt.4).

<table>
<thead>
<tr>
<th></th>
<th>ODDA</th>
<th>PREAM</th>
<th>POSTAM</th>
<th>PREPM</th>
<th>OBB-B</th>
<th>POSTPM</th>
<th>ODD-B</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spring PG</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wt</td>
<td>105±5.9</td>
<td>89±5.1</td>
<td>89±6.5</td>
<td>90±8.8</td>
<td>121±6.5</td>
<td>110±6.7</td>
<td>100±6.2</td>
<td></td>
</tr>
<tr>
<td>Vol</td>
<td>116±3.9</td>
<td>105±6.0</td>
<td>107±5.8</td>
<td>115±7.4</td>
<td>137±9.2</td>
<td>121±6.4</td>
<td>117±6.2</td>
<td></td>
</tr>
<tr>
<td>DM</td>
<td>12.4±1.28</td>
<td>9.4±0.76</td>
<td>9.6±0.73</td>
<td>9.1±1.14</td>
<td>15.0±1.00</td>
<td>13.2±1.03</td>
<td>11.0±0.97</td>
<td></td>
</tr>
<tr>
<td>NDF</td>
<td>7.0±1.27</td>
<td>4.9±0.59</td>
<td>5.3±0.79</td>
<td>5.0±0.78</td>
<td>7.8±0.69</td>
<td>7.2±0.94</td>
<td>6.2±0.81</td>
<td></td>
</tr>
<tr>
<td><strong>Lucerne</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wt</td>
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<td>65±2.2</td>
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<td>113±6.2</td>
<td>112±8.3</td>
<td>118±10.8</td>
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<td>140±16.7</td>
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</tr>
<tr>
<td>DM</td>
<td>10.0±0.71</td>
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<td>7.2±0.41</td>
<td>7.2±0.50</td>
<td>7.0±0.85</td>
<td>11.3±1.19</td>
<td>8.5±0.44</td>
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</tr>
<tr>
<td>NDF</td>
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<td>3.6±0.30</td>
<td>3.0±0.17</td>
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¶ = SEM
Table 5.1.6. The concentration of dry matter (gDM.kg digesta$^{-1}$), organic matter in DM (gOM.kgDM$^{-1}$) and NDF content of rumen OM (gNDF.kgOM$^{-1}$) throughout the day in grazing sheep.

<table>
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<tr>
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<th>ODD-A</th>
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<th>POSTPM</th>
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<tr>
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<td>595±13.9</td>
<td>593±20.1</td>
<td>588±19.4</td>
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<td><strong>Winter PG</strong></td>
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<td>89±3.1</td>
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<td>DM</td>
<td>118±7.2</td>
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<td>107±6.3</td>
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<td><strong>Lucerne</strong></td>
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<td>111±4.2</td>
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<td>106±4.7</td>
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<td>845±4.3</td>
<td>850±8.4</td>
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<td>441±18.4</td>
<td>384±11.5</td>
<td></td>
</tr>
</tbody>
</table>

¶ = SEM
5.1.4.1 Intake

The possibility of animals eating at maintenance levels appeared to be overcome by restricting intake prior to the experiments. In all experiments ME intake exceeded maintenance ME requirements (1.4, 1.6, 1.9 and 2.0 × maintenance for summer PG, winter PG, spring PG and lucerne, respectively), the differences perhaps being due to changes in energy demand.

5.1.4.2 Rumen fill

The grazing pattern was consistent in all experiments, showing a general rise in grazing intensity between sunrise and sunset with a smaller grazing period during the night. There was little evidence of a distinct break between morning and afternoon grazing periods as was observed by Hughes & Reid (1951), Lancashire & Keogh (1966) and Arnold (1981). The total grazing time was within the ranges previously reported of 7.8–10.5 h.d⁻¹ (Hughes & Reid, 1951) and 8.7–9.2 h.d⁻¹ (Arnold, 1975) for mixed grass-legume pastures and 8.6–11.0 and 7.0–8.6 h.d⁻¹ for ryegrass and white clover respectively (Lancashire & Keogh, 1966). However, they are well below the maximum grazing time of 13h.d⁻¹ observed by Allden & Whittaker (1970) for sheep grazing sparse pasture. It is therefore unlikely that grazing time placed any limitation on intake.

The distinctive diurnal pattern of rumen fill was similar to that observed in young lambs grazing pure pasture species (see appendix 2) and 1 year old sheep grazing a mixed species pasture (Ulyatt, 1971). However, these experiments appear to be the first to extend studies over the whole day and to validate the presence and magnitude of these changes. The pattern of rumen fill was unexpected given the importance placed upon physical regulation of intake in grazing animals (Freer, 1981). However, changes in rumen fill were closely related to the grazing pattern, although it is of interest to note that little change in fill occurred during the morning, despite increasing grazing intensity. Thus it would appear that rumen fill was dependent upon the grazing pattern and not vice versa. The concept of physical regulation of intake would suggest the latter.

Regulation of the grazing pattern is not easily explained. Despite a low level of rumen fill in the morning there was not a large increase
in grazing intensity, while in the afternoon grazing intensity was increased to result in a dramatic increase in rumen fill. The ability of the sheep to, in most cases, double the rumen OM content during the day suggests that the intake of these herbages was not limited by rumen fill alone. It was calculated from the following equation, assuming there is no change in the fractional disappearance rate from the rumen, that had rumen OM content been maintained at the maximum observed level, OMI would have increased by 24, 52, 29 and 38% for summer PG, winter PG, spring PG and spring L, respectively.

\[
\text{Potential OMI} = \frac{\text{Maximum rumen content}}{\text{Average rumen content}} \times \text{Actual OMI} ----\text{eqn.5.1.1}
\]

For lucerne the digesta typically contained large quantities of froth, although this was not evident on prairie grass. This is in agreement with the observation of Clarke & Reid (1974) that animals grazing legumes have a higher propensity towards frothy bloat than those grazing grasses. The digesta frequently appeared to be under high pressure in the rumen which resulted in a rapid efflux of a considerable proportion of the digesta upon removal of the rumen bung. Applying Boyle's Law, relating the volume of a gas to pressure, the froth would occupy a lower volume when under pressure and therefore the volume measured would overestimate the actual volume in the rumen. Moreover, for lucerne, there were only small changes in the DM% of rumen digesta throughout the day, therefore changes in rumen DM content were mainly associated with changes in the weight of rumen digesta. This is in contrast to the results for prairie grass where both digesta weight and DM% changed.

5.1.4.3 Prediction of changes in rumen fill

An ability to predict changes in rumen fill is an important aspect of any attempt to model, quantitatively, intake regulation and digestion characteristics in grazing animals. A predictive equation, based on marker kinetics is shown overleaf (see appendix 4 for derivation). This equation was applied to the rumen OM and NDF data for winter PG and spring PG.
\[ C_t = IR.k^{-1} + (C_0 - IR.k^{-1})e^{-kt} \]  

where \( C_t \) = rumen content at time \( t \) (g)  
\( C_0 \) = rumen content at time 0 (g)  
\( IR \) = intake rate (g.h\(^{-1}\))  
\( k \) = fractional disappearance rate (h\(^{-1}\))  
\( t \) = time after time 0 (h)

The fractional disappearance rate was assumed to remain constant at the values obtained in section 5.2, which are given for individual sheep in tables 5.1.7-5.1.10. Rate of intake was calculated by assuming that the intake per minute spent grazing remained constant and by calculating the average time spent grazing per hour during each measurement period. For convenience the interval between ODD-A and PRE-AM is referred to as period 1, PRE-AM and POST-AM as period 2, POST-AM and PRE-PM as period 3, PRE-PM and POST-PM as period 4, POST-PM and ODD-B as period 5 and ODD-B and ODD-A as period 6. For each period the actual rumen content was inserted in the equation along with the computed IR and \( k \). The predicted rumen content at the end of the period was compared with the observed rumen content.

The predicted changes in rumen OM and NDF content were, in general, reasonably accurate (tables 5.1.7-5.1.10). However, the magnitude of the predicted changes tended to vary. The data were not intended to test the validity of the equation and several assumptions were made, particularly in the analysis of average values. The variation between predicted and observed changes in rumen fill was examined to postulate upon the validity of the assumptions, inherent to accurate prediction. Inaccurate prediction was likely to be due to variations in grazing behaviour and digesta kinetics, and comparison of predicted and observed changes allows analysis of possible diurnal variation in the rate of intake per minute spent grazing and in \( k \).

In period 1, prior to sunrise, the equation underestimated the magnitude of the change in rumen fill in 7 sheep, whereas in the other sheep an accurate estimation of NDF and an overestimate of OM was observed. In all sheep the predicted change, as a proportion of the observed change, was lower (\( P<0.01 \)) for NDF (0.61±0.066) than for OM (0.84±0.01). This may be, at least partly, explained by considering the validity of assuming a constant \( k \). Assuming that no intake occurred
during this period, and applying first order kinetics (eqn.2.5.2; given below) to the change in rumen OM and NDF content, the minimum value of $k$ required to explain the change in rumen fill can be calculated.

$$C_t = C_0 e^{-kt}$$

where $C_t$ = rumen content at time $t$
$C_0$ = rumen content at time 0

For NDF this minimum value of $k$ was 61% (0.146 v 0.091; P<0.01) and 9% (0.084 v 0.077; N.S.) higher than the average value of $k$, for winter PG and spring PG respectively. For OM the value was 6% higher (0.135 v 0.128; N.S.) for winter PG and 29% lower (0.074 v 0.104; P<0.05) for spring PG. This strongly suggests that, over this period, $k$ was higher than the average value, particularly with respect to NDF.

Period 2, representing the morning grazing period, was typified by small changes in rumen fill. The equation would therefore be sensitive to small changes in rate of intake and predicted rumen fill was inconsistent.

During period 3, in the middle of the day, an increase in rumen fill was predicted. For winter PG this occurred but for spring PG rumen fill tended to decrease, although one sheep showed an increase. This may reflect a decrease in the rate of intake per minute spent grazing during this period for spring PG. This anomaly may be reconciled by considering the observation of Arnold (1981) that grazing intensity decreased around midday during summer, but not in winter. In the present experiment there was no apparent decrease in grazing intensity, but there may have been an equivalent decrease in the rate of intake per minute spent grazing during spring, which did not occur during winter.

During period 4, the major grazing period, represented by a marked increase in rumen fill, the predicted increase in rumen NDF content was significantly lower (P<0.05) than the observed change. The increase in rumen OM content was underestimated (P<0.01) in winter but not in spring. This may reflect an increase in intake per minute spent grazing in winter and/or a decreased $k$ for OM and NDF in winter and NDF in spring, relative to the average value. The latter may be caused by a time lag prior to the onset of NDF digestion (Mertens & Ely, 1979) and reduction in particle size (Poppi et al, 1980).
During period 5, which followed sunset, the decrease in rumen OM fill was predicted with reasonable accuracy in winter but was overestimated (P<0.01) in spring, suggesting a reduction in k in spring. The data for NDF were conflicting. An increased k, relative to the average value, was suggested in winter, whereas a decreased k was suggested in spring.

During period 6, in the middle of the night, inconsistent predictions were obtained in winter. This may be due to the long time interval (6h). This included the midnight grazing period which violated the assumption of a constant rate of intake. In spring a decrease in rumen fill was predicted but only occurred in two sheep, suggesting a possible reduction in k.

These interpretations suggest that the equation, in its present form, did not predict changes in rumen OM and NDF content accurately, due to changes in the rate of intake per minute spent grazing and rumen function throughout the day. However, comparison of predicted and observed changes in this manner suggested a diurnal variation in k and the rate of intake per minute spent grazing in grazing sheep. With a knowledge of these factors the equation may be modified to predict accurately changes in rumen fill. This appears to be the first study where these changes have been observed in grazing sheep and provides a basis on which to base future, controlled, experiments.

5.1.5 CONCLUSIONS

The rumen fill, in terms of volume and weight of digesta, and OM and NDF content, showed a distinct diurnal pattern of variation. This was associated with changes in grazing intensity, although changes in fractional outflow rate of digesta from the rumen and intake rate per minute spent grazing also appeared to influence the magnitude of the changes. The pattern of fill was affected by daylength, such that the maximum fill always occurred at sunset. The magnitude of the changes was substantial and suggested that substantial increases in intake could be achieved by increasing rumen OM content during periods of the day when rumen content was low. These results seriously challenge the concept that the physical capacity of the rumen is the major limitation to intake in grazing sheep.
Table 5.1.7. Prediction of rumen organic matter content \( (C_t; \text{g}) \) from the rate of intake \( (\text{IR}; \text{g.h}^{-1}) \) grazing time \( (\text{GT}; \text{h}) \), fractional disappearance rate \( (k_{\text{OM}}) \) and the initial rumen OM content \( (C_0; \text{g}) \) in 4 sheep grazing winter PG (expt.2), and comparison with observed \( C_t \).

<table>
<thead>
<tr>
<th>Period</th>
<th>GT</th>
<th>IR</th>
<th>( C_0 )</th>
<th>Predicted ( C_t )</th>
<th>Observed ( C_t )</th>
</tr>
</thead>
<tbody>
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<td>Sheep 1, ( k_{\text{OM}} = 0.121 )</td>
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<tr>
<td>1</td>
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Table 5.1.8. Prediction of rumen NDF content (C_t; g) from the rate of NDF intake (IR; g.h⁻¹) grazing time (GT; h), fractional disappearance rate (k_{NDF}) and the initial rumen NDF content (C_0; g) in 4 sheep grazing winter PG (expt.2), and comparison with observed C_t.

<table>
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<th>Period</th>
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<th>Observed C_t</th>
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<td>16.1</td>
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Table 5.1.9. Prediction of rumen organic matter content \( (C_t; g) \) from the rate of intake \( (IR; g \cdot h^{-1}) \) grazing time \( (GT; h) \), fractional disappearance rate \( (k_{OM}) \) and the initial rumen OM content \( (C_0; g) \) in 4 sheep grazing spring PG (expt.3), and comparison with observed \( C_t \).

<table>
<thead>
<tr>
<th>Period</th>
<th>GT</th>
<th>IR</th>
<th>( C_0 )</th>
<th>Predicted ( C_t )</th>
<th>Observed ( C_t )</th>
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<tr>
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<tr>
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<td>688</td>
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</tr>
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<td>975</td>
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<td>994</td>
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</tr>
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<td>723</td>
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<td>55.7</td>
<td>834</td>
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<td>723</td>
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<td>648</td>
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<td>Sheep 4, ( k = 0.105 )</td>
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<td>674</td>
<td>581</td>
<td>562</td>
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Table 5.1.10. Prediction of rumen NDF content ($C_t; g$) from the rate of NDF intake ($IR; g.h^{-1}$) grazing time ($GT; h$), fractional disappearance rate ($k_{NDF}$) and the initial rumen NDF content ($C_0; g$) in 4 sheep grazing spring PG (expt.3), and comparison with observed $C_t$.

<table>
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<th>Period</th>
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<th>Predicted $C_t$</th>
<th>Observed $C_t$</th>
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</tr>
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<td>666</td>
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<td>24.8</td>
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<td>584</td>
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<td>4</td>
<td>16.2</td>
<td>384</td>
<td>346</td>
<td>320</td>
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5.2 THE RETENTION TIME OF DIGESTA IN THE RUMEN OF SHEEP GRAZING HIGH QUALITY HERBAGES

5.2.1 INTRODUCTION

The importance of retention time of digesta in the rumen (RT) has been discussed in sections 2.2.2 and 2.3.2.2. Briefly, RT is an important determinant of the extent of digestion in the rumen and is therefore important in determining the amount and type of nutrients absorbed by the animal. Secondly, RT is important in determining the quantity of digesta present in the rumen and, as such, may have important implications for intake regulation.

Legumes tend to display lower retention times than grasses (Thornton & Minson, 1972, 1973) and these appear to be very low in grazed herbage (Ulyatt, 1971). However, the absence of steady state conditions in grazing animals has severely hampered attempts to study the RT of grazed herbage and the values obtained have been subject to potentially large errors (Ulyatt, 1971).

In this series of experiments the retention time of digesta in the rumen was estimated from the rate of disappearance of organic matter and NDF from the rumen in fasted sheep and from the average rumen organic matter and NDF content and intake in grazing sheep, following the techniques described in section 2.5.4. Retention time was estimated in early weaned lambs and in older sheep. A total of six experiments were conducted to compare the two techniques and to obtain estimates of the rumen retention time of high quality legumes and grasses.
5.2.2 MATERIALS AND METHODS

5.2.2.1 Animals and management

An outline of the pasture species, animal age and the techniques used in each experiment is given in table 5.2.1.

Expt. 1. Forty Dorset Down x Border Corriedale wether lambs were weaned at 6 weeks of age and allocated to either ryegrass (R) or white clover (C) swards, offered at high allowances of 7 and 6 kgDM/lamb/day, respectively. These were slaughtered at 8 weeks of age to estimate RT from the rate of disappearance of digesta during fasting (techniques are described in section 5.2.2.2).

On the sampling day lambs were removed from pasture at midnight and fasted for 6 hours. At 06.00 hours 4 lambs from each pasture were slaughtered and the remaining 16 returned to pasture. When 10 lambs had stopped grazing (approximately 09.00 hours) all lambs were removed from pasture and placed in yards with free access to water but no food. Four lambs were slaughtered at 45 minutes (R) or 60 minutes (C) after removal from pasture and three groups of four lambs were subsequently slaughtered at 4, 8 and 12 hours thereafter.

Expt. 2. Sixty four South Suffolk x Coopworth ram lambs were weaned at 6 weeks of age and allocated to either ryegrass, white clover, prairie grass (P) or lucerne (L) swards. Management details were outlined in section 4.2. At 8 and 12 weeks of age a total of 8 lambs from each pasture species were slaughtered to estimate RT from the rumen digesta content and intake (techniques are explained in section 5.2.2.2). Four slaughter times were selected to represent pre and post grazing in the morning and afternoon grazing periods and 2 lambs were slaughtered from each pasture species at each time.

Expts. 3 and 4. Four 1-2 year old wethers, each fitted with a large rumen cannula, grazed a prairie grass sward, as described in section 5.1 (expt. 1, summer PG and expt. 2, winter PG). The rumen fill and intake data presented in section 5.1, was used to estimate RT. Immediately following these series of sampling the sheep were housed and fasted for the estimation of RT from the rate of disappearance of digesta from the rumen. The initial sample was obtained at the end of the morning grazing period and 4, 8, 12 and 24 hours thereafter.
Expts. 5 and 6. Five 1-2 year old wethers, each fitted with a large rumen cannula, grazed prairie grass (expt. 5, spring PG) and lucerne (expt. 6) swards, as described in section 5.3 (expts. 3 and 4). Firstly, RT was estimated from the average rumen fill and intake. Following this series of sampling the sheep were housed and fasted for the estimation of RT from the rate of digesta disappearance from the rumen. Consideration was given to the diurnal pattern of rumen fill observed in the previous experiments (see section 5.1) and the initial sample was obtained at the end of the afternoon grazing period and at 4, 8, 12 and 18 hours thereafter.

5.2.2.2 Calculation of rumen retention time

There appears to be some confusion in the literature over the use of RT and k. Although RT is, theoretically, the inverse of k, this relationship does not apply to the average of several observations, i.e. \((RT_1 + \ldots + RT_n)/n - 1 \neq n.((k_1 + \ldots + k_n)/n)^{-1}\). Rumen retention time is a descriptive term, and is used as such in this thesis, whereas k is a biological rate constant and is, therefore, the preferred computational value. To avoid confusion and to retain biological accuracy, k is subsequently used to obtain average values and to describe experimental data, and RT is quoted as a descriptive term to facilitate comparison with previously reported data and perceived concepts.

Expt 1. Serial sampling (SS) technique: The natural logarithm of the rumen content of DM, OM and NDF, expressed as g.kg^{-1}, was regressed against the time of slaughter (removal from pasture = t_0). The fractional disappearance rate from the rumen (k), and therefore RT, was derived from the slope of the regression.

Expt 2. Rumen fill (RF) technique: Rumen fill in grazing animals is a function of intake, k and the time of day. Dividing the average intake of DM, OM and NDF (g.h^{-1}) by the rumen content (g) for each lamb yields a value of k which is dependent upon the time of day. Therefore individual values are meaningless, but the average of all 8 lambs will yield a value approximating the average k. The potential error associated with averaging 4 sampling times was assessed from the data of expts 3, 4, 5 and 6, where average rumen fill was estimated over 24 hours.
Expts 3, 4, 5 and 6. Rumen fill technique: The intake of DM, OM and NDF was divided by the average rumen content (estimated from the results presented in section 5.1) for each sheep to give individual estimates of k.

Serial sampling technique: Fractional disappearance rate was estimated from the slope of the regression of the natural log. of rumen content against time fasted for individual sheep (Reid, 1965). Rumen content was corrected for the removal of subsamples by the following equation, which assumes that the digesta removed would have left the rumen at a similar rate to the digesta remaining in the rumen.

\[
\frac{RC_{n+1}}{CRC_{n+1}} = \frac{CRC_n}{RC_n - DR_n} \times CRC_n \quad \text{eqn.5.2.1}
\]

where
- **CRC**\(_{n+1}\) = corrected rumen contents (g)
- **CRC**\(_n\) = corrected rumen contents at previous sample (g)
- **RC**\(_{n+1}\) = actual rumen content (g)
- **RC**\(_n\) = rumen content at previous sample (g)
- **DR**\(_n\) = weight removed from previous sample (g)

Statistical analysis

The results were analysed by analysis of variance, student's t test and paired t test, where applicable.
Table 5.2.1. Experimental procedures. The age of sheep used, pasture species studied and the techniques used to estimate the retention time of digesta in the rumen.

<table>
<thead>
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<th>Expt.</th>
<th>Pasture species</th>
<th>Age</th>
<th>Technique</th>
</tr>
</thead>
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<tr>
<td></td>
<td></td>
<td></td>
<td>SS RF</td>
</tr>
<tr>
<td>1</td>
<td>Ryegrass</td>
<td>8 weeks</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>White clover</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Ryegrass</td>
<td>8&amp;12 weeks</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>Prairie grass</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>White clover</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lucerne</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Prairie grass</td>
<td>1-2 years</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>4</td>
<td>Prairie grass</td>
<td>1-2 years</td>
<td>X</td>
</tr>
<tr>
<td></td>
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<td>X</td>
</tr>
<tr>
<td>5</td>
<td>Prairie grass</td>
<td>1-2 years</td>
<td>X</td>
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<tr>
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<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>6</td>
<td>Lucerne</td>
<td>1-2 years</td>
<td>X</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>X</td>
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</table>
5.2.3 RESULTS

5.2.3.1 Experiment 1.

The regressions of rumen DM, OM and NDF content (g.kgW\(^{-1}\)) against time fasted, along with the respective rumen retention times of DM, OM and NDF for ryegrass and white clover are shown in table 5.2.2,a. The individual values of rumen OM content and the logarithmic regressions are shown in figure 5.2.1. Due to the similarity in rumen fill between the final two slaughter periods, suggesting a deviation from first-order kinetics, the regressions were recalculated excluding the last period and these are shown in table 5.2.2,b, along with the respective rumen retention times. There was no difference in the retention time of DM, OM or NDF between R and C. Similarly the retention times of DM, OM and NDF were similar within plant species. When the last period was excluded the retention time of DM and OM was reduced, but remained similar for NDF. The rumen content of DM, OM and NDF (g.kgW\(^{-1}\)) was significantly higher (P<0.01) for lambs on R at all times.

5.2.3.2 Experiment 2.

The intake and digestibility of ingested herbage have been discussed in section 4.2. The rumen OM content (g.kgW\(^{-1}\)) is shown in appendix 2. The fractional disappearance rate of DM (k\(_{DM}\)), OM (k\(_{OM}\)) and NDF (k\(_{NDF}\)), together with retention times (RT), are shown for lambs of 8 and 12 weeks of age in table 5.2.3. Legumes had significantly (P<0.05) higher k\(_{DM}\) (0.215-0.374 v 0.090-0.140) and k\(_{OM}\) (0.217-0.367 v 0.088-0.142) than grasses. The difference was reduced for k\(_{NDF}\) (0.112-0.203 v 0.082-0.096, for legumes and grasses respectively), but lucerne still showed the highest value. Within species k\(_{DM}\) and k\(_{OM}\) tended to be similar, but k\(_{NDF}\) was 49 and 22% lower, for legumes and grasses respectively (P<0.01). With the exception of C k tended to be higher at 8 weeks of age than at 12 weeks of age, although this was only significant (P<0.05) for P k\(_{DM}\) and k\(_{OM}\).

The data from expts. 3, 4, 5 and 6 were analysed to assess the difference in rumen fill obtained by averaging 4 sampling times, as compared to the average rumen fill, measured over 24 hours. The rumen fill obtained by averaging 4 sampling points was 0.97 ± 0.007 of the average rumen fill, thus justifying the acceptance of the results of expt.2.
5.2.3.3 Experiments 3, 4, 5 and 6.

The intake, rumen fill and digestibility of ingested herbage have been discussed in section 5.1. The regression relating $\log_e$ rumen content to time fasted tended to deviate from linearity at low rumen fill. This is illustrated in figure 5.2.2 for the average rate of organic matter disappearance from the rumen in expts 3 and 5, when the initial sample was standardised at 1000 for each animal. For this reason the last sampling point was excluded from the analysis. The values for $k$ and RT are given in table 5.2.4.

Estimation of $k$ by the SS technique gave values of $k_{DM}$, $k_{OM}$ and $k_{NDF}$ which were similar within animals. These were, in general, considerably lower than the values of $k$ obtained by the RF technique, particularly in summer PG and winter PG when $k$ (SS technique) was estimated following the morning grazing period. With the exception of summer PG the RF technique yielded values for $k_{DM}$ which were higher than $k_{OM}$. In all experiments the RF technique gave values of $k_{NDF}$ which were markedly lower than $k_{DM}$ and $k_{OM}$. This resulted in a closer agreement of $k_{NDF}$ between the two techniques, particularly in spring PG and L, where $k$ was estimated following the afternoon grazing periods. However, only in spring PG 5 was $k_{NDF}$ similar.

Estimated from the RF technique, sheep grazing L exhibited higher $k_{DM}$ (17-49%, $P<0.01$) and $k_{OM}$ (16-43%, $P<0.01$) than sheep grazing P, but $k_{NDF}$ was similar for L, winter PG and spring PG (0.089-0.095).
Figure 5.2.1 Rumen organic matter content of lambs (gOM.kg$^{-1}$) in expt.1 along with the regressions given in table 5.2.2,a of rumen OM content against time fasted after removal from pasture ($t_0$).
Figure 5.2.2 The disappearance of organic matter from the rumen of fasted sheep, plotted on a logarithmic scale to show deviation from first order kinetics. Initial rumen organic matter content was standardised at 1000.
Table 5.2.2. The retention time (RT) of dry matter (DM), organic matter (OM) and NDF in the rumen of lambs grazing ryegrass (R) and white clover (C) in expt.1, and the regression equations relating $\log_e$ rumen content (g.kg$^{-1}$; y) to time fasted (hours; t) using 4 (a) and 3 (b) sampling times.

(a) 4 sampling times

<table>
<thead>
<tr>
<th></th>
<th>regression equation</th>
<th>$^2$</th>
<th>RT</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>$y = 11.21e^{-0.068t}$</td>
<td>0.672</td>
<td>14.7</td>
</tr>
<tr>
<td>C</td>
<td>$y = 5.31e^{-0.068t}$</td>
<td>0.723</td>
<td>14.6</td>
</tr>
<tr>
<td>OM</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>$y = 9.36e^{-0.072t}$</td>
<td>0.743</td>
<td>13.9</td>
</tr>
<tr>
<td>C</td>
<td>$y = 4.40e^{-0.074t}$</td>
<td>0.790</td>
<td>13.5</td>
</tr>
<tr>
<td>NDF</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>$y = 6.57e^{-0.085t}$</td>
<td>0.654</td>
<td>11.7</td>
</tr>
<tr>
<td>C</td>
<td>$y = 1.65e^{-0.070t}$</td>
<td>0.526</td>
<td>14.2</td>
</tr>
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</table>

(b) 3 sampling times

<table>
<thead>
<tr>
<th></th>
<th>regression equation</th>
<th>$^2$</th>
<th>RT</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>$y = 11.58e^{-0.077t}$</td>
<td>0.645</td>
<td>13.0</td>
</tr>
<tr>
<td>C</td>
<td>$y = 5.65e^{-0.085t}$</td>
<td>0.848</td>
<td>11.8</td>
</tr>
<tr>
<td>OM</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>$y = 9.61e^{-0.080t}$</td>
<td>0.702</td>
<td>12.5</td>
</tr>
<tr>
<td>C</td>
<td>$y = 4.68e^{-0.090t}$</td>
<td>0.726</td>
<td>11.1</td>
</tr>
<tr>
<td>NDF</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>$y = 6.48e^{-0.081t}$</td>
<td>0.575</td>
<td>12.3</td>
</tr>
<tr>
<td>C</td>
<td>$y = 1.66e^{-0.071t}$</td>
<td>0.332</td>
<td>14.0</td>
</tr>
</tbody>
</table>
Table 5.2.3. The fractional disappearance rate \((k; \text{h}^{-1})\) and retention time \((RT)\) of dry matter \((DM)\), organic matter \((OM)\) and NDF in the rumen of lambs grazing prairie grass \((P)\), ryegrass \((R)\), white clover \((C)\) and lucerne \((L)\), estimated by the rumen fill technique at 8 and 12 weeks of age.

<table>
<thead>
<tr>
<th>Plant</th>
<th>Age</th>
<th>DM</th>
<th>OM</th>
<th>NDF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(k)</td>
<td>RT</td>
<td>(k)</td>
</tr>
<tr>
<td>Species</td>
<td></td>
<td>(k)</td>
<td>RT</td>
<td>(k)</td>
</tr>
<tr>
<td>(P)</td>
<td>8</td>
<td>0.130(^b)</td>
<td>7.7</td>
<td>0.129(^b)</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>0.090(^a)</td>
<td>11.1</td>
<td>0.088(^a)</td>
</tr>
<tr>
<td>(R)</td>
<td>8</td>
<td>0.142(^b)</td>
<td>7.0</td>
<td>0.142(^b)</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>0.113(^{ab})</td>
<td>8.9</td>
<td>0.112(^{ab})</td>
</tr>
<tr>
<td>(C)</td>
<td>8</td>
<td>0.215(^c)</td>
<td>4.7</td>
<td>0.217(^c)</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>0.255(^c)</td>
<td>3.9</td>
<td>0.256(^c)</td>
</tr>
<tr>
<td>(L)</td>
<td>8</td>
<td>0.374(^d)</td>
<td>2.7</td>
<td>0.367(^d)</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>0.315(^{cd})</td>
<td>3.2</td>
<td>0.318(^{cd})</td>
</tr>
</tbody>
</table>

Different superscripts within columns represent significant differences \((P<0.05)\)
Table 5.2.4. The fractional disappearance rate ($k$) from, and retention time (RT) in the rumen of dry matter (DM), organic matter (OM) and NDF, estimated by the serial sampling and rumen fill techniques, in sheep grazing prairie grass in summer (expt. 3), winter (expt. 4) and spring (expt. 5), and lucerne (expt. 6).

<table>
<thead>
<tr>
<th>Expt.</th>
<th>Technique</th>
<th>$k_{DM}$</th>
<th>$k_{OM}$</th>
<th>$k_{NDF}$</th>
<th>$RT_{DM}$</th>
<th>$RT_{OM}$</th>
<th>$RT_{NDF}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>RF</td>
<td>0.103</td>
<td>0.104</td>
<td>0.064</td>
<td>9.7</td>
<td>9.6</td>
<td>15.6</td>
</tr>
<tr>
<td></td>
<td>SSa</td>
<td>0.040</td>
<td>0.045</td>
<td>0.045</td>
<td>25.1</td>
<td>22.4</td>
<td>22.4</td>
</tr>
<tr>
<td>4</td>
<td>RF</td>
<td>0.131</td>
<td>0.128</td>
<td>0.091</td>
<td>7.6</td>
<td>7.8</td>
<td>11.0</td>
</tr>
<tr>
<td></td>
<td>SSa</td>
<td>0.046</td>
<td>0.050</td>
<td>0.053</td>
<td>21.7</td>
<td>19.9</td>
<td>18.9</td>
</tr>
<tr>
<td>5</td>
<td>RF</td>
<td>0.116</td>
<td>0.109</td>
<td>0.089</td>
<td>8.6</td>
<td>9.2</td>
<td>11.3</td>
</tr>
<tr>
<td></td>
<td>SSb</td>
<td>0.073</td>
<td>0.079</td>
<td>0.085</td>
<td>13.7</td>
<td>12.7</td>
<td>11.8</td>
</tr>
<tr>
<td>6</td>
<td>RF</td>
<td>0.153</td>
<td>0.149</td>
<td>0.095</td>
<td>6.5</td>
<td>6.7</td>
<td>10.5</td>
</tr>
<tr>
<td></td>
<td>SSb</td>
<td>0.082</td>
<td>0.086</td>
<td>0.077</td>
<td>12.2</td>
<td>11.6</td>
<td>13.0</td>
</tr>
</tbody>
</table>

a SS technique carried out after morning grazing period
b SS technique carried out after afternoon grazing period
5.2.4 DISCUSSION

The estimation of rumen retention time in grazing animals is complicated by the absence of steady state conditions. Two techniques were identified as having potential for accurate estimation. These were employed, and compared, in early weaned lambs and older wethers. The use of older sheep facilitated manual rumen emptying, therefore removing between animal variation and allowing more accurate comparisons to be made. Retention time was then measured on a range of plant species, using both early weaned lambs and older wethers, to assess the differences caused by plant species.

5.2.4.1 Validation of rumen fill technique

The rumen fill (RF) technique was developed by Minson (1966) for application in steady state conditions. Ulyatt (1971) subsequently applied the technique to grazing sheep but did not make any allowance for the diurnal variations in rumen fill. The present experiments appear to be the first to study, quantitatively, the changes in rumen fill over the whole day. Derivation of k from these data requires correction for the diurnal pattern of rumen fill and this can only be achieved by considering the average daily intake and the average rumen fill. Over a 24 hour period the quantity of digesta leaving the rumen will equal the quantity consumed and with a knowledge of the average rumen fill an average value of k can be estimated from the following equation (adapted from Minson, 1966, eqn.2.5.1).

\[
\frac{\text{average intake (g.h}^{-1})}{\text{average rumen fill (g)}} = k
\]

Firstly, average hourly intake was estimated by dividing daily intake by 24. Secondly, the average rumen fill was obtained by graphing rumen content (g) against time of day (0-24h). The area under the graph (gh) was divided by the number of hours to give the average rumen fill (g). These units are the same as used by Minson (1966). It is important to realise that the resultant value of k represents an average hourly value and takes no account of diurnal variations of k. This value was calculated for ease of comparison with existing data.
Accurate estimation of $k$ by the RF technique depends upon the following factors and assumptions.

1. Pattern of rumen fill. An accurate pattern of rumen fill is essential and this requires accurate estimation of the grazing pattern, so that sampling times correspond with major changes in grazing intensity. The most critical period is the end of the afternoon grazing period when grazing intensity changes rapidly from a high value (e.g. 45-50 minutes per hour) to a low value (e.g. 5-10 minutes per hour; see section 5.1), leading to comparatively rapid changes in rumen fill. An error in sampling time would lead to erroneous estimation of the average rumen fill and, therefore, $k$.

2. Calculation of average rumen fill. The change in rumen fill between sampling times was assumed to be linear. This is unlikely to be an accurate representation as changes in rumen fill will probably be curvilinear (see appendix 4 for a theoretical description of rates of change of rumen fill). However, the assumption will lead to minimal error as the rumen fill at the sampling times is the major determinant of average rumen fill.

3. Assumption of a constant $k$. The variation in rumen fill throughout the day is substantial (see section 5.1). It is therefore unlikely that a single constant value of $k$ for a particular plant species exists (see also section 5.1.4.3). However, no technique has been developed to allow measurement of short-term values of $k$ and the paucity of data make the estimation of an "average" $k$ of significant benefit.

4. Sampling technique. The measurement of rumen digesta content requires the manual removal of all rumen contents. Although the entire procedure took under 10 minutes to perform it would disrupt the stratification of digesta in the rumen, possibly leading to a reduction in the rate of passage from the rumen. Also, exposure of the digesta to the low temperature and high oxygen content of the atmosphere may reduce the microbial population, leading to a subsequent decline in the rate of digestion. The latter was minimised by placing the digesta in a heated water bath (39-40°C), which maintained the temperature of the digesta at 37-38°C. No control could be exerted over the disruption of stratification as representative subsampling was essential for accurate analysis. However, the sheep did not appear to suffer any ill effects.
Rumination frequently commenced immediately upon return of digesta and grazing always commenced immediately upon return to pasture. Also, there was no apparent reduction in rumen fill throughout the measurement periods, when replicates were compared. A complete set of data from a sheep grazing winter PG, relating to rumen DM content, is shown in table 5.2.5. Mixing of digesta may have contributed to the reduced values of k obtained by the SS technique, but this is felt to be unimportant as the digesta appeared homogeneous with no apparent stratification.

Recently, Towne et al (1986) studied the influence of manual rumen emptying, mixing and returning rumen contents on microbial populations, VFA concentrations and fractional outflow rate of Cr-EDTA from the rumen of cattle. They concluded that these procedures did not affect microbial activity or liquid passage from the rumen. These results support the acceptance of data obtained by manual rumen emptying.

5.2.4.2 Comparison of techniques

Comparison of the rumen fill technique, modified for use in grazing sheep, and the serial sampling technique was undertaken in expts. 3, 4, 5 and 6. The values of k obtained by the SS technique tended to decrease as the length of fasting increased. This may have been due to changes in the composition of digesta in the rumen but was more probably associated with the decreasing rumen fill. Decreasing intake tends to decrease rumen fill and k (Campling et al, 1961; Minson, 1966) and it is therefore likely that rumen fill will have a direct effect on k. This effect was minimised, but not removed, by excluding the final sample from analysis.

For summer PG and winter PG, where sampling followed the morning grazing period, the SS technique yielded values which were only 37% ($k_{DM}$), 41% ($k_{OM}$) and 64% ($k_{NDF}$) of the values estimated by the RF technique. However, for spring PG and spring L, where sampling followed the afternoon grazing period, the difference was reduced and the values of $k_{DM}$, $k_{OM}$ and $k_{NDF}$ were 58%, 65% and 88%, respectively, of the values obtained by the RF technique. In section 5.1 rumen fill was observed to be considerably higher following the afternoon grazing period than following the morning grazing period. The differences in rumen fill at the start of fasting may have affected the observed value of k in a similar fashion to the level of intake effect mentioned earlier. If this was really the case it suggests that k may vary throughout the day, depending upon rumen fill. However, during fasting the rumen fill soon
fell below the levels observed in grazing sheep and changes in k, caused by changes in rumen fill, may be unimportant at the levels of fill observed in grazing animals.

The SS technique gave higher values of $k_{OM}$ compared to $k_{DM}$, whereas the RF technique tended to do the reverse. Values of $k_{NDF}$ were similar to $k_{OM}$ and $k_{DM}$ for the SS technique but were significantly (P<0.01) lower for the RF technique. This resulted in closer agreement between the techniques for estimated $k_{NDF}$, suggesting that the low values of $k_{DM}$ and $k_{OM}$ obtained by the SS technique were only partly caused by the changes in rumen fill. The major discrepancy was associated with the NDF-free OM and may, at least partly, be explained by the rumen microflora. The SS technique depends upon removal of digesta by passage and digestion and addition of material, e.g. eating, invalidates the technique. Continual renewal of the microflora may influence the accuracy of $k_{OM}$ estimated by the SS technique. This is supported by the data of Moseley (1981) who observed a relatively constant microbial biomass throughout the day in sheep offered fresh herbages once daily (approximately 70-80g microbial DM, equivalent to approximately 16 and 33% of the total rumen DM content at 3 and 24 hours post-feeding, respectively). This constancy will prevent the OM in the rumen from displaying first order kinetics. The lower k values obtained with the SS technique were, therefore, likely to have been caused by low rumen fill and the maintenance of rumen microbial synthesis.

Therefore, it would appear that the RF technique yielded more accurate values of $k_{DM}$ and $k_{OM}$, although similar values of $k_{NDF}$ were obtained by either technique, provided that rumen fill was high prior to estimation by the SS technique. For this reason, only results obtained by the RF technique will be discussed in the following sections.

5.2.4.3 Plant species

The VFC of roughages has been shown to be closely related to the retention time of OM in the rumen (Thornton & Minson, 1972, 1973) and the superior intake by sheep offered legumes, compared to grasses, has been attributed, at least partly, to the higher k observed in legumes (Ulyatt, 1971). However, the only estimates of k in grazing sheep appear to be those of Ulyatt (1971) and none appear to exist for young lambs. It is important to have an appreciation of the influence of plant species on k to understand the differences in intake achieved. Similarly, the higher k
observed with legume diets could have important implications for the quantity and type of nutrients absorbed.

The values of $k_{DM}$ and $k_{OM}$ were higher for legumes than for grasses (expts. 2, 5 and 6). However, the value for $k_{NDF}$ was similar for prairie grass and lucerne (expts. 5 and 6) and for prairie grass, ryegrass and white clover (expt. 2), although lucerne exhibited a higher value than prairie grass and ryegrass (expt. 2). The only data relating to the RT of grazed herbage appear to be those of Ulyatt (1971) who observed a shorter $RT_{OM}$ in sheep grazing white clover (5.6-6.3 h) compared to perennial ryegrass (8.6-10.4 h). However, in that study sheep were removed from pasture between 08.00 and 11.00 hours and slaughtered within 1 hour of removal from pasture. This would lead to an underestimate of the true RT value due to the low level of rumen fill which would be expected at that time of day and to the long interval between removal from pasture and slaughter. Despite this large potential for error the values obtained by Ulyatt (1971) for ryegrass were similar to prairie grass in the present experiment ($RT_{OM}$, 7.0-11.3 h) and for white clover were similar to lucerne in expt. 6 ($RT_{OM}$, 6.7 h). However, the estimates of $RT_{OM}$ obtained for legumes in expt. 2 (2.6-4.6 h) were considerably lower than observed by Ulyatt (1971). No estimates of $k_{NDF}$ were obtained by Ulyatt (1971).

Thornton & Minson (1973), studying a range of dried herbages, observed a similar average $RT_{OM}$ for legumes and grasses. However, the digestibility of the legumes tended to be lower than grasses and $RT_{OM}$ was considerably lower, and DOMI higher, for legumes at a similar digestibility. Again, no estimates of $k_{NDF}$ were obtained.

The consistent observation that rumen fill is lower when white clover is offered than when ryegrass is offered, despite similar or higher intake (McLean et al., 1962, 1965; Johns et al., 1963; Ulyatt, 1971; Jagusch et al., 1976), suggests that clover has a higher k value than grass, as was observed in these experiments.

These data suggest that $k_{DM}$ and $k_{OM}$ varied significantly between plant species. The similarity in $k_{NDF}$ between plant species was unexpected as the higher $k_{OM}$ observed with legumes is generally attributed to increases in the rate of particle breakdown and passage of legumes (Moseley, 1981) which lead to increased passage rate of NDF. This suggested that the major cause of the higher $k_{OM}$ observed with legumes
was due to differences in the fibre content of the plant species, leading to differences in the fractional digestion and passage rates of OM.

5.2.4.4 Influence of age of animal on retention time

Although no direct comparison was made between ages, the pastures grazed by early weaned lambs in expt. 2 and by wethers in expts. 5 and 6 were similar in composition and stage of growth. For grasses, age had little effect on $k_{OM}$ (0.118 and 0.109 for early weaned lambs and wethers, respectively) or $k_{NDF}$ (0.090 and 0.089). However, for legumes there were large differences in $k_{OM}$ (0.290 and 0.149 for early weaned lambs and wethers, respectively) and in $k_{NDF}$ (0.150 and 0.095). These data for early weaned lambs are extremely high, particularly for L. This supports the observation of Jagusch et al. (1976) that young lambs grazing lucerne were susceptible to 'red gut', which appeared to be caused by extremely short RT of digesta in the rumen, but that older lambs and adult sheep were not. It also suggests that rumen function may differ between young lambs and adult sheep consuming high quality legume diets, but not when consuming high quality grass diets.

5.2.5 CONCLUSIONS

It was concluded that the SS technique was not an accurate technique for the estimation of $k_{DM}$ or $k_{OM}$, although $k_{NDF}$ was estimated with reasonable accuracy, provided rumen fill is high initially and the period of fasting is not unduly long. Legumes tend to exhibit higher $k_{DM}$ and $k_{OM}$ than grasses, estimated from the RF technique, although the difference was reduced for $k_{NDF}$. The higher k values observed with legumes were particularly marked in early weaned lambs and suggest that these young lambs had the ability to increase $k_{p}$ and/or $k_{d}$, particularly when grazing lucerne. This was consistent with the occurrence of red gut in young lambs and suggests that, although high values of k are advantageous, very high values may be detrimental to animal health.
Table 5.2.5. A complete set of rumen dry matter content, obtained from expt. 4 (winter PG), showing the constancy between replicates throughout the experiment.

<table>
<thead>
<tr>
<th>TIME</th>
<th>Sampling</th>
<th>04.00</th>
<th>07.00</th>
<th>10.30</th>
<th>14.30</th>
<th>18.00</th>
<th>22.00</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-3</td>
<td></td>
<td>410</td>
<td>307</td>
<td>301</td>
<td>414</td>
<td>628</td>
<td>441</td>
<td>419</td>
</tr>
<tr>
<td>4-6</td>
<td></td>
<td>406</td>
<td>283</td>
<td>313</td>
<td>406</td>
<td>667</td>
<td>468</td>
<td>428</td>
</tr>
<tr>
<td>7-9</td>
<td></td>
<td>419</td>
<td>277</td>
<td>323</td>
<td>426</td>
<td>642</td>
<td>482</td>
<td>434</td>
</tr>
</tbody>
</table>
5.3 THE EFFECT OF Restricting Rumen Capacity ON INtAKE AND Rumen Function

5.3.1 INTRODUCTION

In section 5.1, it was concluded that the pattern of rumen fill appeared to place an unnecessary limitation on intake and that some factor(s), other than just physical regulation, was involved in the regulation of intake. However, it was not possible to determine if rumen fill was limiting VFC, particularly prior to sunset, or why rumen fill remained low during the morning. However, the observed changes in rumen fill were associated with changes in grazing intensity. If physical regulation was the major limitation to intake it should be possible to increase intake by increasing rumen fill in the morning, although this may not be possible in the afternoon. Alternatively, if intake is limited by metabolic regulation the pattern of fill would be related to the pattern of nutrient supply and nutrient requirement, and rumen fill would be irrelevant. It is likely that intake is limited by a combination of physical and metabolic factors, in which case control of the pattern of rumen fill would be more complex. An understanding of the factors which control the pattern of rumen fill will, therefore, enable analysis of the mode of intake regulation and provide solid guidelines for the formulation of an intake regulation model.

This section describes an experiment which studied the effects of restricting rumen capacity, by inserting water filled balloons, on grazing pattern, rumen fill, pattern of rumen fill, fractional disappearance rate of digesta from the rumen and intake in sheep grazing prairie grass and lucerne. The implications of these results on the overall regulation of intake are assessed.
5.3.2 MATERIALS AND METHODS

5.3.2.1 Animals and feeding

Six wethers, approximately 2 years old (average liveweight, 64.8±2.70kg), and fistulated in the rumen, strip-grazed, on 2 day shifts, prairie grass (P) from 2:10:84 - 10:11:84, along with 3 sheep fistulated in the oesophagus. The herbage mass ranged from 1800-2200 kgDM.ha⁻¹ and the herbage allowance averaged 8.3 kgDM.sheep⁻¹.

Five wethers, fistulated in the rumen (average liveweight, 68.5±3.94kg) and 3 sheep fistulated in the oesophagus strip-grazed, on 2 day shifts, lucerne (L) from 20:11:84 - 23:12:83. The herbage mass ranged from 2940-3370 kgDM.ha⁻¹ and herbage allowance averaged 8.6 kgDM.sheep⁻¹.

5.3.2.2 Experimental design

A cross-over design was adopted within each pasture species, which were studied consecutively. Sheep grazed the experimental pastures for a 7 day preliminary period. Following this the sheep were weighed and balloons were inserted into the rumen, when required. A further 7 day period was allowed before sampling commenced. At the end of sampling the sheep were weighed, balloons inserted in the rumen of the remaining sheep and the procedure repeated. Six sheep, fitted with a large rumen cannula, started the experiment. However, one sheep displayed weight loss, low rumen fill and intake and was subsequently removed from the experiment. Another sheep consistently ejected the rumen bung when balloons were present in the rumen. As a result this sheep was omitted from analysis on both prairie grass and lucerne due to insufficient data. Consequently the data reported in this section were obtained from 4 sheep, of which 2 were controls during each measurement period.

5.3.2.3 Manipulation of rumen capacity

Blood bags (hereafter referred to as balloons) were filled with water and heat sealed. The average volume of the full balloons was 416±8.0 ml. A total of 4-5 balloons, including partially filled balloons, were placed in the rumen, depending on the required volume. Each sheep was weighed 7-10 days prior to the sampling period and balloons, equivalent to 25mlH₂O.kg⁻¹, were inserted into the rumen, via the rumen cannula. The volume inserted was calculated, firstly, from section 5.1
(expts.1 and 2), as the difference between the maximum observed volume of rumen digesta and the average daily volume, such that the average daily volume could be maintained by altering the pattern of rumen fill. Secondly, the balloon volume also corresponded to the difference between the average weight of rumen digesta in sheep grazing prairie grass (section 5.1, expt.1) and white clover in summer. The data for white clover was obtained from a preliminary study (Thomson et al., 1985) and is not reported in this thesis. During the measurement periods the balloons were equivalent to 26.4±0.45 and 25.3±0.47 ml.kgW<sup>-1</sup> on P and L respectively.

5.3.2.4 Measurements

Measurement of intake and rumen fill were as detailed in section 5.1. Sampling times were selected in relation to the grazing pattern, which was monitored with automatic grazing recorders (described in appendix 5) for 7 days prior to the start of sampling. As in section 5.1, sampling times represented, where possible, the start (PRE) and end (POST) of the morning (AM) and afternoon (PM) grazing periods, plus 2 intermediate times (ODD-A and ODD-B), such that the 6 sampling times were at approximately 4 hour intervals of a theoretical 24 hour day. Rumen digesta content was measured twice daily for 7 (L) and 9 (P) days. Balloons were removed from the rumen digesta prior to weighing and subsampling digesta, and were replaced prior to return of the digesta. Following removal from the rumen the digesta was stored in tared buckets, which were placed in a water bath, at 39-40°C, to maintain the temperature of the digesta at 37-38°C. The volume and weight of digesta were recorded and subsamples taken for DM, OM and NDF determination. The density of digesta was estimated from the weight and volume of digesta removed. Fractional disappearance rate of OM (k<sub>OM</sub>) and NDF (k<sub>NDF</sub>) from the rumen was estimated by two techniques, the rumen fill (RF) and serial sampling (SS) techniques, as detailed in section 5.2.
5.3.3 RESULTS

5.3.3.1 Grazing behaviour, intake and digestibility

Balloons did not affect the grazing pattern, grazing time or organic matter digestibility (table 5.3.1). However, the presence of balloons reduced OMI and DOMI (g.d\(^{-1}\)) by 23% (P<0.05) on P and by 9% (N.S.) on L. Intake of OM and DOM (g.d\(^{-1}\)) was higher on L than on P (20 and 26%, respectively, for controls, N.S.; 35 and 40%, respectively, for balloons, P<0.01).

5.3.3.2 Fractional disappearance rate

The fractional disappearance rate of OM (k\(_{OM}\)) and NDF (k\(_{NDF}\)), estimated by the rumen fill (RF) and serial sampling (SS) techniques, are given in table 5.3.2. Balloons were associated with an increased k\(_{OM}\) of 17% (P<0.05) and 23% (P<0.01) in P and L respectively, estimated by the RF technique. The k\(_{NDF}\) increased by 14% (P<0.05) and 26% (N.S.) for P and L respectively. Estimated by the SS technique there was no significant difference between control and balloon sheep for k\(_{OM}\) and k\(_{NDF}\).

5.3.3.3 Rumen fill

There was no difference in the pattern of rumen digesta fill between control and balloon sheep (figure 5.3.1). Balloons were associated with a reduction in the average volume (16 and 9% for P and L respectively) and weight (24 and 16% for P and L respectively) of rumen digesta which was significant (P<0.05) in all but L digesta weight. However, there was an increase in the total rumen content (digesta + balloons) in balloon sheep compared to controls (7 and 2% for P volume and weight, respectively and 12 and 17% for L volume and weight respectively) which was only significantly higher (P<0.05) for L volume (tables 5.3.3 and 5.3.4). The rumen OM content was reduced by balloons throughout the day leading to a decrease of 32 and 26% (N.S.) in average OM content for P and L respectively (table 5.3.5). These differences in average rumen fill were similar to the differences at the end of the afternoon grazing period, which was reflected by the similarity of the pattern on rumen fill.

Balloons tended to reduce (N.S.) the DM% of rumen digesta (table 5.3.6).
Table 5.3.1. Grazing time (GT; h), intake of organic matter (OMI) and digestible OM (DOMI), and digestibility of OM (OMD), of sheep grazing prairie grass (P) and lucerne (L) with (BAL) or without (CON) balloons in the rumen.

<table>
<thead>
<tr>
<th></th>
<th>GT (h)</th>
<th>OMI (g.d(^{-1}))</th>
<th>DOMI (g.d(^{-1}))</th>
<th>OMD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>g.kg(^{-1})</td>
<td>g.kg(^{-1})</td>
<td></td>
</tr>
<tr>
<td>Prairie grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BAL</td>
<td>7.7±0.65(</td>
<td>)</td>
<td>1249±233.0(*)</td>
<td>18.8±2.70(*)</td>
</tr>
<tr>
<td>CON</td>
<td>7.7±0.61(</td>
<td>)</td>
<td>1614±228.6</td>
<td>23.8±2.86</td>
</tr>
<tr>
<td>Lucerne</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BAL</td>
<td>6.3±0.82(</td>
<td>)</td>
<td>1770±318.8</td>
<td>25.3±2.96</td>
</tr>
<tr>
<td>CON</td>
<td>6.6±0.99(</td>
<td>)</td>
<td>1943±117.8</td>
<td>28.6±2.53</td>
</tr>
</tbody>
</table>

\(|\) SEM

\(*\) BAL < CON (P<0.05)
Table 5.3.2. Comparison of the fractional disappearance rate of OM ($k_{OM}$) and NDF ($k_{NDF}$), estimated by the rumen fill (RF) and serial sampling (SS) techniques in sheep grazing prairie grass and lucerne with (BAL) and without (CON) balloons placed in the rumen.

<table>
<thead>
<tr>
<th></th>
<th>RF</th>
<th>SS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$k_{OM}$</td>
<td>$k_{NDF}$</td>
</tr>
<tr>
<td>Prairie grass</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BAL</td>
<td>0.131±0.0082</td>
<td>0.113±0.0076</td>
</tr>
<tr>
<td>CON</td>
<td>0.112±0.0060</td>
<td>0.099±0.0148</td>
</tr>
<tr>
<td>Lucerne</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BAL</td>
<td>0.176±0.0143</td>
<td>0.125±0.0178</td>
</tr>
<tr>
<td>CON</td>
<td>0.143±0.0135</td>
<td>0.099±0.0080</td>
</tr>
</tbody>
</table>

* SEM
Figure 5.3.1 The diurnal pattern of rumen organic matter content in sheep grazing prairie grass with (BAL) or without (CON) balloons in the rumen.
Table 5.3.3. The volume of rumen contents (ml.kg\(^{-1}\)) throughout the day in sheep grazing prairie grass and lucerne with (BAL) or without (CON) balloons in the rumen.

<table>
<thead>
<tr>
<th>Prairie grass</th>
<th>ODDA</th>
<th>PREAM</th>
<th>POSTAM</th>
<th>PREPM</th>
<th>POSTPM</th>
<th>ODDB</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>CON</td>
<td>115±3.9</td>
<td>106±5.1</td>
<td>110±3.6</td>
<td>117±6.8</td>
<td>137±8.9</td>
<td>122±5.8</td>
<td>118±5.2</td>
</tr>
<tr>
<td>BAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-Digesta only</td>
<td>104±11.2</td>
<td>-88±11.9</td>
<td>91±7.1</td>
<td>104±13.0</td>
<td>109±7.4</td>
<td>101±7.0</td>
<td>99±9.0</td>
</tr>
<tr>
<td>-Digesta + balloons</td>
<td>130±11.5</td>
<td>114±11.9</td>
<td>117±7.1</td>
<td>131±13.1</td>
<td>136±7.4</td>
<td>127±7.0</td>
<td>126±8.9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Lucerne</th>
<th>ODDA</th>
<th>PREAM</th>
<th>POSTAM</th>
<th>PREPM</th>
<th>ODDB</th>
<th>POSTPM</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>CON</td>
<td>112±6.8</td>
<td>113±7.9</td>
<td>117±11.2</td>
<td>123±13.0</td>
<td>115±11.7</td>
<td>140±15.7</td>
<td>120±7.9</td>
</tr>
<tr>
<td>BAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-Digesta only</td>
<td>104±6.3</td>
<td>89±11.7</td>
<td>105±6.1</td>
<td>116±15.7</td>
<td>108±7.1</td>
<td>133±18.7</td>
<td>109±8.3</td>
</tr>
<tr>
<td>-Digesta + balloons</td>
<td>129±6.2</td>
<td>114±11.7</td>
<td>130±6.0</td>
<td>141±15.6</td>
<td>133±7.1</td>
<td>158±18.8</td>
<td>134±8.4</td>
</tr>
</tbody>
</table>

\(\dagger\) SEM
Table 5.3.4. The weight of rumen contents (g.kg\(^{-1}\)) throughout the day in sheep grazing prairie grass (PG) and lucerne (L) with (BAL) or without (CON) balloons in the rumen.

<table>
<thead>
<tr>
<th>Prairie grass</th>
<th>ODDA</th>
<th>PREAM</th>
<th>POSTAM</th>
<th>PREPM</th>
<th>POSTPM</th>
<th>ODDB</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>CON</td>
<td>103±10.2</td>
<td>89±9.0</td>
<td>90±9.6</td>
<td>90±10.3</td>
<td>119±12.0</td>
<td>108±11.7</td>
<td>99±10.2</td>
</tr>
<tr>
<td>BAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-Digesta only</td>
<td>77±8.3</td>
<td>68±5.4</td>
<td>63±2.4</td>
<td>74±7.2</td>
<td>84±8.7</td>
<td>86±8.5</td>
<td>75±5.4</td>
</tr>
<tr>
<td>-Digesta + balloons</td>
<td>103±7.9</td>
<td>94±5.2</td>
<td>89±2.0</td>
<td>100±7.5</td>
<td>111±8.4</td>
<td>113±8.4</td>
<td>101±5.3</td>
</tr>
<tr>
<td>Lucerne</td>
<td>ODDA</td>
<td>PREAM</td>
<td>POSTAM</td>
<td>PREPM</td>
<td>ODDB</td>
<td>POSTPM</td>
<td>Average</td>
</tr>
<tr>
<td>CON</td>
<td>86±8.2</td>
<td>73±9.9</td>
<td>65±2.6</td>
<td>65±4.3</td>
<td>71±7.6</td>
<td>91±5.87</td>
<td>75±5.2</td>
</tr>
<tr>
<td>BAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-Digesta only</td>
<td>69±9.8</td>
<td>57±5.5</td>
<td>56±5.2</td>
<td>58±4.9</td>
<td>63±6.9</td>
<td>71±4.47</td>
<td>63±5.8</td>
</tr>
<tr>
<td>-Digesta + balloons</td>
<td>94±9.6</td>
<td>82±5.0</td>
<td>81±4.9</td>
<td>83±4.7</td>
<td>89±6.7</td>
<td>97±4.0</td>
<td>88±5.5</td>
</tr>
</tbody>
</table>

¶ SEM
Table 5.3.5. The rumen organic matter content (g.kg\(^{-1}\)) throughout the day in sheep grazing prairie grass and lucerne with (BAL) or without (CON) balloons in the rumen.

<table>
<thead>
<tr>
<th>Prairie grass</th>
<th>ODDA</th>
<th>PREAM</th>
<th>POSTAM</th>
<th>PREPM</th>
<th>POSTPM</th>
<th>ODDB</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>CON</td>
<td>10.1±1.78</td>
<td>7.2±1.22</td>
<td>7.6±1.18</td>
<td>7.7±1.27</td>
<td>11.9±1.72</td>
<td>10.6±1.86</td>
<td>9.1±1.43</td>
</tr>
<tr>
<td>BAL</td>
<td>6.9±1.40</td>
<td>5.3±1.22</td>
<td>4.8±1.13</td>
<td>5.1±0.83</td>
<td>8.4±1.51</td>
<td>7.2±1.24</td>
<td>6.2±1.15</td>
</tr>
<tr>
<td>Lucerne</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CON</td>
<td>7.9±0.81</td>
<td>6.4±0.77</td>
<td>6.0±0.48</td>
<td>5.9±0.59</td>
<td>6.2±0.65</td>
<td>9.7±1.12</td>
<td>7.1±0.57</td>
</tr>
<tr>
<td>BAL</td>
<td>5.9±1.11</td>
<td>4.7±1.08</td>
<td>4.8±0.99</td>
<td>4.9±1.06</td>
<td>5.0±0.82</td>
<td>6.5±1.07</td>
<td>5.3±0.99</td>
</tr>
</tbody>
</table>

† SEM
Table 5.3.6. The dry matter content of rumen digesta (gDM.kg\(^{-1}\)) throughout the day in sheep grazing prairie grass and lucerne with (BAL) or without (CON) balloons in the rumen.

<table>
<thead>
<tr>
<th>Prairie grass</th>
<th>ODDA</th>
<th>PREAM</th>
<th>POSTAM</th>
<th>PREPM</th>
<th>POSTPM</th>
<th>ODDB</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>CON</td>
<td>109±7.9</td>
<td>94±7.7</td>
<td>97±6.0</td>
<td>97±6.4</td>
<td>114±7.0</td>
<td>110±9.6</td>
<td>103±6.8</td>
</tr>
<tr>
<td>BAL</td>
<td>98±11.1</td>
<td>83±11.5</td>
<td>88±11.0</td>
<td>79±11.4</td>
<td>107±8.5</td>
<td>95±9.1</td>
<td>91±10.3</td>
</tr>
<tr>
<td>Lucerne</td>
<td>ODDA</td>
<td>PREAM</td>
<td>POSTAM</td>
<td>PREPM</td>
<td>ODDB</td>
<td>POSTPM</td>
<td>Average</td>
</tr>
<tr>
<td>CON</td>
<td>106±4.5</td>
<td>103±3.2</td>
<td>109±5.3</td>
<td>106±5.9</td>
<td>104±5.6</td>
<td>114±6.1</td>
<td>107±4.0</td>
</tr>
<tr>
<td>BAL</td>
<td>100±7.5</td>
<td>93±12.4</td>
<td>100±9.4</td>
<td>96±13.8</td>
<td>91±8.4</td>
<td>105±11.0</td>
<td>97±9.7</td>
</tr>
</tbody>
</table>

1 SEM
This experiment aimed to study the role of physical regulation in the control of VFC in grazing sheep and attempted to provide some explanations for the marked diurnal pattern of rumen fill. The technique employed was to restrict rumen capacity by inserting water filled balloons into the rumen, thereby introducing a known quantity of permanent ballast which has no direct influence on nutrient absorption.

Previous studies on the effect of placing water filled balloons in the rumen have tended to concentrate on intake, ignoring any effects on rumen function. Results from these studies have been inconclusive. Carr & Jacobson (1967) observed a small, non-significant, decrease in VFC when balloons containing 10.3 and 17.3 gH₂O.kg⁻¹ were present in the rumen of cattle offered chopped alfalfa hay over a 5 day period. Grovum (1979) also observed no decrease in intake when balloons containing 9.7 gH₂O.kg⁻¹ were placed in the rumen of sheep offered ground and pelleted hay. However, he only measured intake over a 30 minute period following a fast of 339 minutes. Campling & Balch (1961) observed a decrease in VFC of 0.045 kgDM.d⁻¹ for every 1kg of water placed in the rumen of cattle offered long hay over a 14 day period. A linear decrease was observed when approximately 45, 68 and 91 gH₂O.kg⁻¹ was placed in the rumen. Lloyd Davies (1962) observed a 27% decrease in VFC when balloons containing 2 litres of water were placed in the rumen of sheep, of unknown weight, offered chaffed lucerne. This represented a decrease of 125 gDM.day⁻¹ per litre of water.

The ability of sheep to increase rumen fill during lactation (Ulyatt & Barton, 1964; Tulloh, 1966) and k during pregnancy (Weston, 1979; Gonzalez et al, 1985) in an attempt to increase nutrient intake in relation to nutrient demand has not been explained and it would be interesting to know if sheep could respond to restriction of rumen capacity in a similar fashion to maintain nutrient intake.

Some possible responses of grazing sheep to reduced rumen capacity are:
1. A reduction in intake and, possibly, grazing time.
2. An increase in rumen volume to accommodate a similar digesta load, and therefore maintain intake.
3. No increase in maximum rumen fill but compensatory filling at other times of the day, leading to an alteration of the grazing pattern.
4. An increased k, i.e. a reduction in rumen retention time.
5. A combination of the above.

Balloons were associated with a reduction in intake, which was greater for P than for L, although there was no alteration of the grazing pattern or the duration of grazing. Therefore, it appears that balloons caused a reduction in intake per minute spent grazing. The reason for this is unclear, but it may have been associated with social interactions between sheep, leading to similar grazing times. The reduction in intake was equivalent to 249 and 125 gDM per litre of balloons, for P and L respectively. This was in agreement with the results of Lloyd Davies (1962) for L, although the difference observed on P illustrates the variation which may occur between feed types.

The analysis of digesta volume was complicated by the presence of froth. The volume of froth is likely to increase when digesta is removed from the rumen due to a reduction in pressure, although extraruminal volume may be of more relevance as a measure of rumen distension than the intraruminal volume or weight (see also section 5.1.4.2). There was no froth present in the P control sheep but froth became apparent in some cases when balloons were inserted. Similarly, the quantity of froth appeared to increase for L in the presence of balloons. This led to a reduction in digesta density (g.ml\(^{-1}\)) from 0.83±0.055 to 0.76±0.031 (N.S.) and 0.63±0.025 to 0.58±0.051 (N.S.) for P and L respectively. The reason for the production of froth when balloons were inserted is unclear. It was unlikely that the rate of digestion was increased, although the lower rate of intake may have been associated with the selection of a diet containing a greater proportion of rapidly fermentable plant components, although no differences in \textit{in vivo} digestibility were observed. The froth may also have been associated with increased salivary production, possibly caused by increased rumination, stimulated by the increased rumen volume and, possibly, by the presence of the balloons, although no measurements were obtained on this aspect.

There was an increase in the total volume of rumen contents (digesta + balloons) which was greater for L than for P. However, the increased volume was insufficient to maintain the volume of digesta. If, however, the volume occupied by the balloons was replaced by digesta similar to that present in the rumen, it was calculated from eqn. 5.3.1 that the average weight of OM in the rumen would increase from 6.2 to
7.8 g.kg\(^{-1}\) for P (CON = 9.1 g.kg\(^{-1}\)) and from 5.3 to 6.5 g.kg\(^{-1}\) for L (CON = 7.1 g.kg\(^{-1}\)). Therefore, rumen OM content would still remain lower than CON sheep. However, as balloons were associated with an increased \(k_{OM}\), the increased rumen OM content would lead to an increase in OMI (eqn. 5.3.2) from 18.8 to 23.7 g.kg\(^{-1}\) for P (CON = 23.8) and 25.3 to 31.2 g.kg\(^{-1}\) for L (CON = 28.6). Thus, sheep grazing L could increase intake by 9% if rumen volume and \(k_{OM}\) were maintained at the levels observed when balloons were present in the rumen. It was, however, surprising that sheep grazing P did not exhibit the potential to increase potential intake, due to the low OM\% of rumen digesta when balloons were present.

\[
OM_c = \frac{RV_t}{RV_d} \times RC_{OM} \quad \text{eqn. 5.3.1}
\]

where \(OM_c\) = corrected rumen OM content (g)

\(RV_t\) = total rumen volume (balloons + digesta; ml)

\(RV_d\) = rumen digesta volume (ml)

\(RC_{OM}\) = rumen OM content (g)

\[
OMI_c = k_{OM} \times OM_c \quad \text{eqn. 5.3.2}
\]

where \(OMI_c\) = corrected OM intake (g.h\(^{-1}\))

\(k_{OM}\) = fractional disappearance rate of OM in BAL sheep

The weight of digesta in the rumen, which would exclude the gas trapped in froth, was decreased by balloons, particularly on P. Including the weight of the balloons led to an increase in the total weight of rumen contents on L but the total weight of rumen contents was similar on P throughout the day. The apparent inability of sheep to increase the weight of rumen contents on P places further emphasis on the relative importance of weight and volume in physical regulation. As mentioned previously, the volume of rumen contents is probably of greater importance, but this observation highlights the necessity for greater understanding of the physical characteristics of rumen digesta which contribute to rumen distension. Leek & Harding (1975) observed two distinct types of nervous receptors in the reticulorumen. The first responded to the volume of digesta in the rumen. The second responded to the consistency of rumen digesta, in particular the pressure required to compress digesta during rumen contractions. It may, therefore, be
possible to distinguish between the effects of volume and consistency and to obtain objective measurements of rumen distension, which would be beneficial in gaining a better understanding of the role of rumen fill in intake regulation.

There was no significant change in the diurnal pattern of rumen OM content, although balloons tended to decrease the magnitude of the variation on L (N.S.). The patterns were, however, similar on P. This was, perhaps, the most surprising observation. The sheep could have maintained intake by modifying the pattern of rumen fill but there was no evidence of this occurring. The fact that this option was not adopted places strong evidence against VFC being controlled solely by physical or metabolic regulation.

Balloons were associated with a decrease in rumen retention time. This was possibly due to the increased volume of total rumen contents per se. Also, if a constant proportion of the total rumen contents flow from the rumen per unit time a reduction in the retention time of digesta will occur because the balloons, although part of the total rumen contents, are not passed from the rumen. Furthermore, if there was an increased salivary production this may also have contributed to the reduced retention time (Owens and Isaacson, 1977), as well as to the reduced DM% of the digesta.

These results suggest that the physical capacity of the rumen, although exerting an influence, was not the sole factor regulating intake in CON and BAL sheep. The presence of balloons exerted a greater effect on intake and rumen fill on P than on L, suggesting that the influence of physical regulation was greater on P and highlighting the importance of diet on the mechanisms of intake regulation. It was probable that an interaction between physical and metabolic regulation occurred.

The diurnal pattern of rumen fill was not altered by balloons and this suggests a variable satiety threshold, possibly caused by a diurnal variation in energy demand. Toutain et al (1977) observed a 20% reduction in heat production between 18.00 and 09.00 hours, in confined sheep. It is therefore possible that a substantial diurnal variation in energy demand occurs. The contribution of energy supply to satiety may be related to nutrient demand and this could, at least partly, explain the diurnal grazing pattern and the subsequent pattern of rumen fill. These
results therefore support the concepts of Forbes (1980b) and place emphasis on an integrated approach to the study of intake regulation. However, the conceptual basis for integrating control mechanisms is poorly defined and, apart from the concepts proposed by Forbes (1980b), the problem of integration does not appear to have been critically examined. The problem will be approached, albeit on a conceptual basis, in the following section.
5.4 PREDICTION OF INTAKE: A CONCEPTUAL MODEL

5.4.1 INTRODUCTION

The problem of integrating physical and metabolic regulation of intake appears, initially, to be complicated by the definition of concepts rather than by computational complexities. However, quantitative interpretation is of crucial importance and must be considered in conjunction with concept formulation.

Forbes (1980b) developed a model, which was based on a combination of physical and metabolic control pathways, to predict intake by sheep. The basic assumptions in the model were that intake was initiated when energy supply, based on the production of VFA in the rumen, fell below a 'hunger threshold'. Meals were terminated when the energy supply rose above a 'satiety threshold', or if the digesta present in the gastrointestinal tract reached an upper limit, based upon abdominal volume. Changes in physiological state were effected by altering energy demand and abdominal capacity. Although the model predicted daily intake and body fat changes with reasonable accuracy, the author conceded that the model only posed a quantitative hypothesis and hoped that further developments would produce improved models.

Forbes' model had several shortcomings, as the importance of the rumen, the balance of nutrients supplied and the additive effect of physical and metabolic stimuli were not considered. Grovum & Phillips (1978) emphasised the limited importance of the intestines in intake regulation and, therefore, the rumen is the preferred site of study. The ability to increase intake by altering the balance of nutrients (Battacharya & Warner, 1968; Weston, 1973) highlights the likely importance of a broader approach to nutrient requirement and the additivity of physical and metabolic stimuli (Adams & Forbes, 1981) suggest a further modification to the model is required.

It is not the objective of this discussion to formulate a complete model, but rather to discuss some basic concepts and to identify future areas of research.
5.4.2 Concept.

A crude representation of the model concept is given in figure 5.4.1. As with Forbes' model the brain integrates satiety signals, e.g. from stretch and acetate receptors in the rumen wall and propionate receptors in the liver, and determines the onset and cessation of feeding. The total satiety input is represented by the sum of the inputs from the various receptor sites. Two thresholds are present in the brain, a satiety threshold, which causes cessation of feeding, and a hunger threshold, which stimulates feeding behaviour (figure 5.4.2). The two major satiety inputs relate to nutrient supply (metabolic) and rumen distension (physical). Both satiety inputs have been further subdivided to permit a more detailed description of the model. The satiety input from nutrient supply was considered to be dependent upon the total nutrient requirement of the host animal and also the composition of the required nutrients. Surplus nutrients, either due to dietary excess or rendered surplus by a deficiency of an essential nutrient, were considered to be monitored separately. These components depend upon the composition of the nutrients supplied by a food and the requirement of the host animal for individual nutrients and are, therefore, closely related. Rumen fill was also considered to consist of two components, as suggested by Leek & Harding (1975). These were the volume of digesta, which is related to the potential rumen volume, and the consistency of digesta in the rumen. Similarly, these two components will be related since, at any given rumen DM content an increase in rumen volume will lead to a decrease in digesta consistency. The role of surplus nutrients is likely to be complex and is poorly understood in ruminants. For example, dramatic changes in intake have been observed in rats when they were offered diets with a high or low protein content or with an unbalanced amino acid profile (see Harper, 1976). The rumen modifies the amino acid composition of absorbed protein in ruminants such that drastic imbalances would be unexpected. However, Weston (1973) observed that intra-abomasal infusion of casein increased intake in sheep, suggesting that protein plays a role in intake control. Therefore, a metabolic sub-model, integrating nutrient supply and nutrient demand (e.g. Gill et al, 1984), would be an essential component of an intake model.

5.4.3 Development

The intensity of metabolic stimuli (satiety input) will depend on nutrient supply and the total and individual nutrient demand, which may
be represented by eqn. 5.4.1, for any given food. Similarly, the satiety input from physical stimuli will be related to the volume and consistency of rumen digesta and the potential maximum rumen volume, and may be represented by eqn. 5.4.2, for any given food. The total satiety input is represented by the sum of the metabolic and physical stimuli. Therefore, individual input variables must be converted to compatible units, to take account of the relative importance of each input and changes in satiety input, in response to changes in input intensity. This is represented by the variables (a, b, c and d) in eqns. 5.4.1 and 5.4.2. Obviously, changes in feed characteristics will alter the relationships between nutrient supply and nutrient demand, and between the relative importance of the volume and consistency of rumen digesta.

\[
\begin{align*}
  y_1 &= (a \times \frac{NS}{PND}) + (b \times EX) \quad \text{---eqn. 5.4.1} \\
  y_2 &= (c \times \frac{RV}{PRV}) + (d \times DC) \quad \text{---eqn. 5.4.2}
\end{align*}
\]

where \( y_1 \) = metabolic satiety input  
\( NS \) = nutrient supply  
\( PND \) = potential nutrient demand  
\( EX \) = surplus nutrients  
\( y_2 \) = physical satiety input  
\( RV \) = volume of rumen digesta  
\( PRV \) = potential rumen volume  
\( DC \) = consistency of rumen digesta  
\( a, b, c, d \) = constant functions of the variables  
and \( y_1 + y_2 \) = total satiety input

No attempt has been made to quantify individual inputs, as the quantitative data required does not exist at present and therefore only two inputs will be considered, energy supply and rumen volume. The functions, a, b, c and d in eqns. 5.4.1 and 5.4.2, are of critical importance and this would be a primary area of future study. It is envisaged that as rumen fill and nutrient supply increase, relative to potential rumen volume and nutrient supply respectively, that the incremental increase in satiety input will also increase, although the exact nature of the response is unclear (e.g. quadratic, logarithmic) and
will possibly alter for different satiety inputs. Prior to completion of a model the response to changes in, for example, rumen digesta volume and consistency, and acetate and propionate production, must be quantified. Data in the literature appear conflicting: for example, Paintal (1954) observed that vagal firing rate in cats increased linearly as stomach distension increased. Similarly, Campling & Balch (1961) observed a linear decrease in intake as the volume of water filled balloons inserted in the rumen of cattle increased. However, in a limited study of sheep, Adams & Forbes (1981) observed an 18% decrease in intake when balloons containing 1 litre of water were placed in the rumen and an 82% decrease when 2 litres were inserted. Therefore, it is unclear whether the response is linear or curvilinear. Similarly, the nature of the metabolic response has not been elucidated. Niijima (1969) observed that vagal firing rate was linearly related to glucose infusion rate in isolated guinea pig liver, whereas the data of Adams & Forbes (1981) suggests a non-linear decrease in intake as intraruminal infusion of acetate and intraportal infusion of propionate in sheep increased. Obviously, more critical experiments must be undertaken to fully understand this problem.

During formulation of the present concept model, linear relationships were fitted to the satiety input data. However, these yielded unrealistic results and were discarded in favour of curvilinear responses. It remains unclear whether all four functions in eqns. 5.4.1 and 5.4.2 are curvilinear, but provided that at least one metabolic and one physical component is curvilinear the final satiety inputs will be of a curvilinear nature. The adoption of a curvilinear response is supported by the data of Adams & Forbes (1981), as discussed previously.

5.4.4 Application

The application of this model to the short term regulation of intake, i.e. individual meals, has not been attempted as no data were obtained on this aspect. However, the model can be applied to the long term regulation of intake, e.g. daily. The results from the previous section, where balloons were inserted into the rumen, provide a useful data set with which to compare predicted responses.

There was insufficient data to carry out a detailed analysis of the effect of balloons on intake and rumen fill. Therefore, a simplified approach has been adopted to analyse the response of animals, consuming two theoretical diets, to restriction of rumen capacity. Several assumptions have been made and these are outlined below.
1. Physical satiety input was related to the volume of rumen contents, as a proportion of the potential rumen volume.

2. Metabolic satiety input was related to the total nutrient supply, as a proportion of the nutrient requirement. Furthermore, nutrient supply was assumed to be equivalent to DOMI.

3. The response, in terms of satiety input, was related to nutrient supply and rumen volume (as a proportion of nutrient demand and potential rumen volume, respectively) by the equation \( y = x^2 \). This function was selected to represent a curvilinear response as no biological evidence is available on the true nature of the response.

4. Selection of theoretical diets. The satiety inputs were calculated for two diets, assumed to represent a legume and a grass diet. The satiety inputs for the grass diet were selected at random and the satiety inputs for the legume diet were selected such that physical input was lower than for the grass diet and the total satiety input was the same for both diets (0.85, table 5.4.1). Diet 1, which represented a legume diet, was assumed to supply 0.74 of the animals nutrient requirements and to promote a rumen digesta volume which was 0.55 of the potential rumen volume. Diet 2, which represented a grass diet, supplied less nutrients (0.6 of the animals nutrient requirement) and promoted a higher rumen digesta volume (0.7 of the potential rumen volume).

5. Rumen digesta volume was assumed to be directly related to DOMI, i.e. the proportion of rumen digesta volume:nutrient supply remained constant, at 0.74 (0.55 + 0.74) and 1.17 (0.7 + 0.6) for diets 1 and 2 respectively.

6. The satiety input, which determines daily intake in this example, was represented by the sum of the physical and metabolic satiety inputs, i.e. \( 0.74^2 + 0.55^2 \) (diet 1) = \( 0.7^2 + 0.6^2 \) (diet 2) = 0.85 (total satiety input). Placing balloons in the rumen causes an alteration of intake and rumen volume such that the total satiety input remains 0.85.

In this example, balloons, equivalent to 10% of the potential rumen volume, were added to the rumen. If intake was to be maintained in the presence of balloons, the satiety input would increase to 0.97 (diet 1) and 1.0 (diet 2) and would, therefore exceed the satiety threshold (0.85). Therefore intake must decrease, causing a related decrease in
The new intake was computed by reducing intake and, proportionally, rumen volume until the satiety input again equalled the satiety threshold.

The assumed values and calculated responses are given in table 5.4.1 and are shown graphically in figure 5.4.3. The increased compensation on the higher quality diet, in terms of rumen volume and DOMI, agrees, qualitatively, with the observed response to intraruminal balloons observed in the previous experiment (section 5.3) and supports the general concept of the model. However, accurate predictions cannot be obtained without a knowledge of potential rumen capacity, potential nutrient demand and the nature of the response curves. Further research is required to quantify these aspects, which should then permit incorporation of additional modifications, e.g. the changes in fractional disappearance rate which were observed when balloons were inserted into the rumen. Moreover, although this example examined the daily response of intake to intraruminal balloons a similar approach could be used to predict short-term responses and, indeed, to explain and predict the pattern of intake and total intake of all ruminants.

5.4.5 CONCLUSIONS

Intake appears to be regulated by a combination of physical and metabolic regulation mechanisms. These appear to be additive but integration of the two mechanisms into an additive model has not been attempted. A conceptual model was proposed which incorporated the additive nature of these mechanisms. Although insufficient data were available to formulate a detailed model, the response of animals consuming two theoretical diets, differing in the relative importance of physical and metabolic regulation, was predicted. The predictions agreed with the responses observed in section 4.3 and supported the concepts of the model. The adoption of a curvilinear response to increases in nutrient supply and rumen volume was of critical importance and the exact nature of the response curve would be a major area of future research. The conceptual model appears to have significant advantages over previous models and provides a basis for the integration of satiety inputs in a detailed model of intake regulation.
Figure 5.4.1. Schematic representation of the derivation and interaction of physical and metabolic stimuli in the regulation of intake.
Figure 5.4.2 Schematic representation of intake regulation. The sum of metabolic and physical inputs regulate feeding behaviour and are integrated in the brain.
Figure 5.4.3. Diagrammatic representation of the effect of inserting balloons in the rumen of animals consuming 2 diets. A represents rumen volume (RV) as a proportion of potential RV (PRV) and B the digestible organic matter intake (DOMI) as a proportion of nutrient demand (ND). A represents the total proportional RV (including balloons), A2 the proportional digesta volume only and B the DOMI following insertion of balloons. Satiety input is related to RV:PRV and DOMI:ND by the relationship $y = x^n$. 

![Diagram](image-url)
Table 5.4.1. The predicted response of animals consuming two diets to insertion of balloons into the rumen. Physical satiety input is assumed to be derived from volume of rumen contents (RV), as a proportion of the potential rumen volume (PRV) and metabolic satiety input is assumed to be derived from DOMI, as a proportion of the potential DOMI requirement (PDR).

<table>
<thead>
<tr>
<th></th>
<th>Diet 1 (legume)</th>
<th>Diet 2 (grass)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. No balloons</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Physical input</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RV/PRV</td>
<td>0.550</td>
<td>0.700</td>
</tr>
<tr>
<td>Satiety input</td>
<td>0.302</td>
<td>0.490</td>
</tr>
<tr>
<td><strong>Metabolic input</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DOMI/PDR</td>
<td>0.740</td>
<td>0.600</td>
</tr>
<tr>
<td>Satiety input</td>
<td>0.548</td>
<td>0.360</td>
</tr>
<tr>
<td><strong>Total satiety input</strong></td>
<td>0.850</td>
<td>0.850</td>
</tr>
<tr>
<td><strong>Decrease in RV(digesta; %)</strong></td>
<td>6.9</td>
<td>8.6</td>
</tr>
<tr>
<td><strong>Decrease in DOMI (%)</strong></td>
<td>6.8</td>
<td>8.5</td>
</tr>
</tbody>
</table>

|                          |                 |                |
| **B. Plus balloons (0.1 PRV), at equilibrium** |     |                |
| **Physical input**       |                 |                |
| RV(total)/PRV            | 0.612           | 0.740          |
| RV(digesta)/PRV          | 0.512           | 0.640          |
| Satiety input            | 0.374           | 0.548          |
| **Metabolic input**      |                 |                |
| DOMI/PDR                 | 0.690           | 0.549          |
| Satiety input            | 0.476           | 0.301          |
| **Total satiety input**  | 0.850           | 0.849          |

Decrease in RV(digesta; %) 6.9 8.6
Decrease in DOMI (%) 6.8 8.5
Sheep production systems in New Zealand are, by necessity, closely integrated with the pattern of pasture growth. Efficiency of production could be improved by increasing lamb growth during spring and early summer, when pasture growth is maximal. This could be achieved by early weaning of lambs, thereby diverting more highly digestible herbage to lambs rather than to ewes. However, widespread adoption of this technique has been limited by the low growth rate of weaned lambs often observed. The major constraints to lamb growth at pasture are herbage intake and the nutrient supply from herbage intake. Technical problems associated with the study of grazing animals have limited study of these aspects.

The objectives of the work described in this thesis were to quantify nutrient supply in grazing lambs and to examine some factors involved with intake regulation. Early weaned lambs were used where possible, due to their high nutrient requirement, particularly for protein, and possible limitations to intake caused by incomplete rumen development. In order to generate differences in intake and nutrient supply a range of pasture species, varying in composition, were used. However, older sheep were used for more detailed studies of intake regulation, as these allowed more precise analysis.

Two legumes, lucerne (L) and white clover (C), and 2 grasses, ryegrass (R) and prairie grass (P) were offered at high dry matter allowances, to encourage maximum intake, to lambs weaned at 6 weeks of age. Liveweight gain (LWG) was higher for lambs grazing legumes (308 and 321 g.d⁻¹ for L and C respectively) than for lambs grazing grasses (230 and 227 g.d⁻¹ for P and R respectively). The superiority of legumes in promoting LWG was similar to previous observations (e.g. McLean et al, 1962, 1965; Ulyatt, 1971) and provided a basis for studying the major factors limiting growth. It was hoped that the plant species used would significantly alter nutrient supply, in particular intake and the proportion of absorbed protein:energy. However, despite differences in plant composition, there were marked differences in protein transactions in the rumen and there was little difference in the balance of nutrients supplied. Therefore, it was not possible to differentiate between the relative importance of protein and energy in determining LWG. However, the marked differences between plant composition and nutrient supply emphasises the importance of using animals in the evaluation of new and
existing plant species. For example, the loss of protein across the stomachs of lambs consuming legumes indicates possible plant breeding strategies for these forages, but this approach would not be appropriate for prairie grass.

The 38% higher LWG of lambs grazing legumes was associated with a 36% higher intake (gOM.kgW⁻¹) and a 33% higher flow of NAN to the small intestine (g.kgW⁻¹). Analysis of the present results with data from the literature suggested that absorbed amino acid nitrogen (aaN) was better correlated with LWG than was ME intake. This observation supports the results of Black et al (1979) and Barry (1981), who observed an increase in LWG when casein was infused into the abomasum of lambs consuming fresh herbage. However, the major factor affecting LWG appeared to be the level of intake achieved, which affected both aaN and ME absorption.

Tentative analysis of the present results suggested that the efficiencies of utilisation of ME for growth (kₑ) and absorbed aaN for N deposition were low (0.34-0.42 and 0.39-0.48 respectively). However, similar values have been observed in sheep consuming herbage diets and this may reflect imbalanced nutrient supply. In particular, absorption of a low proportion of glucogenic:ketogenic precursors, crudely represented by the proportion of propionate:acetate, may lead to a low kₑ (Armstrong & Blaxter, 1957; Armstrong et al, 1958; MacRae & Lobley, 1982; Gill et al, 1984). Furthermore, protein synthesis may be limited by deficiency of (an) essential amino acid(s). This may be of importance in grazing lambs as approximately 70-85% of the NAN flow to the small intestine is of microbial origin and this aaN source may be deficient in methionine for growth (Storm & Ørskov, 1984)

The importance of intake as a determinant of LWG prompted an examination of some factors involved with the regulation of voluntary food consumption (VFC). The major limitation to VFC of herbage diets is generally considered to be the physical capacity of the rumen, i.e. physical regulation (Campling & Balch, 1961; Jones, 1972). If this concept is valid, VFC will be dependent on the rate of removal of digesta from the rumen, by digestion and passage. This aspect has been poorly studied in grazing animals due to the practical difficulties involved in obtaining objective measurements. Sheep grazing legumes tend to have lower rumen fills than sheep grazing grasses (McLean et al, 1962, 1965; Johns et al, 1963; Ulyatt, 1971; Jagusch et al, 1976), despite similar or
higher intakes. This suggests that the retention time in the rumen (RT) of legumes is shorter than the RT of grasses. It also suggests that physical regulation of intake is less important in sheep grazing legumes than in sheep grazing grasses. The primary objective of the present study was to obtain accurate estimates of RT in grazing animals and to assess the importance of retention time in intake regulation.

Two techniques were identified as having potential for the estimation of RT in grazing animals. Firstly RT was estimated from the rate of disappearance of digesta from the rumen in sheep removed from pasture and fasted (SS technique). Secondly, RT was estimated from the average rumen fill and intake of grazing sheep (RF technique). Initially, these techniques were used with early weaned lambs which were slaughtered to obtain estimates of rumen fill. Problems in accurate estimation of RT were encountered due to between animal variation and an apparently large diurnal variation in rumen fill. This latter aspect was studied with older sheep which were fitted with a large rumen cannula to enable manual rumen emptying. This also allowed removal of between animal variation. A consistent diurnal pattern of rumen fill was observed, the lowest level of fill occurring during the forenoon and highest level of fill at the end of the afternoon grazing period, around sunset. The increase in rumen fill through the day was associated with a gradual increase in grazing intensity between sunrise and sunset. An equation was derived, making several assumptions about digesta kinetics in the rumen and grazing behaviour, to predict the rate of change of rumen fill. This proved to be reasonably accurate, but strongly suggested that RT, and possibly intake rate per minute spent grazing, varied through the day. This suggested that intake regulation in grazing animals is extremely complex and could not be explained in terms of physical regulation alone.

In the course of the above experiments RT was estimated from the 2 techniques mentioned previously. The SS technique gave values which were considerably higher than the RF technique, and these were dependent on the rumen fill at the start of fasting. Therefore, these data were excluded from further analysis. The RT of OM was lower in sheep grazing legumes than in sheep grazing grasses, but the RT of NDF tended to be similar. Early weaned lambs and older sheep tended to have similar RT of OM and NDF when grazing grasses in spring (8.5 v 9.2h and 11.1 v 11.3h respectively), but early weaned lambs had a lower RT of OM (3.5h) than older sheep (6.7h) when grazing L in spring. These RT for legumes were
extremely low in early weaned lambs and suggested that the kinetics of digesta disappearance from the rumen may vary with age, depending on the diet. This emphasises the importance of offering young, weaned, lambs high quality legume pasture to maximise LWG.

The ability of sheep to maintain rumen fill throughout the day at the maximum value observed, at sunset, would lead to a significant increase in intake. Therefore, an experiment was designed to examine the ability of sheep, grazing P and L, to alter the pattern of rumen fill, by restricting rumen capacity with water filled balloons. Balloons did not appear to cause a change in the pattern of rumen fill. However, they were associated with a reduction in intake, rumen digesta content and RT. The reduction in intake (gOM.kgW⁻¹) and rumen OM content (g.kgW⁻¹) was greater in sheep grazing P (21 and 32% respectively) than in sheep grazing L (12 and 25% respectively). The reduction in RT of OM was similar for sheep grazing both pastures (15 and 19% for P and L respectively).

These studies on intake regulation suggested that, although rumen fill and, therefore RT, was of importance, some other factor(s) also exert(s) an influence. There has been increasing evidence that a metabolic component, related to nutrient demand (Forbes, 1970; Owen et al, 1980, Weston, 1984) is involved in intake regulation and the concept of integrated regulation now appears irrefutable. Attempts to integrate the influence of physical and metabolic mechanisms (e.g. Forbes, 1977, 1980a,b) have proved partially effective in predicting intake. In this thesis a different approach was adopted to integrate control mechanisms, and although these concepts could not be validated precisely they appear to provide the possibility of integrating physical and metabolic regulation and represent a basis for future research.

It was concluded that high growth rates of early weaned lambs can be achieved, particularly when grazing legumes, and that the major constraints appeared to be intake, which was regulated by a combination of physical and metabolic factors for both grasses and legumes, and the absorption of amino acids.
Appendix 1. References, diet and assumptions used to derive figures 2.1.1 and 4.1.1.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Diet</th>
<th>Assumptions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alam (1985)</td>
<td>grass hay</td>
<td>.5 NAN entering the small intestine of microbial origin</td>
</tr>
<tr>
<td>Barry (1981)</td>
<td>fresh pasture</td>
<td></td>
</tr>
<tr>
<td>Ulyatt (1971) and</td>
<td>grazing pure species pasture</td>
<td>DOMI = 15.83 MJ ME kg⁻¹</td>
</tr>
<tr>
<td>MacRae &amp; Ulyatt (1974)</td>
<td></td>
<td>.5 NAN entering the small intestine of microbial origin</td>
</tr>
<tr>
<td>Corbett et al (1976b)</td>
<td>grazing pure species pasture</td>
<td>DOMI = 15.83 MJ ME kg⁻¹</td>
</tr>
<tr>
<td>Weston (1971)</td>
<td>pelleted lucerne hay, corn, soya bean meal and formaldehyde treated casein</td>
<td>.5 NAN entering the small intestine of microbial origin. NAN supplement absorbed with a similar efficiency to NAN in the basal diet</td>
</tr>
<tr>
<td>Ørskov et al (1974)</td>
<td>barley/fishmeal</td>
<td>DOMI = 15.83 MJ ME kg⁻¹</td>
</tr>
</tbody>
</table>

General assumptions

- Maintenance ME requirement = 0.5 MJ kg⁻₀.⁷⁵ (MAFF, 1975)
- Maintenance aaN requirement = 0.2 g N kg⁻₀.⁷⁵ (Black et al., 1973)
- All data involved extrapolation of aaN absorption from separate sheep consuming similar diets. When necessary NAN entering the small intestine was assumed to be constant, relative to DOMI, within diets and experiments.
Appendix 2

The diurnal variation in rumen dry matter content of lambs at 8 and 12 weeks of age grazing lucerne, white clover, ryegrass and prairie grass. Each measurement is the average of 2 lambs.
Appendix 3

THEORETICAL CONSIDERATIONS IN THE ESTIMATION OF RUMEN FRACTIONAL OUTFLOW RATE FROM VARIOUS SAMPLING SITES IN THE DIGESTIVE TRACT

3.1 INTRODUCTION

Estimation of the fractional outflow rate (FOR) of digesta from the rumen is an important, yet problematical, area of ruminant nutrition. Theoretical considerations of the rate of passage of digesta were given by Blaxter et al. (1956) in a study of the faecal excretion curve of stained food particles. These were subsequently developed to estimate FOR of particulate and solute markers from various segments of the digestive tract (Grovum & Williams, 1973a,b, 1977). Often, marker excretion curves in faeces are used to estimate FOR as animals do not require surgical modification to the gastro-intestinal tract (Grovum & Williams, 1973b; Eliman & Ørskov, 1984). However, there are at least three mixing compartments in the tract; the rumen, abomasum and caecum-large intestine (hereafter referred to as the caecum). Therefore, the marker excretion curve from the rumen may not be accurately represented in the faeces, as suggested by the results of Mira & MacRae (1982) and Mudgal et al. (1982). The rumen itself may consist of two or more pools relating to marker outflow through the reticulo-omasal orifice and particle size reduction, with the additional effect of non-instantaneous mixing of marker in the rumen digesta (Ellis et al, 1979). Furthermore, Dhanoa et al. (1985) have recently suggested that the small intestine may be represented by a series of high turnover pools. Following the cessation of continuous marker infusion only marker outflow from the rumen is of importance, as continuous infusion ensures 'instantaneous' mixing and the effect of particle size will be minimal with respect to particulate markers due to marker migration (Dixon et al, 1983; Faichney & Boston, 1983), and will not affect solute markers.

Compartmental analysis has been used to estimate FOR for these mixing compartments (Grovum & Williams, 1973b, 1977; Faichney & Boston, 1983; Pond et al, 1984), although mixing in the abomasum is generally ignored due to the high FOR compared to the rumen and caecum, and is difficult to detect. The descending portion of the faecal excretion curve
is generally accepted as representing accurately the rumen excretion curve (Grovum & Williams, 1973b, 1977; Pienaar et al, 1983; Eliman & Ørskov, 1984).

In this thesis, FOR from the rumen was estimated in early weaned lambs from the rate of decrease of marker concentration in abomasal digesta and faeces (sections 4.1), and in duodenal digesta and faeces (section 4.2). Further experimental data were used to validate the assumption that abomasal and duodenum sampling yielded values of FOR which reflected accurately FOR from the rumen. These data suggested that the descending portion of the faecal excretion curve did not reflect accurately the excretion curve from the rumen. This prompted an examination of the factors related to the kinetics of marker passage through the gastro-intestinal tract, using compartmental models.
3.2 MATERIALS AND METHODS

Two sections are described. In the first experimental data are described. In the second a simulation of faecal marker excretion curves is obtained by manipulating FOR values in a two pool model.

3.2.1 Experimental

3.2.1.1 Animals and feeding

Experiment 1. Twelve Dorset Down x Border-Corriedale wether lambs were weaned at 6 weeks of age, fitted with a rumen cannula (2.5 cm I.D.) and a simple 'T' piece cannula in the abomasum, and allocated to one of two pasture species. Six lambs grazed a pure species sward of white clover and 6 grazed ryegrass, offered at high dry matter allowances of 6 and 7 kgDM/lamb/day, respectively.

Experiment 2. Animals and management are described in section 4.1. Briefly, 6 Polled Dorset lambs, weaned at 6 weeks of age, were fitted with a simple 'T' piece cannula in the abomasum. They were housed indoors and offered clover hay ad libitum.

Experiment 3. Animals and management are described in section 4.2. Briefly, 24 South Suffolk x Coopworth ram lambs were fitted with a duodenal cannula and weaned at 6 weeks of age. Six lambs were allocated to pure species swards of lucerne, white clover, ryegrass and prairie grass.

3.2.1.2 Marker techniques

The digesta markers $^{103}$Ru-P and $^{51}$Cr-EDTA were continuously infused into the rumen. Following the cessation of infusion, the rate of decline of marker concentration in rumen digesta (expt. 1), abomasal digesta (expts. 1 and 2), duodenal digesta (expt. 3) and faeces (expts. 2 and 3) was measured. Measurements were made at 8 and 12 weeks of age in expts. 1 and 3 and at 8, 12, 16 and 24 weeks of age in expt. 2.

Samples of rumen, abomasal and duodenal digesta were obtained at regular intervals from 0-36 h after the cessation of infusion. Rumen fluid was obtained by suction from a number of sites throughout the rumen, excluding large particles from the sample. However, as the distribution of $^{103}$Ru-P between particle sizes remains constant (Dixon et
al, 1983; Dixon & Milligan, 1985), the fractional rate of decrease of $^{103}$Ru-P concentration will be the same as that of mixed particles. Each sample was thoroughly mixed and duplicate 2.5 ml subsamples transferred to counting vials. Samples of abomasal and duodenal digesta were obtained by free flow from the cannula, thoroughly mixed and duplicate 2.5ml subsamples transferred to counting vials. Grab samples of faeces were obtained at regular intervals from 10-95h after the cessation of infusion and duplicate subsamples placed in counting vials.

Following counting the vials were dried to constant weight at 70°C for dry matter (DM) determination. The concentration of $^{103}$Ru-P per gram DM (all samples) and $^{51}$Cr-EDTA per gram water (rumen, abomasal and duodenal digesta) or per gram DM (faeces) were plotted against time of sampling. The rate of decline of marker concentration was then calculated, assuming first order kinetics, to give estimates of FOR from the rumen. The values measured from rumen, abomasal and duodenal digesta are subsequently referred to as $k_1$ and those from faeces as $k_f$.

3.2.2 Simulation

3.2.2.1 Single pulse of marker

A two-pool, time independent model (Blaxter et al, 1956; Shipley & Clark, 1972) was used to analyse the effect of altering FOR from the rumen and caecum on faecal excretion curves following the administration of a single pulse of marker into the rumen. This assumes instantaneous mixing of markers in the rumen and the caecum. Alternatively, two-pool, time-dependent (Pond et al, 1984) or multicompartmental (Dhanoa et al, 1985) models may be used.

The marker excretion curve in faeces may be described by the following equation, assuming a two-pool time-independent model, modified from Blaxter et al (1956).

$$C_t = Dk_1k_2(e^{-k_1(t-TT)} - e^{-k_2(t-TT)})/V(k_2 - k_1) \quad \text{for } t > TT$$

$$C_t = 0 \quad \text{for } t < TT$$

where:- $C_t = \text{marker concentration in faeces at time } t \ (gDM^{-1})$

$D = \text{quantity of marker introduced into the rumen}$

$V = \text{faecal output } (gDM.h^{-1})$

$t = \text{time after marker introduction into the rumen } (h)$
TT = transit time (i.e. time from marker introduction until first appearance of marker in faeces (h)

\[ k_1 = \text{marker FOR from the rumen (h}^{-1}) \]

\[ k_2 = \text{marker FOR from the caecum (h}^{-1}) \]

### 3.2.2.2 Continuous marker infusion

The faecal excretion curve following the cessation of continuous infusion differs from that following the administration of a single pulse due to marker equilibration in the digestive tract. During continuous infusion the marker concentration in faeces is determined by the infusion rate and the faecal output. Thus the ascending portion of the faecal excretion curve observed following a single pulse of marker is absent following the cessation of continuous infusion. The marker present in the rumen at the cessation of continuous infusion may be considered to behave as a single pulse and thus conform to eqn.1. The caecal marker pool will continue to exhibit steady state characteristics until the arrival of the assumed single pulse from the rumen. The marker present in the caecum at this time will display single compartment first order kinetics. The following equation will thus describe the marker excretion curve in faeces following continuous infusion.

\[ C_t = (k_2C_{oc}e^{-k_2(t-TT)}/V) + (Dk_1k_2(e^{-k_1(t-TT)} - e^{-k_2(t-TT)})/V(k_2-k_1)) \text{app.eqn.3.2} \]

where \( C_{oc} = \text{caecal marker content during continuous infusion} \)

\( D = \text{rumen marker content during continuous infusion} \)

but \( C_{oc} = I/k_2 \) and \( D = I/k_1 \) where \( I = \text{infusion rate (h}^{-1}) \)

substituting in appendix eqn.3.2,

\[ C_t = (Ie^{-k_2(t-TT)}/V) + (Ik_2(e^{-k_1(t-TT)} - e^{-k_2(t-TT)})/V(k_2-k_1)) \text{----app. eqn.3.3} \]

for \( t > TT \)

\[ C_t = I/V \]

For \( t < TT \), \( C_t \neq I/V \)

Altering values of \( k_1 \) and \( k_2 \), in appendix eqns.3.1 and 3.3, generated different faecal excretion curves and the descending portion was analysed to obtain \( k_f \), using the technique described previously. The data generated are perfect data, containing no experimental variation. The descending portion of the generated faecal excretion curve did not
display first order kinetics (i.e. $C_t \neq C_0 e^{-kt}$) although the variation was minimal and was probably undetectable under experimental conditions. The portion of the faecal excretion curve between 80% and 10% of the maximum concentration was analysed to compute $k_f$. Values greater than 80% tended to deviate markedly from first order kinetics, although they may be included in experimental analysis where the starting point is selected by eye. Values of $k_1$ and $k_2$ from 0.025-0.25 were used as these correspond to the range of values in the literature (Eliman & Ørskov, 1984; Dixon et al, 1982; Faichney & Boston, 1983) and the present experiments.
3.3 RESULTS

3.3.1 Experimental

The effect of sampling from the rumen or abomasum on estimation of \( k_1 \) is shown in appendix fig.3.1. There was no difference in estimated \( k_1 \) values. The values were related by:

\[
y = 0.96x + 0.01 \quad (n = 32, \ r^2 = 0.85, \ SE = 0.045)
\]

where \( y = k_1 \) estimated from rumen digesta
\( x = k_1 \) estimated from abomasal or duodenal digesta

There appears to be no reason for the marker excretion curve to alter between the abomasum and the proximal duodenum, therefore abomasal and duodenal estimates of \( k_1 \) were treated similarly. The relationship between \( k_1 \), estimated from abomasal and duodenal digesta, and \( k_f \) for both \( ^{103} \text{Ru-P} \) and \( ^{51} \text{Cr-EDTA} \) are shown in appendix fig.3.2. The values of \( k_1 \) were significantly higher than \( k_f \) \((P<0.01)\), although this only became apparent at high values of \( k_1 \). The result was consistent for both \( ^{103} \text{Ru-P} \) and \( ^{51} \text{Cr-EDTA} \), but the difference was more pronounced for \( ^{51} \text{Cr-EDTA} \) due to the higher values of \( k_1 \) obtained with this marker.

3.3.2 Simulation

An example of the computed faecal excretion curves obtained following a single pulse (appendix eqn.3.1) and continuous infusion (appendix eqn.3.3) are shown in appendix fig.3.3, along with the excretion curve following a single pulse into the caecum (assuming single-pool, first order kinetics). The quantity of marker introduced by the single pulses is assumed to be equal to the quantity of marker present in the rumen and caecum following continuous infusion \((i.e. \frac{I}{k_1} \) and \( \frac{I}{k_2} \) respectively). Thus addition of the two single pulse curves gives the curve following continuous infusion. Calculating \( k_f \) values from appendix eqns.3.1 and 3.3 gave identical results and these are shown in appendix fig.3.4, expressed as a proportion of the \( k_1 \) value inserted in that equation. The ratio of \( k_f:k_1 \), which was always less than one, was associated with the proportion \( k_2:k_1 \) entered in the equation. As \( k_2:k_1 \) decreased below approximately 2.9 the ratio \( k_f:k_1 \) fell below 0.95. If \( k_1 = k_2 \), then \( k_f = 0.69k_1 \) \((approximately, \ from \ appendix \ fig.3.4)\). Thus any value where \( k_f \) is less than 0.69\( k_1 \) signifies that \( k_2 \) is lower than \( k_1 \).
From appendix fig. 3.2 it can be seen that this appears to have occurred in several of the lambs.
Appendix figure 3.1 The relationship between the fractional outflow rate of $^{103}$Ru-P and $^{51}$Cr-EDTA from the rumen, estimated from rumen and abomasal digesta.
Appendix figure 3.2 The relationship between the fractional outflow rate of $^{103}$Ru-P and $^{51}$Cr-EDTA from the rumen, estimated from abomasal or duodenal digesta and faeces.
Appendix figure 3.3 Predicted marker excretion curves in faeces following, 1. continuous ruminal infusion, 2. a single pulse into the rumen and 3. a single pulse into the caecum. Marker concentration is expressed as a proportion of, 1. infusion rate \((\text{I.h}^{-1})\), 2. marker introduced into the rumen \((=\text{I}.\text{I}_{1}^{-1})\) and 3. marker introduced into the caecum \((=\text{I}.\text{I}_{2}^{-1})\).
Appendix figure 3.4 The influence of fractional outflow rate of markers from the caecum ($k_2$) and rumen ($k_1$) on the estimation of $k_1$ from the descending portion of the faecal excretion curve ($k_f$).
DISCUSSION

Site of sampling had a significant effect on estimation of marker \( \text{FOR} \) from the rumen. Little difference was observed between rumen and abomasal sampling and this is in agreement with the data of Poncet & Al Abd (1984) who observed similar \( k_1 \) values for two solute markers when estimated from rumen and duodenal digesta. There was, however, considerable variation between individual animals, possibly due to the difficulty of representative sampling from the rumen. Also, the diurnal variation in rumen digesta content observed in grazing sheep (see section 5.1) leads to fluctuations in marker concentration (G.J. Cruickshank, D.P. Poppi and A.R. Sykes; unpublished observation) which may lead to small errors in estimating \( k_1 \).

Large differences were observed between \( k_1 \) and \( k_f \). Whilst small discrepancies have been noticed previously (Mira and MacRae, 1982; Mudgal et al., 1982) the larger discrepancy noted here prompted an examination of the theoretical implications of changing \( \text{FOR} \) from the rumen and caecum. It was observed that \( k_1 \) in these experiments with early weaned lambs consuming high quality forage was higher than most studies previously reported. The latter usually involved use of adult animals at maintenance or low \textit{ad libitum} levels of feeding, where \( k_1 \) was usually in the range 0.04–0.1. The results of the simulation suggested that this discrepancy between sampling from the primary pool (\( k_1 \)) and the faeces (\( k_f \)) arose because the caecum, acting as a mixing pool, modified the marker excretion curve in faeces such that faecal sampling did not give an accurate representation of the curve leaving the rumen. This finding contradicts the conclusions of Grovum & Williams (1973b) and Eliman & Ørskov (1984). The discrepancy may be due to the low values of \( k_1 \) observed in the latter studies (0.05 and 0.023 – 0.041 respectively) which would cause a minimal change to the faecal excretion curve unless \( k_2 \) was also low. Grovum & Phillips (1973), in a bench top model, observed no difference in estimated \( k_1 \) values between primary and secondary pool sampling even though, in one case, the ratio \( k_2:k_1 \) was 2.0 which would, as shown in appendix fig.3.4, lead to errors in estimating \( k_1 \) from the secondary pool. However, regression analysis appeared to commence when the marker concentration had fallen to under 10% of the maximum concentration observed. The major proportion of the excretion curve, use of which would increase the measured value of \( k_1 \), was thus ignored.
Few data are available on FOR from the caecum and the relationship between FOR from the rumen and caecum is not well defined. Those values available range from 0.163-0.339 in mature wether sheep (Grovum & Williams, 1973a,b; 1977; Dixon et al, 1982) and from 0.057-0.125 in pregnant sheep (Faichney & Boston, 1983). The low FOR from the caecum observed in pregnant sheep may reflect large errors in the estimation of $k_1$ from faecal sampling, as a result of a low proportion $k_2:k_1$.

Accurate analysis of faecal excretion curves clearly requires frequent sampling during the ascending portion of the curve. This may not always be feasible, particularly in grazing studies, and analysis of the descending portion of the faecal excretion curve is often preferred. The latter technique may also be applied following the cessation of continuous infusion, and moreover it has simplicity.

The present results and simulation do, however, suggest that where FOR from the rumen is high analysis of the descending portion of the faecal excretion curve is likely to result in erroneous estimation of $k_1$. These situations are likely to occur in studies with high quality forages, e.g. fresh herbage (Corbett et al, 1976; Corbett & Pickering, 1983), pregnant animals (Weston, 1979; Faichney & Boston, 1983; Gonzalez et al, 1985) and young lambs, as shown in these experiments.

The simulation exercise described provides a powerful tool with which to examine the theoretical implications of changing FOR from the rumen and caecum on faecal marker excretion curves. A major finding of the simulation, not previously recognised, was that the ratio of caecal FOR:rumen FOR influenced the faecal excretion curve, rather than the actual FOR values (appendix fig.3.4), and will dictate how accurately the excretion curve from the rumen is replicated in faeces. Appendix fig.3.4 provides a practical basis on which to assess the circumstances when faecal sampling is appropriate.

When faecal sampling is inappropriate precautions should be taken to ensure accurate estimation of $k_1$. Following the administration of a single dose of marker into the rumen the faecal excretion curve should be analysed using a two-pool model (Faichney & Boston, 1983; Pond et al, 1984) in order to take account of the influence of the caecum. The simplified technique offered by Grovum & Williams (1973b) seems inappropriate, requiring initial estimation of $k_1$ from the descending
portion of the faecal excretion curve. Similarly, application of a two-pool model is inappropriate following the cessation of continuous marker infusion into the rumen as it is not possible to obtain the ascending portion of the faecal excretion curve. However, markers are rarely infused continuously into the rumen without a cannula in the rumen, abomasum or duodenum from which digesta can be obtained for the estimation of FOR from the rumen, thus enabling accurate estimation without any requirement for faecal sampling.

Provided these precautions are observed accurate estimates of FOR from the rumen will be obtained. It is important to recognise that, in all cases, the marker excretion curve in faeces is the product of at least two mixing compartments and mathematical treatment of the descending portion of the excretion curve as the product of a single compartment can lead to large errors in the estimation of FOR from the rumen. The most appropriate method for accurately estimating marker FOR from the rumen may be assessed with a prior knowledge of the expected ratio of caecal FOR:rumen FOR.
Appendix 4

PREDICTION OF CHANGES IN RUMEN DIGESTA CONTENT

4.1 Introduction

The development of models to predict intake (e.g. Forbes, 1980b) require a knowledge of the rate of change of rumen digesta content during and between meals. Moreover, short-term nutrient release, e.g. VFA, for any given feed is dependent on the quantity of digesta in the rumen. Consideration of the kinetics of digesta disappearance from the rumen should allow prediction of changes in rumen digesta content.

Under steady state conditions rumen digesta content may be described by appendix eqn. 4.1 (Minson, 1966).

\[
RC = I \times RT
\]  

where \( RC \) = rumen content (g) 
\( I \) = intake (g.h\(^{-1}\)) 
\( RT \) = retention time (h)

However, in grazing animals rumen digesta content changes dramatically throughout the day (see section 5.1). The rate of change of rumen digesta content will depend upon the rumen digesta content, the rate of herbage intake and the fractional disappearance rate of digesta from the rumen, i.e. the balance between the rate of addition and rate of removal of digesta.

This section adapts equations, developed for tracer kinetics, to changes in rumen digesta content and examines the validity of this application.
4.2 Theory

The theory of tracer kinetics has been well documented (e.g. Shipley & Clark, 1972). However, the derived equations are only valid if tracers abide to certain criteria, and rumen digesta may not adhere to these. The following assumptions have been made to enable extension of tracer kinetics to rumen function.

1. The rumen was considered as a pool of constant size and the digesta was treated as a tracer, displaying first order kinetics. This appears to be a valid assumption, although digesta may not display first order kinetics at low rumen fills (see section 5.2).

2. Rate of intake was assumed to be constant during grazing periods, to mimic continuous tracer infusion. This assumption may be invalidated by changes in grazing intensity over a grazing period. However, selection of short-term measurement periods (e.g. 2-4h) and measurement of grazing intensity would minimise this problem.

3. Fractional disappearance rate \( (k) \) remains constant as rumen fill alters. This appears unlikely, but there are insufficient data at present on which to estimate likely changes in \( k \). If necessary a variable \( k \) could be incorporated into the predictive equation.

4. Fractional disappearance rate of digesta from the rumen is not time dependent, and therefore freshly ingested food exhibits a similar \( k \) to digesta already present in the rumen. This assumption would be invalid if a time lag prior to the onset of digestion exists, e.g. fibre (Mertens, 1977), if particle size reduction affects \( k \) (Poppi et al, 1980) or if particle density changes with time, or extent of digestion (Balch & Kelly, 1950). However, as shown in section 5.2, \( k \) does not appear to increase as residence time in the rumen increases, so this assumption would appear to be valid, at least for fresh herbage.
4.3 Development

Basically, changes in rumen digesta content are due to the difference between food intake (rate of intake x eating time) and digesta disappearance from the rumen (k x rumen digesta content). Therefore, change in rumen content is dependent on the rumen content at the beginning of the observation period, the rate of food intake, k and the duration of the observation period.

Considering the digesta present in the rumen at the start of the measurement period and the ingested food as separate entities, equations can be derived to explain changes in the rumen content of both entities. The sum of these equations represents the predicted change in rumen content. Moreover, if ingesta displays a different k to digesta already present in the rumen this can be incorporated into the equation.

The digesta present in the rumen at the beginning of the measurement period displays first order kinetics, being anomalous with fasting, and may be described by an exponential equation tending to zero (appendix eqn.4.2)

\[ C_t = C_o e^{-kt} \]  

where \( C_t \) = rumen content at time t  
\( C_o \) = rumen content at time 0  
\( t \) = time after time 0

Accretion of rumen digesta is dependent on the rate of intake and k, and increases exponentially, tending towards a maximum rumen content. This may be described by appendix eqn.4.3 and in analogous to continuous intraruminal marker infusion (Shipley & Clark, 1972).

\[ C_t = C_{\text{max}}(1 - e^{-kt}) \]  

where \( C_{\text{max}} \) = maximum rumen content

The maximum rumen content is a measure of the equilibrium rumen content, i.e. when intake rate = disappearance rate, and therefore varies in relation to intake rate and k. Modifying appendix eqn.4.1, which relates to circumstances where intake = disappearance, permits definition of \( C_{\text{max}} \) (appendix eqn.4.4).
\[ C_{\text{max}} = \text{IR} \cdot k^{-1} \]  
\text{-------- appendix eqn.4.4}

where \( \text{IR} \) = intake rate (g.h\(^{-1}\))

The sum of appendix eqns 4.2 and 4.3 represents the net change in rumen content and is given in appendix eqn.4.5, which incorporates appendix eqn.4.4. Solving appendix eqn.4.5 gives a simpler working equation and is represented by appendix eqn.4.6.

\[ C_t = C_o e^{-kt} + \text{IR} \cdot k^{-1}(1 - e^{-kt}) \]  
\text{-------- appendix eqn.4.5}

\[ C_t = \text{IR} \cdot k^{-1} + (C_o - \text{IR} \cdot k^{-1})e^{-kt} \]  
\text{-------- appendix eqn.4.6}

where \( C_t \) = rumen content at time \( t \) (g)

\( C_o \) = rumen content at time 0 (g)

\( t \) = time (h)

\( \text{IR} \) = rate of intake (g.h\(^{-1}\))

\( k \) = fractional disappearance rate

The change in rumen content of feed constituents, e.g. OM, NDF, can be predicted from appendix eqn.4.6.
4.4 Application

The dynamic model proposed in section 5.4, for the prediction and analysis of intake regulation, requires, in future refinements, prediction of short term changes in rumen digesta content. This is necessary as an indicator of rumen fill and the rate of nutrient absorption, particularly VFA. The equation derived above provides a useful basis for these predictions. Although no direct attempt has been made to validate the equation, an indirect evaluation was performed in section 5.1. This highlighted the necessity of accurately measuring the short term rate of intake, which appeared to vary (per minute spent grazing) at different times of the day, particularly in the late afternoon. It also strongly suggested that k varied throughout the day, being highest in the early morning and, possibly, lowest in the afternoon. Therefore, it would appear that modifications to the equation, particularly the incorporation of a variable k, would improve accuracy. However, the predicted changes were reasonably accurate and suggested that the equation was qualitatively correct.

The equation can be used to assess the importance of rate of intake and k on changes in rumen fill, which may be of importance in the grazing situation, where sward characteristics may alter the rate of intake. This was evaluated by selecting a range of intake rates (IR), which could represent a range of herbage allowances (1.5, 3, 4.5 and 6 gDM.kg\(^{-1}\)h\(^{-1}\)), and 2 values of k, which were selected to represent, approximately, a temperate grass (k = 0.1) and legume (k = 0.2). The predicted changes in rumen OM content are shown in appendix figure 4.1, assuming that the initial rumen fill was 8gDM.kg\(^{-1}\) and grazing stopped when rumen fill reached 20gDM.kg\(^{-1}\). These data showed that rumen DM content increased more rapidly as IR increased and k decreased. For example, in the 6h simulated grazing period, only the maximum IR allowed rumen DM to reach 20gDM.kg\(^{-1}\) when k was 0.2 (after 3.9h). However, when k was 0.1, the rumen DM content was predicted to reach 20gDM.kg\(^{-1}\) after 2.6h and 3.9h when IR was 6 and 4.5 respectively. This agrees with the observation that rumen fill is higher in animals grazing grasses than in animals grazing legumes and provides a quantitative model for predicting these differences in rumen fill.
Appendix figure 4.1 Predicted changes in rumen organic matter content (gOM.kg\textsuperscript{-1}), at 4 rates of OM intake, when fractional disappearance rate from the rumen (k) is 0.2 or 0.1.
Appendix 5

DESCRIPTION AND VALIDATION OF AUTOMATIC GRAZING RECORDERS

5.1 Introduction

The measurement of grazing behaviour by visual observation is labour intensive and laborious. Therefore, automatic recording is desirable. Recently, with advances in computer technology, significant developments have been made in this field (e.g. Chambers et al., 1981; Penning, 1983). However, such technology does not come cheaply and the need for a cheaper alternative, specifically designed to record grazing time and pattern, was recognised. In conjunction with DSIR (electronics division), Christchurch, New Zealand a compact grazing recorder was developed. Experimental data have been reported in this thesis.

5.2 Design

Two separate components were developed, grazing recorders, which were lightweight and easily fitted to sheep, and an interrogator unit, which was used to read and programme the recorders.

5.2.1 Recorders

The recording units comprised a low power microprocessor, housed in a waterproof shell, and attached to a mercury switch which was positioned on the sheep's head. The mercury switch was adjusted so that the circuit closed when the sheep's head was in the 'down', i.e. grazing, position and open when the head was 'up'. The microprocessor checked the mercury switch every 1.76 seconds. If, after 14 seconds (8 checks), the circuit was observed to be closed on at least 4 occasions, 1 unit was added to the memory. If the circuit was closed on less than 4 occasions these were ignored. This prevented random contacts being interpreted as grazing behaviour. After 1h (255 potential units) a fresh memory was utilised. This enabled grazing time to be recorded hourly. The microprocessor had the capacity to record for a maximum of 120h, but was only programmed to record a maximum of 48h for the present experiments. The unit was powered by a 9V dry cell which lasted up to 21d.

5.2.2 Interrogator

The interrogator unit, comprising a microprocessor and a printing calculator, was used to communicate with the grazing recorders. The functions available are outlined overleaf.
1. Read. The data stored by the recorder may be accessed and transferred to the interrogator, in under 1 second, and can be printed by the calculator. A simulated printout is shown in appendix table 5.1

2. Reset. When data is read from the recorder it can either be retained in the recorder, or deleted and the recorder initialised.

3. Test. The position if the mercury switch on the sheep's head can be checked to ensure that contact only occurs when the head is in the grazing position.

The only manual recording required was the time when recorders were initialised and read.

5.3 Validation

The mercury switch indicates the position of the head and this may not be an accurate measurement of the time the sheep actually spend grazing. Also, the technique adopted to remove random contacts in the mercury switch may bias results. The accuracy of the recorders was checked by manually recording the time individual sheep spent grazing over hourly intervals and comparing these with the grazing time given by the recorders. A total of 21 hourly observations were made and are shown in appendix fig.5.1. The regression relating observed grazing time to recorded grazing time is given below.

\[ y = 2.2 + 0.96x \quad (r^2 = 0.97) \]

where \( y \) = recorded grazing time (min.h\(^{-1}\))

\( x \) = observed grazing time (min.h\(^{-1}\))

On one occasion playful head butting was observed and this increased the recorded grazing time (21.4 v 13.6 min.h\(^{-1}\)). Another aspect of sheep behaviour which will lead to erroneous estimation of grazing time is the practice of sheep to seek shade, or possibly to escape flies, by lowering their head in the shadow of other sheep in extremely hot weather. This practice was observed on one occasion during an experiment and the resulting data were discarded. These data were markedly higher than normally observed at the same time of day and could have been recognised as erroneous without prior knowledge of the sheep's behaviour.
In conclusion, the grazing recorders gave accurate estimates of grazing time, justifying inclusion of these data in this thesis. Possible inaccuracies due to the incorporation of a mercury switch did not appear to influence the results.
Appendix figure 5.1. Example of printout obtained from grazing recorders.

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<tr>
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<td>M+</td>
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<td>M+</td>
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<tr>
<td>36172</td>
<td>MT</td>
<td>Total of above (irrelevant)</td>
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<tr>
<td>0</td>
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<tr>
<td>0</td>
<td>M+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>152</td>
<td>M+</td>
<td>Hourly records of 'grazing time', in chronological order. 0 = 0min.h⁻¹, 255 = 60min.h⁻¹, 152 = (152 x 60) + 255 = 36min.h⁻¹</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>212</td>
<td>M+</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>M+</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>6</td>
<td>M+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>641</td>
<td>MT</td>
<td>Total 'grazing time'</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix figure 5.2 The relationship between automatically recorded grazing time (min. h\(^{-1}\)) and manually recorded grazing time (min. h\(^{-1}\)).


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Last, but not least, I am indebted to my parents and family, who always encouraged my continuing education. This thesis is as much for them as it is for me.
Papers published during the course of the study.
Influence of age of early weaned lambs on intake, digestibility and retention time of clover hay

G. J. CRUICKSHANK, D. P. POPPI AND A. R. SYKES
Lincoln College, Canterbury.

ABSTRACT

Twelve lambs, weaned at 6 weeks of age, were used to study the development of rumen function from 6 to 24 weeks of age when offered clover hay ad libitum. Six of the lambs were cannulated at the abomasum on weaning and the remaining 6 remained intact.

Dry matter intake (g/kg live weight) increased rapidly until 10 weeks of age and subsequently remained constant at 33 to 37 g DM/kg LW. in vivo DM digestibility and marker rumen retention time decreased initially (0.693 in week 7 v 0.664 in week 9 and 14.5 hours in week 8 v 10.9 hours in week 12 respectively) but were constant thereafter. The proportion of digestible DM apparently digested in the rumen was low (0.45) but was similar at 8, 12 and 16 weeks of age.

There were no differences between the intact and cannulated lambs in DM intake and digestibility or in marker retention time in the rumen.

Keywords Sheep; early-weaning; dry matter intake; digestibility; site of digestion; marker rumen retention time

INTRODUCTION

The increasing emphasis on efficient pasture utilisation and possible introduction of high fecundity sheep flocks mean that early weaning of lambs will become an increasingly critical and frequently used management technique. Our ability to meet the high nutrient requirements of these lambs from pasture will require an intimate knowledge of the development of rumen function in very young lambs and its effect on intake and site of digestion of nutrients.

Rumen development has been considered to reach adult status by 8 to 10 weeks of age in lambs given access to solid feed (Wardrop and Coombe, 1961) and it has been demonstrated that the ability of rumen microflora to digest herbage (in vitro) reaches adult status by 3 weeks of age (Joyce and Rattray, 1970). We have few data, however, on quantitative aspects of intake and digestion in very early weaned lambs. Recent research has concentrated on older lambs and has ignored the immediate post-weaning period (Weston and Margan, 1979; Egan and Doyle, 1982). High quality forages appear to be digested less in the reticulorumen and more in the caecum and proximal large intestine (Ulyatt, 1971; Ulyatt and MacRae, 1974) and it has been suggested that this effect is more pronounced in young lambs (Jagusch et al., 1976).

This paper describes a study of rumen development in early weaned lambs and the quantitative changes in dry matter (DM) intake, rumen retention time of marker, site of DM digestion and apparent DM digestibility.

MATERIALS AND METHODS

Animals and Housing

Twelve Polled Dorset lambs were obtained from a synchronised lambing. Six lambs were weaned at 38 days of age (average live weight 14.9 kg) and were fitted with a simple 'T' cannula in the abomasum. A further 6 lambs were weaned at 44 days of age (average body weight 16.2 kg) and remained intact. All lambs were then placed in metabolism crates where they remained for the duration of the experiment. A continuous lighting regime was adopted to eliminate effect of changing daylength on intake.

Diets and Feeding

Chaffed clover hay (clover content 73%) was offered ad libitum; i.e., previous days intake plus 25%. Feed was delivered every 2 h from an automatic feeder.

Measurements

Dry matter intake (DMI) was recorded daily and in vivo DM digestibility determined during weeks 7, 9, 11, 13, 15, 17 and 23. During weeks 8, 12 and 16 abomasal flow and retention time in the rumen of the DM marker 103ruthenium phenanthroline (103Ru-P) was estimated. Retention time of 103Ru-P was also estimated in week 24.

Live weight was determined at weekly intervals. Abomasal flow of DM was measured by the technique of Faichney (1975). A solution containing the digesta markers 103Ru-P and 51chromium ethylene
diamine tetra-acetic acid ($^{11}\text{Cr-EDTA}$) was continuously infused into the rumen of cannulated lambs via a temporary catheter for 8 days. Samples of abomasal digesta (approx. 50g) were collected at 8 hourly intervals over the last 4 days. Of this a 20 g sample of whole digesta was bulked. The remainder was strained through pantyhose and a 20 g sample of filtrate was also bulked. Samples were bulked within lambs over the first and last 2-day period.

Retention time of $^{103}\text{Ru-P}$ in the rumen was calculated from the rate of decline of $^{103}\text{Ru}$ concentration in faeces (counts/g DM) (Grovum and Williams, 1973). Samples of faeces were collected at approximately 4 h intervals during the 10 to 95 h after the cessation of infusion in cannulated lambs and 25 to 110 h after the injection of $^{103}\text{Ru-P}$ directly into the rumen of intact lambs.

RESULTS

Dry matter intake and apparent DM digestibility of feed in cannulated and intact lambs are given in Fig. 1 and Table 1 and indicate no apparent effect of simultaneous weaning and surgery.

Feed intake (g DM/d) increased throughout the duration of the experiment. When related to body weight

\[ \text{Table 1: Effect of cannulation on in vivo DM digestibility.} \]

<table>
<thead>
<tr>
<th>Age (weeks)</th>
<th>Intact</th>
<th>Cannulated</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>0.682</td>
<td>0.705</td>
</tr>
<tr>
<td>9</td>
<td>0.656</td>
<td>0.672</td>
</tr>
<tr>
<td>11</td>
<td>0.662</td>
<td>0.675</td>
</tr>
<tr>
<td>13</td>
<td>0.637</td>
<td>0.635</td>
</tr>
<tr>
<td>15</td>
<td>0.671</td>
<td>0.672</td>
</tr>
<tr>
<td>17</td>
<td>0.663</td>
<td>0.665</td>
</tr>
<tr>
<td>23</td>
<td>0.661</td>
<td>0.675</td>
</tr>
<tr>
<td>S.E.</td>
<td>0.017</td>
<td></td>
</tr>
</tbody>
</table>

**FIG. 1** Comparison of DMI between cannulated and intact lambs.

The increase was rapid until week 10 after which no further change occurred (Fig. 1).

Marker retention time in the rumen and in vivo $\text{DM}$ digestibility decreased initially and subsequently remained relatively constant (Table 2).

The proportion of DMI apparently disappearing in the rumen did not change with age (Fig. 2). The overall regression equation was:

\[ \text{Abomasal DM flow} = 0.706 (\pm 0.033) \times \text{DMI} - 14. (n = 14, r^2 = 0.975) \]

That for week 8 above was:

\[ \text{Abomasal DM flow} = 0.693 (\pm 0.056) \times \text{DMI} - 15. (n = 5, r^2 = 0.92) \]

Thus 29.4% of ingested DM apparently disappeared from the rumen irrespective of age, live weight or intake. This represents 45% of the total DM digestion occurring in the alimentary tract.

The average body weight gain over the experiment was 130 g/d.

**TABLE 2** Average in vivo DM digestibility and marker rumen retention time.

<table>
<thead>
<tr>
<th>Age (weeks)</th>
<th>DM digestibility</th>
<th>RRT (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>0.693a</td>
<td>14.5a</td>
</tr>
<tr>
<td>8</td>
<td>0.664b</td>
<td>9.6b</td>
</tr>
<tr>
<td>9</td>
<td>0.668b</td>
<td>6.7b</td>
</tr>
<tr>
<td>12</td>
<td>0.636c</td>
<td>12.3b</td>
</tr>
<tr>
<td>13</td>
<td>0.671b</td>
<td>12.3b</td>
</tr>
<tr>
<td>15</td>
<td>0.669b</td>
<td>12.3b</td>
</tr>
<tr>
<td>23</td>
<td>0.668b</td>
<td>12.3b</td>
</tr>
<tr>
<td>S.E.</td>
<td>0.017</td>
<td>1.7</td>
</tr>
</tbody>
</table>

**FIG. 2** Dry matter digestion in the rumen.
DISCUSSION

Bomasal cannulation of these young lambs had no effect on DMI, DM digestibility and marker rumen retention time. This result agrees with other studies in the effect of cannulation on adult sheep (MacRae et al., 1982; MacRae and Wilson, 1977).

Dry matter intake (g/kg LW) increased rapidly until week 10 and was constant thereafter which agrees with the results of Wardrop and Coombe (1961) who studied lambs weaned at 6 weeks of age and offered sorne hay.

The higher DM digestibility during week 7 and marker rumen retention time in week 8 were associated with the lower DMI. As the DMI increased here was a decrease in DM digestibility and marker rumen retention time which agrees with the results obtained by Grovum and Williams (1977) studying the effects of level of intake on digestion. The marker rumen retention times in the rumen measured in this experiment were low (8.4 to 14.5 h) when compared to those observed by Egan and Doyle (1982) (16.2 to 24.3 h).

Age, live weight or DMI were shown to have no influence on the proportion of DM digestion occurring in the rumen despite the changes in DMI and marker rumen retention time.

Digestion in the rumen accounted for 45% of the total apparent DM digested. This is comparable with the results obtained with calves offered fresh clover (Beever et al., 1980), lambs offered a ground and pelleted ration (Morgan et al., 1962) and chopped hay (M. R. Alam, pers. comm.). It is, however, lower than that observed in lambs (0.625) by Weston and Morgan (1979) and adult sheep (0.65) by Hogan (1973) and Egan et al. (1975), all of whom offered dried subterranean clover.

It is concluded that intake increased rapidly following early weaning of these lambs and, in this experiment, no change in the proportion of DM apparently digested in the rumen was observed between 8 and 16 weeks of age. Abomasal cannulation of 6-week old lambs had no effect on intake, DM digestibility and marker retention time in the rumen.

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Diurnal patterns of rumen fill in grazing sheep

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ABSTRACT
The diurnal pattern of grazing and of rumen fill was studied to assess whether the initiation and cessation of eating were associated with any particular level of rumen fill.

Four wethers fitted with large rumen cannulae grazed Huia white clover or Matua prairie grass for 14 to 21 days. Animals grazed longer on the prairie grass than on the white clover (8.9 ± 5.8 h). Major grazing periods were evident in the morning and afternoon, although the animals generally spent more of each hour in grazing during the afternoon.

Rumen fill (volume, wet weight and dry weight) showed diurnal patterns of change similar to the grazing pattern. The maximum level of rumen fill (9.5 and 7.0 g OM/kg live weight (W) on grass and clover respectively) was observed at the end of the afternoon grazing period and the minimum at 0900 h on the grass (5.2 g DM/kg W) and at 1300 h on the clover (3.9 g DM/kg W).

The implication of these results is that the intake of these roughages is less than that which is physically possible if the animal ate consistently to its maximum fill.

Keywords Sheep; white clover; prairie grass; wet weight; dry weight; rumen; volume.

INTRODUCTION
The major factor limiting animal production is the level of intake achieved. With roughage diets intake is thought to be controlled by the amount of digesta that can be accommodated in the rumen and the rate of its removal (Balch and Campling, 1962). Thus with animals within any physiological state rumen fill is relatively constant across a range of roughage diets and hence intake is proportional to the rate of digesta removal from the rumen (Ulyatt et al., 1967; Thornton and Minson, 1973; Poppi et al., 1981). However, animals on a legume diet have lower levels of rumen fill than those on a grass diet (Thornton and Minson, 1973).

This concept of a physical regulation of intake implies that animals experience satiety at a particular level of fill. However, Forbes (1980) has proposed that there is an interaction of physical and metabolic control mechanisms whereby the intake at a single meal need not necessarily cease at a particular level of rumen distension. This may partly explain why rumen fill increases in lactating animals (Hutton et al., 1964).

In a study on intake regulation of grazing animals it is necessary to know the extent to which the level of rumen fill influences the initiation and cessation of grazing. Such data are also required in intake models incorporating both physical and metabolic control systems. In this study the relationship between grazing pattern and rumen fill was examined in wethers grazing white clover or prairie grass pastures.

MATERIALS AND METHODS
Four wethers (65 ± 1.8 kg) fitted with large rumen cannulae (85 mm) were set stocked on Matua prairie grass (Bromus catharticus, Grasslands Matua) or Huia white clover (Trifolium repens) swards for 14 to 21 days during March and April with sunrise and sunset approximately 0600 and 1900 h. The prairie grass sward had an average height of 9.4 cm with a range of 1.5 to 18 cm and a herbage mass of 2100 kg DM/ha. The white clover sward had an average height of 12.3 cm with a range of 4 to 18 cm and a herbage mass of 2400 kg DM/ha. Allowance was liberal at 10 and 11.5 kg DM/head/d for prairie grass and white clover swards respectively. Grazing pattern was established by using grazing clocks designed to measure the time the animal's head was in the down position. The sampling times were organised to coincide with the beginning and end of each major grazing period — 0100 h, 0500 h (start morning), 0900 h (end morning), 1300 h (start afternoon), 2100 h (end afternoon) and 1700 h on the grass sward only. In the case of the clover studies, sampling was carried out over one 24 h period. With the prairie grass studies each sampling time was replicated and only 2 rumen emptyings were carried out each day. Rumen emptying thus was extended over a 6 d period.

At each sampling the rumen was emptied via the rumen cannula and digesta stored in a water bath at 37 to 39°C. The wet weight and volume of digesta were recorded and 2 samples (approximately 50 g) were taken for dry matter determination. The
Each sheep was infused continuously with approximately 0.9 g ytterbium/d as YbCl₃. Grab samples of faeces were taken regularly, ytterbium analysed and faecal organic matter output calculated. Three oesophageal fistulated animals were used to obtain representative samples of the diet selected and in-vitro organic matter digestibility of the extrusa was determined. From the faecal output and in-vitro digestibility, organic matter intake was calculated.

RESULTS AND DISCUSSION

As these trials were done consecutively, it is not statistically valid to compare results from grass and legume swards. The average organic matter intake (OMI) achieved by the animals was 16.1 (± 0.81) and 14.6 (± 0.71) g/kg live weight (W) for grass and legume respectively, with organic matter digestibilities of 0.67 and 0.74. Thus DOMI was similar on grass and legume pastures (10.8 g/kg W) and supplied approximately 11 MJ metabolizable energy (Beever et al., 1985). Calculated maintenance was 10.5 MJ metabolizable energy (MAFF 1975) and these animals subsequently reached live weights of approximately 80 kg. Thus intake appeared to be regulated metabolically to achieve a constant DOMI slightly in excess of calculated maintenance.

The grazing times of animals on these pastures were 8.9 (± 0.8) and 5.8 (± 0.8) h/d for grass and legume respectively which agrees with previous published reports (Lancashire and Keogh, 1966). The higher rate of intake of legume could be due in part to the easy accessibility of its green leaf for grazing (Hodgson, 1982). Of interest are the actual grazing times achieved as these are less than the potential grazing time available for animals which is assumed to be the maximum grazing time observed in sheep i.e. 12 to 13 h/d (Arnold and Dudzinski, 1981). If it is assumed that animals grazing both swards had a potential requirement in excess of that achieved then there appears to be no physical reason in terms of grazing time available why this could not have been achieved. However, the fact that a similar DOMI was achieved on both pastures suggests that the animals were regulating intake metabolically and in that case grazing time differences reflect differences in rate of intake.

There was a diurnal pattern of grazing (Fig. 1, 2) which differed slightly between animals on the grass and legume swards. Animals started grazing at approximately sunrise and stopped close to sunset with another grazing period around midnight or the early hours of the morning. Such a pattern has been observed previously but the daylight grazing has often been divided into a morning grazing and an afternoon grazing with a distinct break around midday (Pearson et al., 1951; Scott and Sutherland, 1981). Such a pattern occurred on the legume sward (Fig. 2) but not on the grass sward (Fig. 1). Most grazing was done during daylight hours (0.74 and 0.80 of total grazing time on grass and clover, respectively) and these proportions are similar to other reports (Hughes and Reid, 1951).

The intensity of grazing, defined as the proportion of each hour spent grazing (●) and the percentage of the total grazing time spent grazing (●) are shown in Fig. 1. There was a diurnal pattern of grazing across all hours of the day with the highest proportion of the maximum dry matter fill in the rumen and the grazing pattern of wethers grazing white clover.
grazing as the day progressed from 0500 h to the end of grazing at approximately 1800 h (Fig. 1, 2). The morning grazing on grass was characterised by an hourly proportion of time spent grazing being generally less than 0.5 while in the afternoon it was greater than 0.5. Eating patterns indoors were similar to that observed on grass (Forbes, 1980).

Changes in intensity of grazing must inevitably lead to changes in rate of intake over a grazing period. Rumen fill (dry matter content, wet digesta content and digesta volume) would be expected to alter accordingly and a diurnal pattern of rumen fill was observed (Table 1). The actual pattern (an increase during the day) was unexpected, given the concept of a morning and afternoon grazing but was closely associated with the pattern of intensity of grazing. Thus animals only reached a maximum rumen load at the cessation of the afternoon grazing and the rate of intake over the morning grazing was insufficient to markedly increase rumen fill. The changes in rumen fill were particularly consistent on grass but animals on the legume showed more variation. However, as the results for the legume sward were obtained during a single 24 h period they need further rigorous confirmation. The results are generally in agreement with values obtained from animals slaughtered at different times of the day (Ulyatt, 1971).

**TABLE 1** Volume (ml/kg W), wet and dry weight of rumen digesta (g/kg W) in animals grazing prairie grass or white clover.

<table>
<thead>
<tr>
<th>Time</th>
<th>0100</th>
<th>0500</th>
<th>0900</th>
<th>1300</th>
<th>1700</th>
<th>2100</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prairie grass Volume</td>
<td>97.62</td>
<td>90.22</td>
<td>74.15</td>
<td>88.99</td>
<td>108.97</td>
<td>102.13</td>
</tr>
<tr>
<td>SE</td>
<td>7.38</td>
<td>5.56</td>
<td>6.69</td>
<td>8.11</td>
<td>7.04</td>
<td>7.8</td>
</tr>
<tr>
<td>Wet weight</td>
<td>82.73</td>
<td>77.15</td>
<td>62.39</td>
<td>78.8</td>
<td>96.78</td>
<td>92.5</td>
</tr>
<tr>
<td>SE</td>
<td>5.75</td>
<td>5.19</td>
<td>5.78</td>
<td>6.52</td>
<td>5.94</td>
<td>6.34</td>
</tr>
<tr>
<td>Dry weight</td>
<td>8.36</td>
<td>7.43</td>
<td>5.14</td>
<td>7.47</td>
<td>9.02</td>
<td>9.48</td>
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<tr>
<td>SE</td>
<td>0.7</td>
<td>0.69</td>
<td>0.57</td>
<td>0.83</td>
<td>0.77</td>
<td>1.01</td>
</tr>
<tr>
<td>White clover Volume</td>
<td>79.41</td>
<td>75.77</td>
<td>87.23</td>
<td>71.13</td>
<td>96.36</td>
<td></td>
</tr>
<tr>
<td>SE</td>
<td>4.2</td>
<td>6.54</td>
<td>7.18</td>
<td>9.85</td>
<td>5.53</td>
<td></td>
</tr>
<tr>
<td>Wet weight</td>
<td>53.91</td>
<td>49.58</td>
<td>44.27</td>
<td>77.02</td>
<td>66.69</td>
<td></td>
</tr>
<tr>
<td>SE</td>
<td>7.92</td>
<td>6.3</td>
<td>7.36</td>
<td>7.31</td>
<td>6.44</td>
<td></td>
</tr>
<tr>
<td>Dry weight</td>
<td>5.34</td>
<td>4.70</td>
<td>4.21</td>
<td>3.88</td>
<td>6.99</td>
<td></td>
</tr>
<tr>
<td>SE</td>
<td>1.01</td>
<td>0.68</td>
<td>0.84</td>
<td>0.75</td>
<td>1.02</td>
<td></td>
</tr>
</tbody>
</table>

Animals grazing legume swards generally had lower rumen dry matter, wet weight and volume throughout the day when compared to those on grass which agrees with results from indoor trials (Thornton and Minson, 1973). The maximum dry matter content of 9.5 g/kg live weight on grass and 7.0 g/kg live weight on clover swards is much lower than that observed in sheep under indoor, steady-state feeding conditions (21 g/kg W; Poppi et al., 1981).

Grazing animals do not appear to regulate grazing pattern by reference to the level of rumen fill. The rumen appears to reach its maximum level of fill only at the end of the afternoon grazing. Examination of the proportion of grazing done in each hour indicates that there is considerable scope for increasing this over the morning grazing or in the midnight grazing period. The implications of such a pattern of rumen fill and grazing intensity is that physical limitation is unlikely to be the primary obstacle to increasing the intake of these forages. There may have been an apparent physical limitation against continuing the afternoon grazing on the grass as the rumen was very distended. These results suggest that simple models based on either physical or metabolic regulators of intake are not applicable to the grazing animal. Models such as that proposed by Forbes (1980) are required which incorporate physical and metabolic regulators, the relative importance of which may vary throughout the day.

**ACKNOWLEDGEMENTS**

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Intake and duodenal protein flow in early weaned lambs grazing white clover, lucerne, ryegrass and prairie grass

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Animal Sciences Group, Lincoln College, Canterbury

ABSTRACT

Protein (NAN) flow to the small intestine was measured in early-weaned ram lambs grazing pure swards of white clover (W), lucerne (L), ryegrass (R) and prairie grass (P) at high allowances.

Lambs were weaned at 6 weeks of age and measurements made at 8 and 12 weeks of age. Live-weight gain (LWG) measured over 6 weeks after weaning was higher for lambs grazing on legumes (308 ± 25, 321 ± 18 for L and W) than on grasses (230 ± 8, 227 ± 9 for P and R).

No differences were observed within species in duodenal NAN flow between measurements made at 8 and 12 weeks of age. Duodenal NAN flow (g NAN/kg LW/d) was significantly higher for legumes (1.24 ± 0.11, 1.20 ± 0.09 for L and W) than for grasses (0.87 ± 0.006, 0.96 ± 0.06 for P and R). Duodenal NAN flow, expressed as g NAN/kg DOMI, showed a similar pattern (44.9 ± 2.1, 45.0 ± 1.3, 42.8 ± 2.2, 39.3 ± 2.2 respectively for L, W, P and R) though differences between species were lower than when expressed /kg LW.

The rumen retention time (h) of a dry matter marker (103 Ru_P) was lower for legumes (8.4 ± 0.43, 9.5 ± 0.74 for L and W) than for grasses (11.5 ± 0.73, 15.1 ± 0.98 for P and R).

Intake (g OM/kg LW/d) was 30% higher for legumes than for grasses.

It was concluded that the higher LWG observed in lambs grazing legumes was associated more with a higher organic matter intake than with an increase in the duodenal NAN/DOMI ratio.

Keywords Sheep; early-weaning; grazing intake; duodenal protein flow; pure pasture species.

INTRODUCTION

Growth rates of lambs at pasture tend to fall below those of 350 to 400 g/day recorded indoors (Fraser and Orskov, 1974; Orskov et al., 1976) although legumes have the ability to promote growth rates in excess of 300 g/d (McLean et al., 1965; Ulyatt, 1971). Lambs do not obtain sufficient nutrients from pasture to realise their genetic potential for growth and protein supply to the small intestine has been implicated as a major factor (MacRae and Ulyatt, 1974; MacRae, 1976; Barry, 1981).

Limited data are available for protein supply to the small intestine in ruminants offered fresh herbage indoors (MacRae and Ulyatt, 1974; Ulyatt and Egan, 1979; Beever et al., 1980) and grazing (Corbett and Pickering, 1979; Corbett et al., 1982; Ulyatt et al., 1980; Losada et al., 1982). No data appear to exist on protein flow to the small intestine in early-weaned lambs, either offered herbage indoors or grazing fresh herbage.

The experiment described here quantifies the intake and non ammonia nitrogen (NAN) flow at the duodenum in early-weaned lambs grazing pure pasture swards of Huia white clover (Trifolium repens), Rere lucerne (Medicago sativa), Matua prairie grass (Bromus catharticus) and Ruanui ryegrass (Lolium perenne) at high allowances.
Digesta markers (10 μCi 103Ru-P and 50 μCi 51Cr-EDTA in 150 ml water) were continuously infused into the rumen by portable peristaltic pumps (Everest Electronics, Seaford, South Australia) via a temporary rumen catheter.

Samples of duodenal digesta and faeces were collected over the last 4 days of infusion on 8 separate occasions, staggered to represent 3-hourly intervals over a theoretical 24 hour day. After the cessation of infusion at approximately 1000 h, the rumen retention time of 103Ru-P and 51Cr-EDTA was calculated from the rate of decrease of marker concentration in whole duodenal digesta and faeces respectively.

Intake

Faecal output was calculated from the dilution of 103Ru-P in the faeces. The double marker technique of Faichney (1975) appeared to be largely due to the high DM digestibility (Table 1). Lambs grazing legumes had higher duodenal NAN flow/kg DOMI but this was not statistically significant (P>0.05).

Previous studies on digestion of fresh herbage have used much older lambs and adult sheep or cattle and this appears to be the first study in which these digestion characteristics have been determined in early weaned lambs in a grazing situation with realistic animal production data. No data appear to have been published for prairie grass.

In comparison to previously published reports the duodenal flow of NAN (g/kg LW) was higher than those observed in sheep grazing lucerne (Corbett et al., 1982) and in cattle grazing ryegrass and white clover (Losada et al., 1982) (Table 1). This appeared to be largely due to the high OM (g/kg LW) achieved, as the duodenal flow of NAN (g/kg DOMI) observed was similar in all studies.

The differences in growth rate, therefore, appeared to be associated more with a difference in DOMI than with differences in protein:energy ratio of absorbed nutrients.

The OM digestibility at 8 and 12 weeks respectively was 0.87 and 0.84, L; 0.84 and 0.83, W; 0.82 and 0.83, R; 0.85 and 0.77, P. With the exception of prairie grass at 12 weeks these values are 1 to 9 percentage units higher than previously published data for grazed herbage estimated from in-vitro in-vivo relationships (Geenty and Sykes, 1982; 1984).

Live-weight gain was 321 ± 18, 308 ± 25, 230 ± 8 and 227 ± 9 for lambs grazing white clover, lucerne, prairie grass and ryegrass respectively. These values agree with those reported by McLean et al. (1965) but are considerably less than the 360 to 409 g/d reported by Fraser and Orskov (1974) for lambs of a similar age consuming a barley-fishmeal diet.

The reasons for the higher growth rate on legumes appear to be related to the higher DOMI (21 to 53%) and NAN flow (g/kg LW) to the small intestine (25 to 43%) (Table 1). Lambs grazing legumes had higher duodenal NAN flow/kg DOMI but this was not statistically significant (P>0.05).

As no differences were observed between 8 and 12 weeks of age in intake (g OMI/kg live weight (LW)) or duodenal NAN flow (g NAN/kg LW or g NAN/kg DOMI), results have been grouped within pasture species.

RESULTS AND DISCUSSION

TABLE 1 Intake (g/kg LW/d) of organic matter (OMI), digestible organic matter (DOMI) and nitrogen (NI) and duodenal NAN flow in grazing ruminants.

<table>
<thead>
<tr>
<th></th>
<th>OMI</th>
<th>DOMI</th>
<th>NI</th>
<th>Duodenal flow (g/kg LW/d)</th>
<th>NAN flow (g/kg DOMI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>This experiment</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lucerne</td>
<td>36.5 ± 1.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>31.2 ± 1.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.15 ± 0.11&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.24 ± 0.11&lt;sup&gt;a&lt;/sup&gt;</td>
<td>44.9 ± 2.1&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>White clover</td>
<td>33.4 ± 1.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>27.9 ± 1.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.69 ± 0.15&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.20 ± 0.09&lt;sup&gt;a&lt;/sup&gt;</td>
<td>45.0 ± 2.3&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Ryegrass</td>
<td>28.8 ± 1.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>23.1 ± 1.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.24 ± 0.05&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.96 ± 0.06&lt;sup&gt;b&lt;/sup&gt;</td>
<td>39.2 ± 2.2&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Prairie grass</td>
<td>25.1 ± 1.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>20.4 ± 1.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.90 ± 0.07&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0.87 ± 0.07&lt;sup&gt;b&lt;/sup&gt;</td>
<td>42.8 ± 1.7&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Other experiments</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ryegrass&lt;sup&gt;1&lt;/sup&gt;</td>
<td>—</td>
<td>Approx. 13-18</td>
<td>—</td>
<td>0.47-0.68</td>
<td>27-41</td>
</tr>
<tr>
<td>White clover&lt;sup&gt;1&lt;/sup&gt;</td>
<td>—</td>
<td>Approx. 18-23</td>
<td>—</td>
<td>0.74-0.81</td>
<td>29-43</td>
</tr>
<tr>
<td>Lucerne&lt;sup&gt;1&lt;/sup&gt;</td>
<td>22-30</td>
<td>15-22</td>
<td>0.86-1.41</td>
<td>0.59-1.11</td>
<td>32-56</td>
</tr>
</tbody>
</table>

<sup>1</sup>Losada et al. (1982) grazing cattle
<sup>2</sup>Corbett and Pickering (1979), Corbett et al., (1982) grazing sheep
Corbett et al., 1982; Hughes et al., 1984) and may reflect the generally high pasture quality and potential for diet selection in the present study. They may also reflect a difference between the in-vitro and the indigestible ADF techniques in the estimation of the in-vivo digestibility of high quality ingesta.

The higher OM and duodenal NAN flows were associated with very low values for marker retention time in the rumen (Table 2). These values are much lower than those observed in animals offered dried forage by Egan and Doyle (1982) (13.9 to 17.1 h) and Margan et al. (1982) (16.2 to 24.3 h) and highlight the need to examine critically the extension of data from animals offered dried forage indoors to grazing animals.

**TABLE 2 Retention time (h) of markers in the rumen of lambs grazing white clover (W), lucerne (L), prairie grass (P) and ryegrass (R).**

<table>
<thead>
<tr>
<th></th>
<th>W</th>
<th>L</th>
<th>P</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ru-P</td>
<td>9.6±0.74ab</td>
<td>8.5±0.43a</td>
<td>11.5±0.73b</td>
<td>15.1±0.98c</td>
</tr>
<tr>
<td>Cr-EDTA</td>
<td>7.7±0.53a</td>
<td>8.2±0.75ab</td>
<td>7.3±0.41bc</td>
<td>10.3±0.47c</td>
</tr>
</tbody>
</table>

The values may, however, reflect the age of the animal as they are similar to those of 10.8 to 14.5 h observed for early-weaned lambs offered clover hay (Cruickshank et al., 1984). This also supports the concept of working with animals in the appropriate physiological state.

The practical significance of these results is the higher LWG achieved by animals on legume pasture and the lack of a difference in LWG between lucerne and white clover and between ryegrass and prairie grass. Based on the LWG achieved by animals consuming a barley/fishmeal diet, the animals grazing legume pastures did not appear to reach their genetic potential for growth.

It is concluded that the higher LWG observed on legume pastures was associated more with a higher DOMI than with the higher duodenal NAN/DOMI ratio.

**ACKNOWLEDGEMENTS**

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