EFFECT OF PARTICLE SIZE DISTRIBUTION IN THE RETICULO-RUMEN, OMASUM AND ABOMASUM OF SHEEP ON VOLUNTARY INTAKE AND DIGESTIBILITY OF FORAGES

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Abstract

This study was designed to provide information on some of the factors affecting voluntary consumption and digestibility of forages by sheep. A wet sieving procedure was used to determine particle size distribution in the reticulo-rumen, omasum and abomasum of sheep fed 100 % prebloom alfalfa or 100 % second-cut Altai wild ryegrass hays or mixtures of these with tall wheatgrass or Altai wild ryegrass straws. The study also compared second-cut Altai wild ryegrass and prebloom alfalfa as components in an all forage diet for sheep. Each diet was fed ad libitum to eight Romanov x Western whiteface wether lambs weighing 22 to 25 kg during the intake and digestibility trials. For the determination of particle size distribution, the animals were slaughtered at 12, 24, 36, and 48 hours after feed removal and the contents of the reticulo-rumen, omasum and abomasum sampled.

Five different methods of describing digesta particle size distribution were compared as to their ability to predict voluntary intake and digestibility of the forages by sheep.

The best method for expressing particle size distribution in the reticulo-rumen in terms of ability to predict dry matter digestibility (DMD) was the proportion of soluble dry matter in total dry matter (PSDM). A significant (P< 0.05) correlation (r = 0.84) between PSDM and dry matter digestibility, 12 hours after feed removal was obtained. PSDM in omasal digesta 24 hours after feed removal was also highly correlated with DMD and energy digestibility (r = 0.97, 0.91, respectively). Very high correlations were obtained between PSDM in abomasal digesta 24 hours after feed removal and digestibility of cellulose, NDF and ADF (r = 0.99, 0.97 and 0.97 respectively). The proportion of particles less than 1mm to the total particles (PIP) in the reticulo-rumen gave the most
consistent correlations with intake of dry matter and energy.

Voluntary intake of dry matter by the animals on the alfalfa–based diets were significantly higher (P < 0.05) than those on the second–cut Altai wild ryegrass–based diets. However, the apparent digestibility coefficients of the proximate fractions in the Altai wild ryegrass diets were significantly higher (P < 0.05) than those of diets containing alfalfa. Daily intake of digestible energy by animals on 100 % alfalfa was not significantly different from that of animals on 100 % second–cut Altai wild ryegrass. The difference between their respective combinations with tall wheatgrass and Altai wild ryegrass straws were also not significant.

It was concluded that PIP and PSDM are indeces based on biologically significant fractions and may therefore have greater relevance than purely mathematical or statistical descriptions of particle size distribution in digesta. In this regard, the relationship between PSDM and digestibility and, PIP and intake are consistent with published theory and can be used in mathematical models to examine control processes in feed intake, rate of passage and digestion. The study also indicated that second–cut Altai wild ryegrass harvested at the prebloom stage can be used as a substitute for alfalfa in an all–forage diet for winter feeding of sheep.
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Ruminants are the predominant food producing livestock in the world. They supply nearly all the milk and approximately one-half the meat consumed by humans. Ruminants have a specialized compartment (reticulo-rumen) in their digestive system capable of predigesting feed prior to its passage through the rest of the digestive system. The predigestion that takes place is brought about by the action of the large bacterial and protozoal populations inhabiting the reticulo-rumen (Hungate, 1966).

Forages are the major source of feed for ruminant livestock in most parts of the world. The quality of a forage has its ultimate expression in terms of animal performance when it is fed as the sole source of digestible nutrients and when the amount offered is not limited. The anatomical and cell wall characteristics of forage plants confer on them the necessary strength and rigidity to maintain their erectness. The same features are also responsible for the relative indigestibility of forages. This dietary limitation arises mainly from the physical properties of forages. In particular their resistance to breakdown in the gastro-intestinal tract of animals limits their dietary usefulness (Akin, 1986).

The nutritive quality of a forage diet therefore depends, in part, on the efficiency of its initial processing. The initial processing occurs both as the forage is eaten and during passage through the reticulo-rumen. As a result the forage is reduced to a form which is more easily utilized by the rest of the digestive system. This initial, rate-limiting step in ruminant digestion is governed by two major factors; 1) the physical breakdown of the forage which occurs as a result of mastication during ingestion and
rumination, and 2) detritus by the muscular activity of the rumen wall and microbial digestion (Moseley and Jones, 1984). Since these processes are responsible for controlling the physical breakdown of feed they may also influence its passage from the rumen and, consequently, the voluntary intake of feed by the animal (Balch and Campling, 1962). Thus variations in physical breakdown may affect the extent, rate and nature of digestion within the reticulo-rumen and the ultimate supply of nutrients to the intestine.

While the digestibilities of different forages can be accurately estimated under laboratory conditions, measurement of voluntary intake can only be done in feeding trials. This is both time consuming and expensive. The inability of researchers to predict successfully the level of forage intake by ruminants may be due to the scientists' failure to describe forage digestion and passage in terms of dynamic processes in the rumen (Worrell et al., 1986).

Several recent studies have investigated the physical attributes of forages emphasizing particle degradation and passage kinetics (Mertens and Ely, 1982; Ehle and Stern 1986; Pond et al., 1987). The manner by which the outflow of particles from the rumen is controlled continues to attract interest, especially in terms of the possible effect on voluntary intake. The considerable space that feed particles occupy in the reticulo-rumen potentially limits intake. It is therefore desirable that digested particles are passed as rapidly as possible from the rumen. Clearance of feed particles depends on two interacting processes, breakdown (physical reduction in particle size plus microbial digestion) and passage through the reticulo-omasal orifice (Ulyatt et al., 1986). Although the qualitative aspects of these processes are well understood, emphasis is now been placed on understanding their quantitative contributions.

This study was designed to provide more information on some of the factors affecting intake and digestibility of forages in sheep. Factors such as rate of particle size reduction
and distribution in the reticulo-rumen, omasum and abomasum of sheep were characterized and/or quantified. Such information is urgently required because the increased use of mathematical models to examine control processes in feed intake, rate of passage and rate of fermentation demands that these factors be identified and measured precisely. Different methods of describing digesta particle size and distribution were also compared as to their ability to relate to intake and digestion in sheep. In addition to information on particle size, this study also compared second-cut Altai wild ryegrass with alfalfa as components in an all-forage diet for sheep.
Chapter 2

LITERATURE REVIEW

2.1 REVIEW OF METHODS OF NUTRITIONAL EVALUATION OF FORAGES

The nutritional value of forages as well as the nutritional requirements of animals must be known before suitable rations can be formulated for livestock. The nutritive value of a forage is an intrinsic characteristic which enables the forage to supply nutrients in adequate quantities to help meet the physiological requirements of an animal (Seoane, 1983). Nutritive value is divided into three components; relative proportion of nutrients, the digestibility of the nutrients, and the animal’s voluntary intake of the forage.

Methods for forage evaluation are categorized according to type of procedure; either a) compositional analysis—the use of analytical methods to determine the composition of dietary ingredients, or b) in vitro procedures.

Analyses describing carbohydrate, protein and fiber fractions attempt as their first objective a characterization and division of the dry matter of the forage into categories relative to their nutritional character or availability. The proximate analysis and detergent system of analysis are examples (Van Soest, 1984). These systems provide analytical values of composition of dietary ingredients upon which balanced feed formulations are based; alternatively, animal responses are predicted from dietary composition.

On the other hand, in vitro methods involving rumen bacteria or enzymes are designed primarily to estimate nutritive value of the total feed or the availability of a particular
fraction. These methods reveal little about the chemical nature of the material being assayed (Van Soest, 1984). Nutritional properties that must be inferred from such relationships are prone to varying degrees of uncertainty and error. The association between any feed fraction and animal performance presumes a cause–effect relationship whereby the isolated components either contain (a) unavailable fractions or, (b) nutritionally available fractions or (c) fractions which promote or reduce the efficient utilization of other nutrients (Minson, 1982).

For the purposes of this review it is assumed that mineral and vitamin requirements are separate estimations, and that one can relatively easily make adjustments in their levels in rations. The prime factors for consideration are therefore protein and energy.

2.2 CHEMICAL COMPOSITION OF FORAGES

2.2.1 Introduction

Forages contain a wide diversity of chemical constituents many of which may be considered as nutrients because they are either used as an energy source or satisfy a specific nutrient requirement. The chemical constituents of forages are divided into those making up the structure of the plant (cell wall constituents) and those contained within the cell structure (cell contents). This division is nutritionally meaningful because it lends itself to simple chemical analysis by extraction in neutral and acid detergent (Van Soest and Moore, 1965).

The cell contents consist of the sugars and 'storage' carbohydrates (fructosans or starch), proteins and non-protein nitrogenous constituents, lipids, organic acids, vitamins and minerals. The cell wall components are mainly cellulose, hemicellulose, pectin, lignin and structural amino acids. The availability or digestibility of these constituents varies from the completely digestible sugars to the largely indigestible lignin. The digestibility
of cellulose and hemicellulose is influenced by the degree of lignification, the conditions and duration of enzymes present in the gastrointestinal tract while cell wall constituents are degraded mainly by enzymes of microbial origin in the rumen (Jones and Wilson, 1987).

The starting point of forage evaluation is often, the determination of the chemical composition which is then used as an index of forage quality. The quantity of carbohydrate, fat, and protein provide a measure of the usefulness of a feed. Unless the components making up a ration have a certain minimum amount of each of these nutrients, the animal cannot be adequately fed. The chemical composition of forages has consistently been positively correlated with animal performance. Van Soest (1968) noted that some of the chemical constituents may impose a limit on the availability of some nutrients and may influence the rate of digestion.

The main factors influencing the chemical composition and nutritive quality of forages have been the subject of several extensive reviews (Minson, 1982; Norton, 1982; Wilson, 1982). The chemical composition of plants varies not only within and between species, but is also affected by environmental factors. As a plant matures there is usually an increase in the proportion of fiber and a reduction in protein and non-structural carbohydrates of cell contents. Associated with these changes is a reduction in intake and digestibility of the plant by animals.

The most commonly used system of feed evaluation is the proximate system of analysis. The background and limitations of this system in its ability to predict the nutritive value of feedstuffs have been reviewed by Van Soest (1982). In the period prior to the late 1950s, a major emphasis in quality evaluation was directed to the definition of relationships between estimates of digestibility (dry matter, organic matter TDN etc.) and components of the proximate analysis (primarily, crude fiber and protein) or chemically isolated fractions of the cell wall such as cellulose or lignin.
Two main components are measured during the chemical evaluation of forages; a) protein and other nitrogen containing compounds, and b) carbohydrates.

2.2.2 Protein and Nitrogen Fractions

Nitrogen in forages exist in several forms; non–protein nitrogen (NPN), which is generally soluble, protein nitrogen (variable solubility) and unavailable nitrogen (mostly insoluble) associated with or recovered in acid detergent fiber (ADF). The NPN and protein nitrogen constituents of herbage are important nutrients for the ruminant, needed to satisfy the nitrogen requirements of rumen microorganisms and that of host animal (Jones and Wilson, 1987).

Protein deficiencies are a major limitation to the intake and utilization of herbage. Crude protein (CP) content below 6–8 percent in forages depresses appetite (Doyle, 1987). The depressing effect on intake appears to be caused by a deficiency of circulating amino acids since intake of a protein deficient diet can be increased if casein (but not urea) is infused into the duodenum (Egan, 1965). Filmer (1982) and Beever (1982) reported that the protein content of temperate forages is seldom a limiting factor, but that its high degradability in the rumen may result in a high proportion of protein being inefficiently used by the ruminant. Jones and Wilson (1987) on the other hand, suggested that the balance of soluble carbohydrates and nitrogen constituents in a forage is of greater importance than total protein content.

The crude protein content of forages is influenced by the stage of growth and the level of nitrogen fertilizer applied during growth (Jones and Wilson, 1987). General trends in relative crude protein content are evident in comparisons between species and particularly between grasses and legumes. Minson (1976b) compared the frequency distribution of protein content in grasses and legumes in the literature. The analysis showed a considerably higher median for legumes (150–180g CP/kg DM) than grasses (60–90g CP/kg
Chapter 2. LITERATURE REVIEW

Tropical grasses showed skewed distributions with 22% of the protein values below 60g CP/kg DM. The lower protein content of many tropical grasses has been related to the higher efficiency with which C\textsubscript{4} plants use nitrogen for growth. Norton (1982) concluded that the low protein content often found in tropical grasses, even when fertilized with nitrogen, is an inherent characteristic of C\textsubscript{4} plants closely related to their survival under conditions of low soil fertility.

Protein content is also influenced by vegetative stage. Young vegetative growth is high in protein but the protein content rapidly falls as the proportion of leaf decreases. Protein content decreases in both the leaves and the stems as the plant ages. Yet there is a slower decline in the protein content of the leaf than of the stem with advancing age. This reflects the decrease in the proportion of cell contents in the stem as the stem lignifies and cell walls thicken (Norton, 1982; Jones and Wilson, 1987). Although protein content alone is not a good indicator of forage quality, it is an important consideration in quality evaluation.

2.2.3 Carbohydrate Content

The carbohydrate fraction of forages consists of the crude fiber and nitrogen–free–extract (NFE) portions of the forage. Fiber is defined nutritionally as the insoluble organic matter indigestible by animal enzymes (Van Soest, 1967). The three main components of forage fiber are; hemicellulose, cellulose and lignin. The digestibility of hemicellulose and cellulose varies depending on the animal species being fed. Lignin, however, is generally regarded as indigestible. NFE is calculated by deducting from the initial weight of the sample, the sum of the moisture, ether extract, crude protein, crude fiber, and ash. Feeds that are high in starches and sugars are high in NFE.

The development of the crude fiber technique and the proximate system of analysis during the 19th century was an attempt to partition feeds on the basis of the potential
availability of the carbohydrate components. The crude fiber was designated as the 'indigestible portion' while the NFE contained the relatively soluble carbohydrate. More recent research determined that crude fiber is not a homogenous entity and contains both digestible and somewhat less digestible substances. Lignin is recovered only to the extent of 10-50 %, hemicellulose 15-25 %, and cellulose 50-80 %. In fact, the crude fiber, especially in roughages, may be as well or better digested than the NFE fraction (Van Soest, 1982).

A significant improvement in forage quality evaluation methodology was the description of plant composition in terms of cell contents and cell walls by Van Soest (1967). This method separated the plant material into two fractions of high and low availability to the ruminant animal. The cell contents are generally considered to be of high digestibility and are therefore an important nutritive consideration. Van Soest (1982) obtained an average digestibility estimate of 98 %. With such a high digestibility it is of importance to know what proportion of a forage is present as cell content. The cell wall is also an important source of nutrients. Methods have, therefore, been developed for fractionating the cell wall, loosely referred to as fiber, into its various constituent parts.

Neutral detergent fiber (NDF) is a measure of the plant cell wall. NDF refers to all of the constituents in a feed which are not soluble in neutral detergent. The NDF fraction recovers the portion of a forage not readily digestible to a greater extent than any other fiber fraction (Van Soest, 1984). NDF includes hemicellulose, cellulose, lignin, cell wall nitrogen, ash and cutin. The NDF value is a measure of palatability or expected voluntary intake by an animal of a feed. That is, a relatively low NDF value would indicate a high proportion of soluble starches and sugars. It is these components (soluble starches and sugars) which contribute the greatest amount to the overall palatability of a feed.

Acid detergent dissolves hemicellulose, acid soluble ash and some cell wall nitrogen.
Acid detergent fiber (ADF), therefore contains cellulose, lignin and acid insoluble ash. The ADF value is a rough index of digestibility of a forage. A low ADF value indicates a low proportion of lignocellulose complexes in the forage and therefore a relatively high digestibility.

The refluxing of forage with acid detergent was originally intended to be a preparatory means of recovering lignin from the interfering matter. However, the acid detergent fiber recovers cellulose as well as lignin, cutin, heat damaged protein, and silica (Van Soest, 1975). The use of ADF as a preparatory step for the determination of the above fractions outweigh its importance as a measure of fiber. Other uses of acid detergent extraction are: (1) the fractionation of plant cell walls so that hemicellulose, which the acid detergent solution dissolves, is partitioned from the cellulose and lignin; (2) the determination of its nitrogen content which has been shown to be highly correlated (negatively) with protein digestibility (Van Soest, 1975).

2.2.4 Available energy in forages

In most tropical countries the primary purpose served by forages in the diet of ruminants is the provision of energy. A shift in emphasis from protein and other chemical entities to available energy content of forages as the primary factor limiting animal response started in the late 1950s. During the same period the importance of level of intake as a principal component of the feeding value of a forage was recognized. Blaxter (1956) in a review of the nutritive value of feeds as sources of energy concluded that the primary consideration in the feeding of the individual animal is the adequacy of energy supply. He further stated that shortages of dietary energy are usually more important causes of low productivity in farm animals, than are dietary deficiencies of vitamins, minerals or protein. Crampton (1957) also noted that available energy rather than some specific nutrient was the fundamental limiting factor in the nutritive value of forages. He concluded that if a
forage is consumed in amounts sufficient to meet the animal's energy requirements, the forage will also probably meet the animal's needs for protein, calcium and phosphorus.

Crampton (1957) suggested that a numerical rating of quality might be assigned to a forage on the basis of the animal's level of consumption of the forage as a percentage of an 'expected' value, and subsequently proposed adoption of a Nutritive Value Index (NVI) as a measure of relative intake of digestible energy (Crampton et al., 1960). Reid and Klopfenstein (1983) noted that the principle involved in the determination of the NVI led to the introduction of periods of ad libitum feeding into feeding trials. This resulted in an intensification of efforts by many scientists to define both forage and animal characteristics that regulate intake.

Blaxter et al. (1961) reported that the voluntary intake of hays by sheep was directly related to both energy digestibility and rate of passage of the forage. They concluded that within the range of forage quality examined, appetite was controlled by physical rather than physiological factors.

Since the gross energy content of different herbages of varying maturity is relatively constant (Minson, 1980) digestible energy content is closely related to the digestibility of dry matter or organic matter. The energy losses in urine and fermentation gases also tend to remain relatively constant (Jones and Wilson, 1987). Therefore assessment of the digestibility of dry matter or organic matter of a forage is, regarded as an acceptable measurement of the metabolizable energy of the forage.

2.3 EFFECT OF CHEMICAL COMPOSITION ON VOLUNTARY INTAKE

2.3.1 Introduction

Minson (1982) categorized the chemical factors in plants which influence the intake of forage by animals into three classes;
1. chemical fractions that are related to the quantity and composition of the fiber in the forage,

2. chemical fractions that are essential nutrients for the microbial population of the rumen and the host animal, and

3. toxic factors.

Van Soest (1965) determined that chemical composition was much more closely related to digestibility than voluntary intake. In some forage species eg. orchardgrass, bromegrass and sudangrass, the correlation between voluntary intake and chemical components was very high, and a nutritive value index could be predicted with some degree of accuracy. In other species such as alfalfa and Kentucky bluegrass, relationships were confounded, and there was not a significant relationship between voluntary intake and digestibility or between chemical composition and voluntary intake. Van Soest (1965) also found that the interrelationships between intake, digestibility and chemical composition were highly species-oriented. The only consistent effect that could be observed for all forages was that as the total fibrous fraction (cell wall constituents) increases, voluntary intake declines with an increasing negative slope.

### 2.3.2 Effect of cellular components on voluntary intake

The relationship between cellular components and intake depends on the contribution made by a specific constituent to the structure or volume of the plant. The amount of forage ingested by ruminants depends on both the bulk and filling effect of feed particles. In other words, it depends on the ingestive capacity of the animal (Seoane, 1983). The bulk or density of a forage is primarily due to an inherited characteristic but is affected by age, light, temperature, humidity, and other environmental conditions. These factors are difficult to control under practical conditions. By comparison, the filling effect of a
forage, is a more predictable phenomenon. The filling effect depends almost entirely on the rate of cell wall degradation in the rumen and on the rate of passage of degraded material to the lower parts of the gastrointestinal tract. Cell wall degradation is mainly influenced by two factors: (a) the chemical composition of the wall which determines its resistance to both chewing and microbial attack and, (b) the activity of the exogenous microbial population of the rumen which affects the rate of cell wall degradation (Minson, 1982).

Mertens (1973) demonstrated the importance of cell walls as determinants of voluntary intake. He reported that sheep eat a fairly constant amount of cell walls, which is approximately 40g/kgBW\(^{0.75}\). Seoane (1982) also found that dry matter intake was highly correlated with cell wall and cellulose contents of hays, both of which are structural components of the plant. Seoane (1982) reported that when voluntary intake was expressed as grams of cell walls ingested per kgBW\(^{0.75}\), intake varied between 41.4 to 47.2g/kgBW\(^{0.75}\). These values are slightly higher than those reported by Mertens (1973).

As forage plants mature there is usually an increase in the proportion of fiber and a reduction in the protein and non-structural carbohydrates of the cell contents. Associated with these changes, digestibility and intake by animals are reduced. Van Soest (1965) found significant correlations between intake and neutral detergent fiber (\(r = -0.65\)), protein (\(r = 0.54\)) and acid detergent fiber (\(r = -0.53\)). In a study with 35 grasses and 14 legume samples Donefer et al. (1966) found that intake of grass and legume samples was significantly correlated (\(r = 0.94\)) with the quantity of dry matter soluble in acid pepsin.
2.3.3 Essential nutrients

Protein

The intake of a forage by an animal will only be limited by the level of fiber and its physical composition if protein, vitamin and minerals are available in sufficient quantities. Morris (1966) found that a decline in crude protein content below 6–8 %, depressed appetite and significantly reduced forage intake by cattle. Feeding a protein supplement or urea, however, increased intake by 16–82 %. Adequate levels of dietary sulphur are required for the conversion of urea into microbial protein and where the forage is deficient in sulphur then feeding urea has little effect on intake (Kennedy and Siebert, 1973).

Sulphur

Sulphur is required for the formation of bacterial protein in the rumen so any deficiency of sulphur is likely to lead to a protein deficiency and reduced intake. Feeding sulphur supplements has increased the intake of grasses with less than 0.10 % sulphur by 21–49 % (Kennedy and Siebert, 1972, 1973). This increase only occurs when nitrogen levels in the diet are adequate for the utilization of the sulphur by the microbial population in the rumen (Kennedy and Siebert, 1973). Subsequent work showed that the intake response was related to the sulphur content of the grass and that no increase in intake by sheep would be expected when the grass contained more than 0.17 % sulphur (Ress and Minson, 1978).

Thus the nutrient availability of a feed is basically limited by its chemical composition. But the chemical composition of forage is an imperfect standard by which to judge its nutritive value. The first consideration in evaluating the nutritive value of a forage is digestibility, since undigested nutrients do not enter the body proper (Schneider and Flatt, 1975).
2.4 EFFECT OF CHEMICAL COMPOSITION ON DIGESTIBILITY

A number of factors influence the digestibility of a forage; a) proportion of stem, b) amount of lignin, and c) method of digestibility determination.

Sullivan (1964), reviewed research on harvested forages in the northeastern United States. He noted that one of the problems with using chemical components to predict digestibility was the discrepancies between different classes of forages and particularly between legumes and grasses. Of the many components examined, the lignin concentration of the forages showed the highest association with dry matter or organic matter digestibility. None of the variants of the fiber analysis (acid detergent fiber, cellulose, acetic acid fiber, or non–protein ammonium oxalate fiber) were better correlated with digestibility than crude fiber.

Plant cell wall content, as measured by neutral detergent fiber (NDF), has proved to be the most fundamental feed characteristic determining feeding value of forages. Van Soest (1975), however, reported poor correlation between NDF and digestibility. He attributed this to the high variability in digestibility of plant cell walls. It therefore follows that the problem of digestibility prediction is that of estimating cell wall digestibility. Several techniques have been established which take this factor into account. Two examples are in vitro digestibility using rumen inoculum (Tilley and Terry, 1963) and enzyme solubility (Jones and Hayward, 1975). The results of these tests have been found to be more successful in predicting in vivo digestibility than those based simply on fiber content or fiber constituents such as cellulose and lignin.

Ideally, predicting digestibility from chemical components could be achieved if the chemical entities could be separated and sorted according to their nutritional uniformity. This concept was applied by Lucas (1964) in a mathematical model cited by Van Soest (1982). The results of analysis by the Lucas model showed that only the non–cell wall
portion of feeds behave in a nutritionally uniform fashion and that the cellulosic carbohydrates were non-uniform subfractions (Van Soest, 1982). The non-uniformity of cellulosic carbohydrates is associated with lignification and secondary factors which tend to influence the availability of other cell substances.

A consequence of this external effect is that analyses for sugar components and carbohydrate fractions are of limited value in accounting for nutritional effects, although they may explain much about composition. This implies that the physico-chemical nature of the plant cell carbohydrates is of greater nutritional significance than is its chemical constitution and intrinsic composition. Van Soest (1984) suggested that the chemical basis for this effect is that physico-chemical associations of the respective constituent macropolymers are more important factors determining availability than the intrinsic chemical structure and its linkages.

The lignin content of forages has generally been associated with poor digestibility of the forage. As the proportion of lignin in a forage goes up, digestibility of the forage decreases. The negative relationship between degree of lignification and cell wall digestion in forages is well recognized (Van Soest, 1982). ‘Crude lignin’, which generally represents the non-carbohydrate fraction of plant cell matrix, is chemically non-homogeneous. True lignin is a polymer derived mainly from three closely related phenylpropanoid monomers, p-coumaryl, coniferyl and sinapyl alcohols, interconnected in varying proportions and random sequences. True lignin in forages is divided into two different kinds; those in monocotyledons are cinnamic acid derivatives with ester linkages to carbohydrate, while dicotyledons and conifers contain cinnamyl alcohol derivatives with ether linkages to carbohydrate. Legume and grass lignins respond differently to alkali hydrolysis. Grass (monocotyledonous) types are susceptible to cold alkali whereas legume (dicotyledonous) types are not.

Jung and Fahey (1983) found that the decline in fiber digestion in mature alfalfa was
associated with increased lignin. The presence of the phenylpropanoid units, p-coumaric and ferulic acids, or their complexes with hemicellulose and cellulose have been shown to reduce ruminal digestion (Burritt et al., 1984; Hartley, 1972). Digestibility depressions in tall fescue were associated with increased concentrations of p-coumaric and ferulic acids (Jung and Fahey, 1983). Akin (1982) using in vitro methods also demonstrated that purified p-coumaric acid and, to a lesser degree, ferulic acid depressed growth rates of microbes and reduced the degradation of cellulose in the form of filter paper.

Although lignin and their polyphenols are not digestible per se, they may not necessarily be recovered in feces. Hartley (1972) reported that depolymerization can occur to create soluble forms but these forms may not be recovered with the usual methods of analysis or are excreted in urine if of sufficiently low molecular weight. Reeves (1985) found that the composition of lignin in feeds varied considerably and was not directly related to the amount of lignin present.

The reduction in cell wall digestion of lignified mature forages can, to a greater extent, be attributed to the 'encrusting' effect of lignin rather than to the total lignin concentration. Chandler et al. (1980) reported that lignin obligately protects about 2.4-3 times its own weight of plant cell wall from digestion.

### 2.5 OTHER FACTORS AFFECTING DIGESTIBILITY OF FORAGES

Digestibility is also influenced by forage maturity at harvest. The stem is less digestible than the leaf and because the proportion of the stem increases as the plant matures there is a progressive decline in digestibility with plant age (Jones and Wilson, 1987). At the same time the digestibility of the stem, and to a lesser extent the leaf, decreases as the tissues become more lignified. According to Minson et al. (1964) digestibility remains high during vegetative growth and early stages of stem elongation but falls
rapidly after ear emergence. The decline in stem digestibility is particularly marked. Hacker and Minson (1981) reported a mean daily decline of 0.5–0.8 percentage units of stem digestibility compared to 0.1–0.4 units for leaves in a range of temperate grasses. Care is therefore needed in the interpretation of differences between species since the apparent interspecies differences may merely reflect differences in maturity at the harvest date.

Characteristic differences have been established between species. Minson et al. (1964) showed clear differences in the in vivo digestibility of a range of temperate grasses. They found that cocksfoot grass has a lower digestibility compared to perennial ryegrass at the same growth stage. Tropical grasses are generally less digestible than temperate grasses (Hacker and Minson, 1981). Minson and Wilson (1980) determined from a survey of the literature that the mean dry matter digestibility for tropical legumes and grasses was 56.6 percent and 55.4 percent respectively compared to 60.7 percent and 68.2 percent for temperate species. Considerable variation has also been found between varieties within species. Early flowering varieties are more digestible than late flowering varieties at the same growth stage (Jones and Wilson, 1987).

Forage species which maintain high digestibility for long periods during the growth season are of higher value for animal production than those which may have high digestibility at a young stage of growth but in which digestibility decreases rapidly. The effects of environmental and nutritional factors on the herbage digestibility has been extensively reviewed by Wilson (1982). He concluded from the review that the most important environmental influence on nutritive quality was growth temperature. High growth temperatures were found to accelerate stem development and the maturation process in plants. This led to an increase in cell wall content and lignification and a subsequent decrease in herbage dry matter digestibility. It was also reported that high irradiation and moderate soil water stress during growth improved the feeding value of
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Grasses.

Chemical composition does not account for all the variation in intake between forage samples. Some of the residual variation is caused by errors in estimating intake by animals and in analysis, but most of it is caused by true differences in intake of different forage species or varieties with the same chemical composition. In the case of pepsin soluble dry matter, Minson (1982) reported large differences between regressions for six different cultivars of Panicum; when pepsin soluble dry matter was 14%, intake of the cultivars Kabulabula and Hamil was 40 and 62g/kgBW^{0.75}/day respectively. Differences in intake regressions have also been found between leaf and stem fractions of grasses; the intake of the leaf fraction was significantly higher than that of the stem fraction when compared at the same levels of neutral detergent fiber, acid detergent fiber and lignin (Minson, 1982).

2.6 RELATIONSHIP BETWEEN DIGESTIBILITY AND VOLUNTARY INTAKE

The performance of an animal being fed a particular forage is affected by four major factors; 1) nutrient requirements of the animal, 2) feed intake, 3) digestibility and 4) efficiency of utilization of absorbed nutrients. A great deal of earlier research on forage quality evaluation expressed nutritive value in terms of the concentration of total digestible nutrients (TDN), starch equivalent (SE) or net energy (NE).

The realization that in practice, animal production depended on the level of nutrient intake was a significant development. Crampton et al. (1960) determined that the nutritive value of forages was proportional to the yield of digestible nutrients per unit weight multiplied by the weight eaten. Forbes (1986), however, calculated that the nutritive value was proportional to the square of the digestibility. This holds true only for feeds for which intake is limited predominantly by physical factors, and thus dependent
on digestibility (Forbes, 1986).

Many studies with sheep and cattle have shown the existence of a correlation between intake and digestibility but deviations from the general trend have also been found.

Blaxter et al. (1961) demonstrated the relationship between herbage intake and digestibility, rate of passage and rumen fill. They used poor, medium and good quality hays to show that low intake was associated with low digestibility and feed intake by sheep was inversely related to the transit time of stained particles through the rumen. From the fecal excretion curves of stained particles they estimated that the dry matter contained in the digestive tract was similar for all three hays. They therefore concluded that intake of hays by sheep was mainly controlled by rumen capacity. Grovum and Phillips (1978), however, did not find evidence to show that intake of herbage was limited by the capacity of the small and large intestines to transport bulk.

If it could be shown that intake was always closely related to digestibility then it would be possible to predict intake from digestibility estimated by in vitro techniques based on rumen fluid (Tilley and Terry, 1963) or cellulase (McLeod and Minson, 1978).

2.7 ASSOCIATIVE EFFECTS OF COMBINING FORAGES

Attempts to improve the nutritive value of low quality forages have emphasized physical and chemical treatments of the forage (Kiflewahid et al., 1983). The technology required for such treatments is expensive and at times hazardous. An alternative approach to achieve increased utilization of low quality roughages is proper supplementation.

Associative effects of different components of a diet on digestibility, intake and performance have been recorded in several cases where high quality forages have been fed in conjunction with low quality forages (Schneider and Flatt, 1975). The performance of ruminants on mixtures of grasses and legumes, either fed as harvested forage or grazed
is generally superior to that of animals on grass alone (Ulyatt, 1981). The net effect of adding forage supplements to many basal rations is to increase the metabolizable energy intake by the animals. Legume straws fed as supplements to a basal diet of rice straws to sheep increased significantly metabolizable energy intakes (kJ/kg/BW/day) from 68 for the control rice straw diet to 138, 118, 127, 115, and 136 for sheep supplemented with mungbean, cowpea, peanut, pigeonpea and lucerne, respectively. Similar large increases in metabolizable energy intakes were reported by Mosi and Butterworth (1985) who fed combinations of cereal crop residues with *Trifolium ternbense* hay. The increases in metabolizable energy intakes were similar, if not superior, to those expected following chemical treatment of straws with strong alkalis.

Klopfenstein and Owen (1981) analyzed weight gain and dry matter intake data when sheep were fed with crop residues supplemented with good quality hay. They determined positive associative effects in terms of animal weight gain and dry matter intake in all cases when chemically treated and untreated crop residues were supplemented with alfalfa hay. Substitution of legumes for low quality forage has been shown to increase dry matter consumption compared with diets consisting only of low quality forage (Soofi *et al.*, 1982; Ndlovu and Buchanan-Smith, 1985). Moseley (1974) reported greater organic matter digestibility and increased rate of weight gain for sheep fed a perennial ryegrass–red clover combination diet compared with sheep fed only perennial ryegrass or red clover alone. Paterson *et al.* (1982) found increased dry matter digestibility and better steer performance with a 50 % alfalfa–50 % corn cob diet compared with either an 100 % alfalfa or 100 % corn cob diet.

Preston and Leng (1984) listed rumen available nitrogen as first priority in a supplement in order to stimulate digestion of low quality roughages. Satter and Slyter (1974) showed that adequate rumen ammonia concentrations should not be less than 70–80mg/l for optimum stimulation of microbial activity.
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It is believed that a sustained degradation of protein in the rumen leads to a more efficient utilization of the ammonia produced; the slow ammonia production matches the slow degradation of the structural polysaccharides in the plant fibers (Elliott and McMeniman, 1987). Aii and Stobbs (1980) showed that there is considerable variation in the rate at which the nitrogen in legumes and grasses is digested in the rumen. Forage supplements which contain significant quantities of soluble nutrients could also influence the rate of fiber digestion in the rumen by stimulating colonization of plant materials by microflora. Bauchop (1981) noted that the extent of colonization of wheat straw by microfungi varied in sheep fed different diets.

2.8 CONCLUSION

The prediction of animal response to the feeding of forages on the basis of routine evaluation procedures is not sufficiently reliable to estimate potential levels of intake and production. This does not mean that animal production cannot be predicted from laboratory analyses of feedstuffs; the problem lies in the accuracy to be expected from the predictions. Forages with gross differences can be identified by present laboratory analyses. For example, laboratory assessment supports the fact that higher production will generally be obtained by animals fed legume hay compared with cereal stubble. It appears that laboratory assessment of forages can only divide forages into a number of broad categories. Present laboratory techniques are not accurate enough to predict the feeding value of a forage within a category. The accuracy of prediction of animal production from such analyses is also influenced by the quantity of the forage that will be voluntarily consumed by the animal.

Considering the complexity of the ruminant digestive system it appears no single laboratory measurement will enable scientists to predict intake and animal production
from a forage. To solve this problem researchers need to identify and understand the factors that affect the passage of plant material through the ruminant digestive system.
2.9 PARTICLE SIZE REDUCTION IN THE DIGESTIVE TRACT OF RUMINANTS

2.9.1 Introduction

Voluntary intake is a major factor in determining the nutritional value of forages. This was first recognized by Crampton (1957). His work stimulated studies on the mechanisms which control feed intake. A number of mechanisms have been described; including the length of time forage particles were retained in the reticulo-rumen.

The rate of passage of digesta from the rumen of animals fed roughage is an important determinant of their feed intake. This is because rumen fill can physically limit intake in ruminants on forage diets. Feed residues must escape the rumen by either digestion or passage for further intake to occur. The amount and pattern of nutrients eventually absorbed by a ruminant also can be affected by fermentation and passage rate effects on site and extent of digestion (Murphy and Nicoletti, 1984). Passage rate itself depends on rate of microbial and mechanical digesta breakdown in reticulo-rumen and fluid flow from it (Poppi et al., 1981a). It has been demonstrated that although the reticulo-rumen of sheep normally contain large proportions of long fibrous material, the digestive organs beyond the reticulo-omasal orifice contain few particles more than 1mm in length (Poppi et al., 1980; Ulyatt, 1983; Ulyatt et al., 1986). Factors which contribute to particle size reduction and clearance of particles from the digestive tract of ruminants are reviewed below.

2.9.2 Particle size reduction

Since particle size is one factor in the passage of digested forage from the reticulo-rumen to the omasum, and because it is the smaller particles which tend to pass into the omasum, particle size reduction is an important aspect of the efficiency of forage digestion. The
reduction in size of large forage particles is carried out by four processes in the animal. These are 1) primary mastication during ingestion, 2) mastication during rumination, 3) digestion and 4) detrition accomplished by the action of rumen contractions (Moseley and Jones, 1984).

Primary mastication

According to Ulyatt et al., (1986) primary mastication serves three purposes:

1. Long forages are reduced to a size that can be incorporated into a bolus and swallowed.

2. Soluble nutrients, especially from fresh forages, are released for fermentation.

3. The crushing and crimping during mastication exposes the inner structures of forage material, facilitating the effective invasion of the tissue by the reticulo-rumen microbes.

Without the physical disruption of mastication the microflora would be unable to penetrate the cuticle or the vascular bundles of the plant tissue (Pond et al., 1984).

The frequency of chewing is reasonably constant within animal species. Sheep have a high frequency of chewing during primary mastication (125–150 chews per minute) versus 72–81 chews per minute in cattle (Ulyatt et al., 1986). The overall effect of primary mastication on digestion has been investigated by Poppi et al. (1981a). They found that the rate of digestion of tropical grasses in nylon bags was faster for chewed (0.022 per hour) than unchewed (0.016 per hour) grasses. They also reported that the lag time before significant digestion occurred was considerably greater in unchewed (15.5 hours), than in chewed material (3.1 hours). Approximately 35 % of the dry matter of fresh
forage is solubilized by chewing, while only 20–30 % of the dry matter is released from dried forages (Ulyatt, 1986).

Poppi et al. (1981b), Pond et al. (1984) and Ulyatt (1983) measured the contribution of primary mastication to particle size reduction by wet sieving material collected from oesophageal fistulas. Poppi et al. (1981b) measured the percentage of dry matter reduced to less than 1.18mm as a criterion for the effectiveness of chewing. They found that the effectiveness in sheep was 22.4 % compared to 18.2 % in cattle. They also noted that chewing reduced the leaf dry matter by 27.2 % compared to 13.2 % for stem material, 17.8 % for six-week regrowths (leaf and stem) compared to 23.0 % for twelve-week regrowths (leaf and stem). Pond et al. (1984) reported that in cattle primary mastication reduced 15.5 %, 51.9 % and 25.8 % of coastal bermuda hay, grazed coastal bermuda, and grazed ryegrass, respectively, to less than 1.0mm.

Ulyatt (1983) investigated the effectiveness of chewing in sheep fed three types of fresh forages and a hay; perennial ryegrass at early vegetative and early bloom stages, fresh white clover and chaffed lucerne hay. Significant differences were observed in the large particle fraction: the immature, high digestibility feeds were less reduced than the more mature feeds. He attributed this to a brittleness effect—that is, the more mature feeds are more brittle and easier to fracture. Despite this effect, neither the amount of dry matter solubilized nor the efficiency of chewing ( % dry matter reduced to less than 1.00mm) were different between diets. From the results of his experiment he hypothesized that ingested feed is chewed until some common end point is reached and then the bolus is swallowed. He further noted that during one episode of chewing approximately 50 % of feed dry matter is reduced to less than 1.0mm.
Mastication during rumination or secondary mastication

Secondary mastication serves two purposes; 1) it damages regurgitated digesta to further expose internal plant structures for microbial attack, and 2) it reduces the particle size of refractory material. The subject of rumination has been reviewed by Dulphy et al. (1980). The rumination cycle starts with a reticular contraction followed by the aspiration of digesta into the mouth where excess liquid and small particles are expressed and swallowed prior to bolus chewing (Weston and Kennedy, 1984). Radiological studies on sheep have indicated that digesta is regurgitated from the ventral (Rousseau et al., 1982) or the middle (Reid, 1984) regions of the reticulum. A measure of the importance of rumination is the time the animal spends ruminating. On a high forage diet the animal might ruminate as much as 10 hours per day. This time decreases as digestibility increases and fiber content of the diet decreases (Welch, 1982; Dulphy et al., 1980).

The rumination pattern during the day may be influenced by the feeding regime imposed. Dulphy et al., (1980) observed in sheep that, with once daily feeding ruminating activity was often low for several hours after feeding ceased but progressively increased thereafter. With ad libitum feeding on the other hand, eating and ruminating activities were interspersed during the day, and no pronounced circadian pattern was apparent. The control of the initiation and termination of periods of rumination are not well understood. Evans et al. (1973) have, however, observed that the onset of rumination is closely related to the attainment in reticulorumen digesta of the maximum concentration of low density particles and the minimum concentration of high density particles.

The physical properties of the diet affect time spent ruminating. Diet particle size consistently affects rumination. With oat straw a reduction in particle size decreased rumination from 94–133min/kg dry matter to 0–20min/kg dry matter (Balch, 1971). Under conditions of ad libitum feeding, time spent ruminating may be below the animal’s
ruminating capacity (Weston, 1984). Extensive breakdown of large particles occur during each cycle of rumination. A value of 69% has been obtained with sheep (Ulyatt, 1983).

Reid et al. (1979) demonstrated that, in sheep fed a chaffed lucerne hay once a day, the proportion of the reticulo-rumen dry matter pool that was ruminated at any given time increased from 4% at four hours after feeding to 96% in the period 20−24 hours after feeding. Ulyatt (1983) reported that in sheep fed hourly on lucerne hay, the fractional flow rates of the reticulo-rumen dry matter pool subjected to rumination, digestion, and passage were 3.38, 0.62, and 0.97 per day, respectively. He concluded that the major role of rumination was to reduce the particle size of refractory material so that it could be cleared from the reticulo-rumen. The much higher fractional flow rate of ruminated material also points to the possibility that rumination could be the major rate-limiting step in clearing the rumen.

Microbial digestion and detrition

Microbial digestion contributes significantly to the reduction of the dry weight of particles in the rumen (Murphy and Nicoletti, 1984). However, the contribution of microbial digestion to particle size reduction in vivo is apparently limited to a weakening of the forage cell-wall structure so that breakdown by rumination can be facilitated (Ulyatt et al., 1986). McLeod and Minson (1988a) showed by difference that microbial digestion plus detrition (rubbing), was responsible for 17% of the breakdown of forage large particles to small particles. This finding was in conflict with the suggestion of Ulyatt et al. (1986) that, although digestion weakens large particles, it had no direct effect on particle size reduction.

Using a digestion-detrition simulator, McLeod and Minson (1988b) determined the importance of digestion and detrition in the rumen on the breakdown of large particles in leaf and stem fractions of temperate and tropical forages. Large particle breakdown
was measured in forage samples subjected to 48-hour digestion or 48-hour digestion plus detrition. Digestion caused a breakdown of 14% of the large particles while detrition reduced large particles by 8%. There was no difference in breakdown between temperate and tropical forages.

Microbial metabolism of the dry matter in the reticulo-rumen accomplishes;

1. fermentation of the soluble material released by primary and secondary mastication, and

2. erosion of the cut ends and damaged surfaces of the plant tissue.

Microbes invade the plant tissue in a specific order. The general order of tissue invasion is mesophyll, phloem, epidermis, parenchyma bundle sheath, sclerenchyma, lignified vascular tissue. The spatial architecture of the plant therefore remains comparatively intact (Van Soest, 1975). This may be the reason why there is only a small change in particle size as a result of microbial digestion. This reasoning is supported by the finding that very little particle size reduction occurs distal to the reticulum despite the fact that there is considerable fermentation in the cecum and proximal colon (Poppi et al., 1980; Uden and Van Soest, 1982).

The reticulo-rumen undergoes very strong contractions during its mixing cycle, and it is possible that the movement of digesta can reduce the particle size of plant cell wall structures that have been weakened by chewing and microbial attack (Ulyatt et al., 1986).

2.10 DISTRIBUTION OF PARTICLES IN THE DIGESTIVE TRACT

Much information has been gathered about particle distribution in the digestive tract of sheep fed forage diets by Reid et al., (1979); Ulyatt et al., (1984); and Waghorn
et al., (1986). It seems well established that the discrimination against the passage of large particles occurs before the omasum. The factors which control the movement and separation of particles within the digestive tract are discussed below.

2.10.1 Distribution of particles within the reticulo–rumen

The distribution of materials within the reticulo–rumen is the result of;

1. mixing action of the cycles of ruminoreticular contractions,

2. unmixing tendencies due to the spontaneous movements of the particles themselves, and

3. the effects of particle interactions (Sutherland, 1986).

The separation velocity of a group of particles is the measure of their unmixing tendency. The forces acting to maintain these velocities against the resistance to flow or apparent viscosity are the differences between the weights of the particles and that of the medium or more strictly, the contents displaced; thus, they depend markedly on particle density (Evans et al., 1973).

Waghorn et al., (1986) using sheep fed once daily found that reticular digesta is more fluid than rumen digesta at all times, except immediately prior to feeding. The dry matter percent of reticular contents is 7–8.5 % compared to 11–13.7 % of ruminal digesta. The same authors suggested that the form and frequency of reticulum contractions may be responsible for its lower dry matter percentage and particle size distribution.

2.10.2 Distribution of particles within the omasum and abomasum

The distribution of dry matter within particle size fractions in the omasum and abomasum is not affected by feeding frequency. Omasal digesta has a higher dry matter
percentage (19–22 %) than abomasal digesta (7–9 %). However, abomasal digesta has a higher proportion of soluble dry matter (15–21 %), compared to 6–7 % for omasal digesta. Waghorn et al. (1986) found that the 2 and 4mm sieves used to separate omasal and abomasal digesta did not retain any particulate material.

McBride et al., (1984) established that liquid flows in both directions through the reticulo–omasal orifice. This happens with a normal pulse of digesta leaving the reticulum with the second reticular contraction and the intermittent return of material from the omasum to reticulum. This may explain the differences in particle size distribution between the omasum and abomasum.

2.11 PASSAGE OF PARTICLES FROM THE RETICULO–RUMEN

2.11.1 Introduction

As stated earlier the regulation of digesta flow from the reticulum to the omasum is poorly understood. Various factors have been found to influence flow rate to the omasum. The flow has been demonstrated to be proportional to feed intake within the range of intake studied by Ulyatt et al., (1984). Further the physical attributes of the diet appear to exert a significant effect on flow rate (Weston and Kennedy, 1984). Mertens and Ely (1979) suggested that indigestible matter was the primary factor limiting rumen digesta turnover. They concluded from their studies that the considerable space that such particles occupy has a potential limitation on intake; and that the optimum strategy for the animal is to pass the particles as rapidly as possible. This rapid clearance requires high liquid concentrations or rapid liquid flows, or both, in the rumen because the particles must leave in suspension.
2.11.2 The concept of critical particle size

Critical particle size is a concept that has been used in the development of models for digesta flow. This concept divides rumen particles into two pools; a large particle pool, which cannot pass out of the rumen easily, and a small particle pool which can leave the rumen rapidly (Poppi et al., 1980). Balch and Campling (1962), and later Ulyatt et al., (1986), deduced from their experiments that the site that discriminates passage in favor of small particles occurred before the omasum and was subsequently identified as the reticulo-omasal orifice.

Several other researchers have noted that, although particle size reduction is a pre-requisite for passage through the reticulo-omasal orifice, the material present in the reticulo-rumen at any time is predominantly below the threshold size of 1mm (Evans et al., 1973; Poppi et al., 1981b). McBride et al., (1984) refined this concept as a result of studies using endoscopy to study the movement of particles through the reticulo-omasal orifice. They found that particle size relative to the size of the orifice is not the rate-limiting 'step' in clearance of digesta from the reticulo-rumen.

2.11.3 Factors affecting movement of digesta

Movement of digesta within the rumen of sheep has been described as following two streams; one which circulates in the dorsal sac as the raft of floating particles, the other with counter circulation moving through the ventral sac (Kennedy and Murphy, 1988). Evans et al., (1973) demonstrated that in the rumen of cows given hay the density of smaller particles was greater than that of coarser particles. They also observed that a greater proportion of the smaller, denser particles occurred in the ventral region of the rumen. Evans et al., (1973) suggested that there was a cyclic movement of digesta in the rumen which carried the smaller particles towards the reticulum. This circulating
pattern has been confirmed by radiological observations in sheep by Wyburn (1980).

Reid (1986), cited by Kennedy and Murphy (1988), stated that the subsequent movement of particles depended on factors such as:

1. concentration of particles eligible for passage and delivery to the reticulum;

2. selection of appropriate material in the reticulum and its presentation to the reticulo-omasal orifice;

3. factors affecting entry of digesta into the omasum; and

4. the motility of the omasum and digesta flow within.

Within the reticulo-rumen it appears that the material passed to the reticulo-omasal orifice is also from the underlying layers and that raft materials must pass through infranatent layers to exit. Hooper and Welch (1985) reported that large forage particles have low densities and slow gas exchanges. These features make the large particles buoyant, forcing them into the dorsal rumen and keeping them away from the infranatent ventral layers. Sorting of digesta particles in the reticulo-rumen is also a time-dependent process. The segregation of large and light particles in the 'raft' by floatation in the dorsal sac has the effect of reducing passage into the reticulum, ensuring that such particles stay in the rumen longer. This gives the larger particles more time for further comminution during rumination (Kennedy and Murphy, 1988).

Sutherland (1986) examined raft particles in sheep fed lucerne hay daily. It was found that the raft particles were almost entirely of stalk origin and that the relative enrichment of particles in the raft compared to their concentration in the ventral sac was positively related to particle size. The raft entraps small particles which would otherwise sink into the ventral sac, thereby delaying their entry to the pool which can pass from
the reticulum–rumen. The raft thus constitutes an effective barrier to passage of small particles.

Campling and Freer (1962) investigated the relationship between the specific gravity of particles and their retention time in the digestive tract of cows. They reported that the effect of specific gravity on the mean retention time of particles in the reticulo–rumen depended on the rate at which the particles separate from the main mass of digesta, sink to the fluid layer in the ventral rumen and reticulum and so pass to the omasum. They observed that the shortest mean time of retention in the whole gut was found with particles of specific gravity 1.2 and the longest time with particles of specific gravity 1.02. Mean retention time in the reticulo–rumen fell with increasing specific gravity from 73 hours on average, for particles of specific gravity 1.02 to 28 hours, on average, for particles of specific gravity 1.21. Mean retention time in the hindgut, in contrast was directly related to specific gravity, increasing on average from 29 to 52 hours as the specific gravity of the particles increased from 1.02 to 1.21. Ehle and Stern (1986) concluded from their experiments that even though both particle size and density influenced passage of particulate matter through the alimentary tract of cows, density appeared to be a more important criterion.

Reid (1984) reported that the passage of digesta through the reticulo–omasal orifice is also affected by the frequency and amplitude of contractions in the reticulo–rumen, the pressure differential between reticulum and omasum, and the presence of receptive space within the omasum. These factors, he stated further, were modulated by the degree of tactile stimulation afforded by the digesta to tension receptors in the wall of the reticulo–rumen.
Chapter 2. LITERATURE REVIEW

2.12 MEASUREMENT OF PARTICLE SIZE DISTRIBUTION IN DIGESTA

2.12.1 Introduction

The ultimate goal in livestock research is to develop means of manipulating various components of the production system to economic advantage. The effective exploitation of available techniques is dependent on the identification of rate limiting physiological processes in production systems and the assessment of the magnitude of the limitations. This assessment and identification depends on the availability of suitable methods for measuring the value of appropriate variables. There is widespread agreement among researchers that particle size of ruminant diets and of the digesta within the reticulorumen is related to level of feed intake and to rate of digesta passage within the digestive tract (Kennedy, 1984; Weston and Kennedy, 1984). It is within this context that the measurement of particle size is important.

A number of difficulties exist in measuring particle size. The foremost of these is the lack of uniformity of particle shape in most biological materials of interest. A further problem is the lack of homogeneity with respect to particles of different size. Further, within organs such as the reticulorumen, particle size can vary from place to place (Weston and Kennedy, 1984). Despite these problems, a diverse range of techniques has arisen over the years and their use has permitted much useful qualitative and semi-quantitative data on particle size that relate to diet description and various physiological processes that contribute to digestion and voluntary intake.

2.12.2 Techniques of measuring particle size

Several techniques have been used to measure particle size distribution in digesta. Most of these techniques involve the separation of size fractions using a series of sieves with descending aperture size. These sieving techniques vary in the state and size of sample,
the number and sizes of the sieve fractions and the special conditions used to effect separation e.g. wet or dry sieving, vibration, reciprocal motion in water etc. (Allen et al., 1984). Due to the variations in techniques used to measure particle size and variations in reporting the data it is difficult to make quantitative comparisons between laboratories.  

Troelsen and Campbell (1968) and Poppi et al. (1980) used a technique in which samples were placed on the top of a bank of sieves immersed in water and oscillated in a vertical plane. Evans et al. (1973) described an apparatus in which samples were washed through a set of sieves, each of which was rotated and agitated with soft rubber brushes. A similar apparatus was used by Reid et al. (1979) and Ulyatt et al. (1984). The time allocated for sieving has varied from 5 minutes (Reid et al., 1979) to 16 hours (Troelsen and Campbell, 1968).

Forage digesta particulate matter is approximately cylindrical in shape although it can vary in shape, size and density. Due to the cylindrical shape of the particles, it is possible for particulate material to pass end-on through a sieve pore considerably smaller than its length. McLeod (1986) found that the 1.18mm (linear aperture) sieve, used to discriminate large and small particles, retained fecal particles measuring up to 10mm in length, while allowing passage of other particles up to 5mm in length. In addition, small particles were found to be enmeshed in larger material and prevented from passing to the next sieve in the sequence. Thus at the end of an analysis, the material retained on any sieve represented a distribution of particle sizes (Evans et al., 1973). The methods are thus not well defined and variations in technique, especially with regard to sieving time and degree of agitation, can markedly influence the result.

In addition, methods of presenting data vary widely. Poppi et al., (1981b) presented their results as proportions of total dry matter of samples retained on each sieve. Ulyatt (1983), on the other hand, reported results as proportions of particulate dry matter only. Abomasal digesta commonly contains 30–40 % soluble dry matter, so presenting results
on a particulate dry matter basis, by excluding the solubles, will change the apparent distribution (Ulyatt et al., 1986). The need therefore exists for standardization of both sieving methods and presentation of results.

2.12.3 Analyzing particle size distribution data

Numerous statistical procedures have been used to describe the distribution of particles measured. The American Society of Animal Science (ASAS), American Dairy Science Association (ADSA) and the American Society of Agricultural Engineers (ASAE), recommended the adoption of the log-normal distribution for describing ground concentrate feeds (ASAS, 1969; ADSA, 1970). Zenz and Othmer (1960) showed that the particle sizes of ground homogenous material can usually be plotted on log probability paper and the mean particle size and standard deviation read directly from the graph.

Waldo et al. (1971) suggested that forage digesta sizes were suitably described using a log normal distribution. They proposed that a log_{10} mean (\mu) and log_{10} standard deviation (\delta) can be calculated from the regression of standard normal deviates of cumulative weight undersize on log_{10} sieve size. The antilog of log \mu is then used as a measure of median particle size. The use of this method, however, relies on the distribution conforming to the log normal distribution. A log normal distribution has been reported to be adequate by some investigators (Ehle, 1984; Smith and Waldo, 1969) but inappropriate by others (Merten et al., 1984; Moseley, 1984; Pond et al., 1984).

Smith et al., (1983) utilized this approach to determine the log mean particle size of different forages, as well as samples collected from the duodenum and feces of a wether, to determine the rate of plant cell wall particle size reduction in the rumen. They concluded that the high R^2 represented a good fit to the log-normal distribution. The log-normal plots of their data, however, showed a curvilinear relationship between probits of the
cumulative particle size distribution and particle size. Allen et al., (1984) have, however, shown that goodness of fit determined by examining $R^2$ from the regression of a cumulative distribution on particle size or log particle size will usually lead to a high $R^2$, as each point is a function of the previous points. If particle size of forages are accurately described by a log-normal distribution, the log-normal plots of the cumulative distributions should be linear.

Allen et al., (1984) reviewed the literature on methods of expressing particle size distribution data and concluded that the work by Kolmogoroff (1941) has been incorrectly used as a theoretical justification for fitting the log-normal distribution to forage, digesta and feces particle size data. They noted that both Kolmogoroff (1941) as well as Zenz and Othmer (1960) made the assumption that a homogenous material was used. Both investigators had made the observation that the log-normal law was not applicable if particles of different sizes have different rates of disintegration. Furthermore, work by Ehle et al., (1982) and subsequently by Smith et al., (1983) has shown that the rate of reduction of particle size in the rumen is a function of particle size both with rumination and without rumination. Because of the above reasons and the fact that feedstuffs are not homogenous substances the use of the log-normal law to describe particle size data may not be appropriate.

Gates et al., (1988) argued that mass-size frequency data, as generated from particle sieving, are inter-dependent and therefore contravenes the assumption of both normality of errors and independence of data from the dependent variable needed for the application of linear regression procedures adopted by Waldo et al., (1971). Gates et al., (1988) further argued that because moments can be calculated without assumptions of normality for the particle size distribution or without resorting to transformations it is a more appropriate statistical approach for describing the distribution of digesta particulate material.
Certain advantages are realized when particle size data of feedstuffs, digesta and feces follow the log-normal distribution. For example, the log mean is equal to the log median and the log standard deviation has meaning. But because most data with feedstuffs and digesta are not log-normally distributed, this seeming advantage is of no consequence. Furthermore, Allen et al., (1984) demonstrated that analysis of variance of log transformed medians will not lead to the same reductions in sums of squares as the untransformed median. As a result one could possibly draw wrong conclusions from such an analysis.

Because different forage particle sizes vary in their composition and rate of breakdown, it is doubtful that a theoretical basis for choosing any particular distribution will be found. However, attempts should be made to identify important particle sizes that can be correlated with specific physiological functions of ruminant digestion so as to enable their use in modelling ruminant feed intake and digesta passage through the digestive tract.
Chapter 3

OBJECTIVES

The main objectives of this research were;

1. to determine the effect of forage type on particle size reduction and distribution in the gastrointestinal tract of sheep,

2. to compare various methods of expressing digesta particle size distribution as to their ability to relate to forage intake and digestion in sheep, and

3. to determine the voluntary intake and \textit{in vivo} digestibilities of alfalfa, second-cut Altai wild ryegrass fed separately, or in combination with tall wheatgrass or Altai wild ryegrass straws by sheep.

To accomplish these objectives two experiments were conducted. The first study determined the voluntary intake and \textit{in vivo} digestibilities of the forage diets by sheep (objective 3). The second experiment provided information on particle size reduction and distribution in the reticulo-rumen, omasum and abomasum of sheep using the comparative slaughter technique (objective 1). Data from the second experiment were expressed in different forms and related to the chemical compositions, digestion coefficients and voluntary intake of the forages by sheep (objective 2).
Chapter 4

VOLUNTARY INTAKE AND DIGESTIBILITY EXPERIMENT

4.1 INTRODUCTION

The performance of ruminants fed all-forage diets depends largely on the amount of the forage consumed and its digestibility. Substitution of legumes for low quality forage or grass hays increases crude protein content and has been shown to increase consumption and digestibility of the original forage diets. This is a positive associative effect and is observed whenever legumes are fed in combination with other non-legume forages. Few experiments have, however, examined the possibility of associative effects between grass-grass combinations. The overall objective of this study was to investigate the effects of feeding alfalfa (legume) and Altai wild ryegrass (grass) hays, individually and in combination with tall wheatgrass or Altai wild ryegrass straw to wethers. Feeding conditions were designed to simulate an intensive forage feeding situation, in which forage would be provided in *ad libitum* amounts and be the only source of organic matter.

The specific objectives of this experiment were:

1. to compare the voluntary feed intake of sheep fed second-cut Altai wild ryegrass and alfalfa and their combinations with tall wheatgrass or Altai wild ryegrass straw;

2. to estimate and compare the digestibilities of the proximate fractions of the diets; and

3. to assess the value of second-cut Altai wild ryegrass as part of the diet for sheep fed all-forage diets.
Chapter 4. VOLUNTARY INTAKE AND DIGESTIBILITY EXPERIMENT

4.2 MATERIALS AND METHODS

4.2.1 Forages

Alfalfa *Medicago sativa*, (A), second cut Altai wild ryegrass *Elymus angustus* Trin., (AWR2), tall wheatgrass *Agropyron elongatum*, (TWG) and Altai wild ryegrass straw (AWR1) were the forages used in this study. The alfalfa and AWR2 were harvested at the same time (25% bloom stage). Tall wheatgrass was harvested at full maturity. Tall wheatgrass at this stage of maturity is very stemmy and unpalatable to sheep (Knipfel, personal communication). The Altai wild ryegrass straw was cut after seed harvest. The tall wheatgrass and Altai wild ryegrass straw were therefore regarded as low quality forages in this study. Alfalfa and AWR2 were the high quality forages.

4.2.2 Diets

The forages were weighed, chopped in a hammer-mill with a 5-cm screen and mixed to provide the following dietary treatments;

1. 100% Alfalfa hay,

2. 60% Alfalfa hay + 40% AWR1,

3. 60% Alfalfa hay + 40% TWG hay,

4. 100% AWR2 hay,

5. 60% AWR2 hay + 40% AWR1, and

6. 60% AWR2 hay + 40% TWG hay.

All animals were given vitamin A and D injections prior to the beginning of the experiment. Water and a (1:2) mixture of dicalcium phosphate and cobalt-iodized salt were supplied *ad libitum*. 
4.2.3 Experimental design

The experiment was designed as a replicated randomized complete block with two periods and six dietary treatments. A total of forty-eight wethers were used. Twenty-four animals were used in each period. Four animals were allocated to each dietary treatment in each period. The periods were regarded as replicates. There were two sets of eighteen metabolic crates in the metabolism barn which were regarded as blocks.

4.3 PERIOD ONE

4.3.1 Animals

Twenty-four Romanov x Western Whiteface wethers weighing approximately 22kg each were randomly divided into six groups of four animals each. Each group was randomly assigned to a dietary treatment. The four animals on each dietary treatment were randomly allocated to the metabolic crates within each experimental block to give two animals per treatment in each block.

4.3.2 Measurement of intake

The experiment was conducted for a total of twenty-four days. The animals were fed their respective diets ad libitum, with a 5–20 % refusal level. The first twelve days of the experiment constituted the adjustment period. This was followed by a seven-day period during which voluntary feed intake was determined. Voluntary feed intake was determined by feeding each animal ad libitum a known weight of its experimental diet every morning at 0900hrs. Refused feed was weighed and subtracted from the amount offered the previous day to obtain the amount of feed consumed. Fresh feed was offered each morning, and all refused feed was discarded prior to each feeding.
4.3.3 Measurement of digestibility

Following the voluntary feed intake measurement the animals were fed for another five days. Total feces collection was performed during this period. Feces were collected every morning, the total weight recorded and a 20% subsample taken and frozen. Daily feed intake was recorded for each animal. Refused feed from each animal was weighed and subsampled. Refused feed and feces from each animal were pooled for the entire collection period. A grab sample of each diet was obtained during each feeding and pooled over the five-day collection period.

4.3.4 Analytical procedures

Subsamples of the diets, refused feeds and feces were dried at 105°C for 24 hours for dry matter (DM) determination. Samples of diets and refused feeds were dried in a vacuum oven for chemical analysis. Feces samples were freeze-dried. Dried samples were ground through a 1-mm stainless steel screen in a Wiley mill. Neutral detergent fiber (NDF), acid detergent fiber (ADF) and cellulose contents of samples were determined according to Goering and Van Soest, (1970). Organic matter (OM) and nitrogen were determined according to AOAC (1975) procedures. Gross energy (GE) content of samples was determined using a Parr adiabatic bomb calorimeter.

4.4 PERIOD TWO

The procedures above were repeated using a second set of wethers (average weight 20kg). The adjustment period for this part of the study was nine days. The adjustment period was reduced since these animals had been separated into pens and randomly allocated to the dietary treatments at the beginning of period one. The nine-day adjustment period was therefore intended primarily to get them adapted to the metabolic crates and
stabilize feed intake. Measurement of voluntary feed intake commenced on day ten and was followed immediately by digestibility determination.

4.5 CALCULATIONS

4.5.1 Apparent digestibility coefficients

Apparent digestibility coefficients of dry matter (DM), organic matter (OM), nitrogen (N), cellulose, neutral detergent fiber (NDF), acid detergent fiber (ADF) and gross energy (GE) were calculated as the difference between the nutrient’s intake and excretion in the feces expressed as a percent of nutrient intake. Since no corrections were made for fecal components of endogenous origin it was assumed that the feces represented residues of dietary origin only. The term apparent digestibility was therefore used to describe all coefficients calculated in this manner. All data were expressed on dry matter basis.

4.5.2 Digestible nutrients

The digestible nutrient content in the diets and forages was obtained by multiplying the coefficient of digestibility of the nutrient by the content of the nutrient present in the dry matter of the diet or forage.

4.5.3 Intake

Voluntary intake per day of dry matter, organic matter, nitrogen, cellulose, neutral detergent fiber and acid detergent fiber were expressed as gram per kilogram metabolic size of the animal (g/kgBW\(^{0.75}\)). Energy intake per day was expressed as kcal. per metabolic size (kcal/gkBW\(^{0.75}\)).
4.5.4 Nutritive Value Index

Nutritive Value Index for each diet was calculated as daily digestible energy intake.

4.5.5 Statistical analysis

Intake and digestibility data were analysed statistically as a randomized complete block design using the general linear model procedure of the SAS (1985). The model used was:

\[ X_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\gamma)_{ik} + \epsilon_{ijk} \]

where;
\[ X = \text{observation}, \]
\[ \mu = \text{overall mean}, \]
\[ \alpha = \text{effect of treatment}, \]
\[ \beta = \text{effect of block}, \]
\[ \gamma = \text{effect of period}, \]
\[ \epsilon = \text{overall error}, \]
\[ i = 1, 2, ..., 6 \]
\[ j = 1, 2 \]
\[ k = 1, 2. \]

Simple correlation tests were performed on some of the data to determine relationships between some of the variables measured during the intake and digestibility trials.
Table 4.1: Chemical composition of diets (% DM)

<table>
<thead>
<tr>
<th>Item</th>
<th>100 % Alfalfa</th>
<th>60 % Alfalfa + 40 % AWR1</th>
<th>60 % Alfalfa + 40 % TWG</th>
<th>100 % AWR2</th>
<th>60 % AWR2 + 40 % AWR1</th>
<th>60 % AWR2 + 40 % TWG</th>
</tr>
</thead>
<tbody>
<tr>
<td>OM</td>
<td>87.17</td>
<td>87.23</td>
<td>86.58</td>
<td>90.19</td>
<td>90.35</td>
<td>89.30</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>2.55</td>
<td>1.97</td>
<td>1.70</td>
<td>2.69</td>
<td>2.45</td>
<td>1.78</td>
</tr>
<tr>
<td>Cellulose</td>
<td>24.79</td>
<td>32.26</td>
<td>31.82</td>
<td>29.84</td>
<td>32.41</td>
<td>33.50</td>
</tr>
<tr>
<td>NDF</td>
<td>32.19</td>
<td>51.54</td>
<td>49.24</td>
<td>53.64</td>
<td>60.55</td>
<td>60.63</td>
</tr>
<tr>
<td>ADF</td>
<td>23.97</td>
<td>33.18</td>
<td>33.81</td>
<td>29.09</td>
<td>33.36</td>
<td>34.90</td>
</tr>
<tr>
<td>GE (Mcal/kg)</td>
<td>4.35</td>
<td>4.38</td>
<td>4.32</td>
<td>4.41</td>
<td>4.44</td>
<td>4.33</td>
</tr>
<tr>
<td>DM (%)</td>
<td>92.92</td>
<td>93.48</td>
<td>93.00</td>
<td>93.76</td>
<td>93.98</td>
<td>93.98</td>
</tr>
</tbody>
</table>

Values are for the composited samples for the two experimental periods.

4.6 RESULTS AND DISCUSSION

4.6.1 Chemical composition of diets

Chemical composition of alfalfa (A) and secondcut Altai wild ryegrass (AWR2) diets and their mixtures with Altai wild ryegrass straw (AWR1) and Tall wheatgrass (TWG) are presented in Table 4.1. The dry matter (DM) content of all diets was similar. It ranged from 92.92 to 93.98 %. However, the content of organic matter (OM), nitrogen (N), neutral detergent fiber (NDF), acid detergent fiber (ADF), cellulose (C) and gross energy (GE) was higher in the AWR2 diet than in the alfalfa diet. Combinations of AWR2 and AWR1 or TWG straws therefore, resulted in diets with higher levels of the above fractions than corresponding combinations with alfalfa.

Nitrogen content ranged from 1.70 % for alfalfa + tall wheatgrass mixture to 2.69 % for the AWR2 diet. Cell wall components (percentage NDF) was lowest for 100 % alfalfa diet (32.19 %) and highest for AWR2 and Tall wheatgrass mixture (60.63 %). This is in agreement with the finding of Van Soest (1982) which indicated that grasses generally have higher NDF levels. Lignocellulose content (percentage ADF) of 100 % alfalfa diet...
Table 4.2: Least square means and standard errors of digestible nutrient content of diets (% DM)

<table>
<thead>
<tr>
<th>Item</th>
<th>Diet</th>
<th>100 % Alfalfa</th>
<th>60 % Alfalfa + 40 % AWR1</th>
<th>60 % Alfalfa + 40 % TWG</th>
<th>100 % AWR2</th>
<th>60 % AWR2 + 40 % AWR1</th>
<th>60 % AWR2 + 40 % TWG</th>
</tr>
</thead>
<tbody>
<tr>
<td>DOM</td>
<td></td>
<td>53.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>48.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>45.4&lt;sup&gt;c&lt;/sup&gt;</td>
<td>59.0&lt;sup&gt;d&lt;/sup&gt;</td>
<td>56.7&lt;sup&gt;d&lt;/sup&gt;</td>
<td>49.9&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.07)</td>
<td>(0.99)</td>
<td>(1.07)</td>
<td>(0.98)</td>
<td>(0.98)</td>
<td>(1.07)</td>
</tr>
<tr>
<td>DN</td>
<td></td>
<td>1.83&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.24&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.11&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.99&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1.69&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.21&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.050)</td>
<td>(0.039)</td>
<td>(0.039)</td>
<td>(0.050)</td>
<td>(0.039)</td>
<td>(0.039)</td>
</tr>
<tr>
<td>DCell</td>
<td></td>
<td>14.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>19.8&lt;sup&gt;c&lt;/sup&gt;</td>
<td>17.0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>21.7&lt;sup&gt;d&lt;/sup&gt;</td>
<td>22.7&lt;sup&gt;d&lt;/sup&gt;</td>
<td>20.7&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.45)</td>
<td>(0.42)</td>
<td>(0.45)</td>
<td>(0.45)</td>
<td>(0.42)</td>
<td>(0.45)</td>
</tr>
<tr>
<td>DNDF</td>
<td></td>
<td>13.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>27.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>21.2&lt;sup&gt;c&lt;/sup&gt;</td>
<td>37.9&lt;sup&gt;d&lt;/sup&gt;</td>
<td>41.6&lt;sup&gt;c&lt;/sup&gt;</td>
<td>36.5&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.70)</td>
<td>(0.65)</td>
<td>(0.70)</td>
<td>(0.65)</td>
<td>(0.65)</td>
<td>(0.70)</td>
</tr>
<tr>
<td>DADF</td>
<td></td>
<td>9.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>16.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>14.5&lt;sup&gt;c&lt;/sup&gt;</td>
<td>19.8&lt;sup&gt;d&lt;/sup&gt;</td>
<td>22.0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>19.7&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.43)</td>
<td>(0.40)</td>
<td>(0.43)</td>
<td>(0.40)</td>
<td>(0.40)</td>
<td>(0.43)</td>
</tr>
<tr>
<td>DE</td>
<td>(Mcal/kg)</td>
<td>2.63&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.41&lt;sup&gt;cd&lt;/sup&gt;</td>
<td>2.30&lt;sup&gt;c&lt;/sup&gt;</td>
<td>2.85&lt;sup&gt;c&lt;/sup&gt;</td>
<td>2.79&lt;sup&gt;c&lt;/sup&gt;</td>
<td>2.49&lt;sup&gt;bc&lt;/sup&gt;</td>
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<tr>
<td></td>
<td></td>
<td>(0.048)</td>
<td>(0.047)</td>
<td>(0.047)</td>
<td>(0.048)</td>
<td>(0.048)</td>
<td>(0.047)</td>
</tr>
</tbody>
</table>

Means within rows with different letters are significantly different (P < 0.05).

(23.97 %) was the lowest among the diets. The ADF content of the rest of the diets varied slightly, ranging from 29.09 % for AWR2 diet to 34.90 the AWR2 and TWG mixture. The gross energy content of the diets did not vary much. It ranged from 4.32 Mcal/kg DM for alfalfa and TWG mixture to 4.44 Mcal/kg DM for AWR2 and AWR1 mixture.

The digestible nutrient content of the diets are presented in Table 4.2. The concentration of digestible nutrients in the diets followed a pattern similar to that reported for chemical composition above. Digestible organic matter (DOM) and digestible nitrogen (DN) were highly correlated (r = 0.95 and 0.82, respectively) with digestible energy (DE). The DE content of AWR2–based diets were higher than the corresponding values for the alfalfa–based diets. This observation is most likely a reflection of the DOM and DN in the respective diets and is further supported by the highly significant (P < 0.001) correlation coefficients obtained in this study.
Table 4.3: Least square means and standard errors of apparent digestibility coefficients of proximate fractions of diets (%)

<table>
<thead>
<tr>
<th>Item</th>
<th>Diet</th>
<th>Item</th>
<th>Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100 % Alfalfa 60 % Alfalfa + 40 % AWR1</td>
<td></td>
<td>100 % AWR2 60 % AWR2 + 40 % TWG</td>
</tr>
<tr>
<td>DMD</td>
<td>61.0&lt;sup&gt;a&lt;/sup&gt; 55.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>DMD</td>
<td>65.3&lt;sup&gt;c&lt;/sup&gt; 62.9&lt;sup&gt;ac&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(1.14) (1.05)</td>
<td></td>
<td>56.0&lt;sup&gt;b&lt;/sup&gt; (1.14)</td>
</tr>
<tr>
<td>OMD</td>
<td>63.4&lt;sup&gt;c&lt;/sup&gt; 57.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>OMD</td>
<td>69.2&lt;sup&gt;c&lt;/sup&gt; 66.9&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(1.02) (0.95)</td>
<td></td>
<td>(1.02) (0.95)</td>
</tr>
<tr>
<td>ND</td>
<td>71.9&lt;sup&gt;a&lt;/sup&gt; 62.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>ND</td>
<td>72.0&lt;sup&gt;d&lt;/sup&gt; 70.4&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(1.12) (1.03)</td>
<td></td>
<td>(1.12) (1.03)</td>
</tr>
<tr>
<td>CD</td>
<td>57.6&lt;sup&gt;a&lt;/sup&gt; 61.2&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>CD</td>
<td>72.0&lt;sup&gt;c&lt;/sup&gt; 70.5&lt;sup&gt;ac&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(1.34) (1.23)</td>
<td></td>
<td>(1.34) (1.23)</td>
</tr>
<tr>
<td>NDFD</td>
<td>40.0&lt;sup&gt;a&lt;/sup&gt; 52.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>NDFD</td>
<td>69.5&lt;sup&gt;d&lt;/sup&gt; 68.3&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(1.23) (1.14)</td>
<td></td>
<td>(1.23) (1.14)</td>
</tr>
<tr>
<td>ADFD</td>
<td>38.8&lt;sup&gt;a&lt;/sup&gt; 50.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>ADFD</td>
<td>67.0&lt;sup&gt;d&lt;/sup&gt; 65.7&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(1.26) (1.16)</td>
<td></td>
<td>(1.26) (1.16)</td>
</tr>
<tr>
<td>GED</td>
<td>60.5&lt;sup&gt;ac&lt;/sup&gt; 55.0&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>GED</td>
<td>64.7&lt;sup&gt;d&lt;/sup&gt; 62.8&lt;sup&gt;ad&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>(1.14) (1.05)</td>
<td></td>
<td>(1.14) (1.05)</td>
</tr>
</tbody>
</table>

<sup>a,b,c,d,e</sup> Means within rows with different letters are significantly different (P < 0.05).

4.6.2 Digestibility of nutrients

Least square means and standard errors of apparent digestibility coefficients of DM, OM, N cellulose, NDF, ADF and energy for all diets are presented in Table 4.3.

Digestibility of dry matter, organic matter, nitrogen, cellulose, neutral detergent fiber and acid detergent fiber

Mean apparent digestibility coefficients of DM, OM, and cellulose, of 100 % AWR2 diet were significantly (P < 0.05) higher than the corresponding values for 100 % alfalfa diet. Nitrogen digestibility (ND) coefficients for the two diets were, however, not significantly different. Mixtures of AWR2 and AWR1 or TWG straw had significantly higher dry matter digestibility (DMD) coefficients than mixtures of alfalfa with AWR1 or TWG.
straw. The ND coefficients were not significantly different. The pattern of results obtained for the digestibility of organic matter (DOM) was similar to that observed for DM digestibility. This similarity can be attributed to the fact that the dry matter fraction excluding the ash is basically OM. It was therefore apparent that the positive associative effect on digestibility of DM, OM and cellulose for the grass-grass mixtures was greater than that of the legume-grass mixtures. This effect was the reverse of what was observed during the voluntary intake trial.

Nitrogen digestibility of AWR2 diet though higher, was not significantly different from that of alfalfa diet. AWR2+TWG, alfalfa+AWR1 and alfalfa+TWG diets had similar coefficients of digestibility for nitrogen. This implies that addition of alfalfa to the straw diets did not offer any advantage in terms of digestibility of the nitrogen over that obtained from the addition of AWR2 to the straws.

Positive associative effects for DM digestibility of grass-legume mixtures have been reported (Moseley, 1974; Moseley and Jones 1979). Hunt et al. (1985), however, noted that associative effects may not exist for legumes and grasses of very low quality. Another possible reason for the higher digestibility coefficients for the grass-grass combinations compared to the grass-legume combinations may probably be a reflection of the chemical composition of the NDF fraction in alfalfa. The resistance of the NDF fraction to digestion as observed in the present study may be associated with the greater lignin content of the alfalfa NDF fraction. Knipfel (1978) reported higher levels of lignin in alfalfa compared to AWR2.

The availability of cellulosics to cellulolytic organisms varies from 0 to 100 % depending on intrinsic factors such as the crystallinity of the cellulose and its association with lignin, cutin and silica (Van Soest, 1973). Cellulose digestibility data reported in this study are higher than those reported by Van Soest (1973), who found digestibilities of between 40 and 60 % for both alfalfa and straw cellulose. Fonnesbeck et al. (1981), however, found
that grass cellulose was more digestible than alfalfa cellulose. Reduced digestibility of cellulose in alfalfa diets has been attributed to rapid passage through the reticulo-rumen (Moore, 1964).

Significantly (P< 0.05) higher neutral detergent fiber digestibility (NDFD) coefficients were observed in AWR2-based diets compared to alfalfa-based diets. The resistance of the NDF fraction may be associated with the greater lignin content of the alfalfa NDF fraction as mentioned earlier. Coefficients of ADF digestibility were similar to those of NDF but were slightly lower than those for NDF digestibility. The effect of combining AWR2 with AWR1 straw or TWG straw led to an increase in digestibility of these nutrients in the resulting diets.

A possible reason for the higher digestibility coefficients observed for the AWR2 diet and its mixtures may be due to the higher levels of digestible nutrients in these diets. This hypothesis is justified when the digestible nutrient content of the diets are compared, Table 4.2. AWR2 had higher levels of digestible nutrients. Addition of legumes to low quality grass diets has usually increased digestion (Hunt et al., 1985). This observation has been attributed to increased levels of rapidly available soluble nutrients, especially nitrogenous compounds. These substances provide nutrients needed for maximal microbial growth and digestion.

**Gross energy digestibility**

The legume (alfalfa) and legume-grass diets had significantly lower (P< 0.05) gross energy digestibility (GED) coefficients compared to the all-grass diets i.e. (AWR2, AWR2+AWR1 and AWR2+TWG, Table 4.3). It is worthy of note that the pattern of results obtained for DMD and OMD and discussed above is similar to that obtained for the gross energy digestibility. This similarity can be explained by the fact that the DM fraction excluding the ash is predominantly a source of energy. The coefficient of
Table 4.4: Simple correlation coefficients between proximate fractions and apparent digestibility coefficients

<table>
<thead>
<tr>
<th>Component</th>
<th>DMD</th>
<th>OMD</th>
<th>ND</th>
<th>CD</th>
<th>NDFD</th>
<th>ADFD</th>
<th>GED</th>
</tr>
</thead>
<tbody>
<tr>
<td>OM</td>
<td>0.44&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.62&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.33&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.53&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.62&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.64&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.46&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>0.77&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.73&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.82&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.53&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.33&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.35&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.72&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Cellulose</td>
<td>-0.33&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.32&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.45&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.28&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.47&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.42&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.32&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>NDF</td>
<td>-0.02</td>
<td>0.13</td>
<td>-0.14</td>
<td>0.59&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.81&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.79&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.07&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>ADF</td>
<td>-0.39&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.33&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.52&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.16&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.41&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.39&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.35&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>GE</td>
<td>0.65&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.61&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.55&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.74&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.69&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.69&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.61&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

P< 0.001; b P< 0.01; c P< 0.05.

Gross energy digestibility values were, however, slightly lower than those reported for DMD and OMD.

Energy digestibility of 100 % AWR2 diet was significantly higher than that of 100 % alfalfa. Gross energy digestibility of the AWR2+AWR1 mixture was higher than that of alfalfa diet even though the difference was not significant. The lower energy digestibility of the alfalfa based diets can partially be attributed to the significantly lower digestibility of the cellulose fraction in alfalfa. The reason for saying this is the highly significant (P< 0.001) correlation (r = 0.77) between cellulose digestibility and energy digestibility found in this study. Thus the depression in gross energy digestibility can be attributed to the decline in cellulose digestibility.

To determine the effect of chemical composition on digestibility of the proximate fractions, apparent digestibility coefficients were regressed on percent of individual chemical fraction (Table 4.4). Nitrogen and GE content of diet were the only fractions which correlated positively and significantly with apparent digestibility coefficients of all proximate fractions. This positive relationship between both dietary energy and nitrogen and digestibility of diets can be attributed to the stimulatory effect both fractions have on
Table 4.5: Least Square Means and Standard Errors of Nutrient Intake (g/kgBW^{0.75}/day) of diets

<table>
<thead>
<tr>
<th>Item</th>
<th>Diet</th>
<th>DM</th>
<th>OM</th>
<th>Nitrogen</th>
<th>Cellulose</th>
<th>NDF</th>
<th>ADF</th>
<th>GE</th>
<th>kcal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100 % Alfalfa</td>
<td>102.1(^a) (4.11)</td>
<td>89.3 (3.60)</td>
<td>2.60(^a) (0.098)</td>
<td>25.8(^a) (1.13)</td>
<td>34.2(^a) (1.80)</td>
<td>25.6(^a) (1.14)</td>
<td>443.71(^a) (17.928)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>+ 40 % AWR1</td>
<td>95.4(^ab) (3.80)</td>
<td>82.9 (3.33)</td>
<td>1.90(^b) (0.094)</td>
<td>30.7(^ab) (1.05)</td>
<td>49.3(^b) (1.66)</td>
<td>31.6(^b) (1.05)</td>
<td>417.67(^ab) (16.560)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>+ 40 % TWG</td>
<td>88.8(^bc) (4.11)</td>
<td>76.4 (3.60)</td>
<td>1.62(^c) (0.098)</td>
<td>27.4(^bc) (1.13)</td>
<td>42.2(^c) (1.80)</td>
<td>29.0(^bc) (1.14)</td>
<td>383.96(^bc) (17.928)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>100 % AWR2</td>
<td>83.4(^cd) (4.11)</td>
<td>75.3 (3.60)</td>
<td>2.30(^d) (0.098)</td>
<td>25.1(^bc) (1.13)</td>
<td>45.6(^bc) (1.80)</td>
<td>24.7(^a) (1.14)</td>
<td>367.58(^cd) (17.928)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>+ 40 % AWR1</td>
<td>73.8(^d) (3.80)</td>
<td>66.6 (3.33)</td>
<td>1.77(^bc) (0.094)</td>
<td>23.8(^a) (1.05)</td>
<td>45.0(^bc) (1.66)</td>
<td>24.7(^a) (1.05)</td>
<td>327.85(^d) (16.560)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>+ 40 % TWG</td>
<td>75.5(^d) (4.11)</td>
<td>76.1 (3.60)</td>
<td>1.43(^bc) (0.098)</td>
<td>24.8(^ac) (1.13)</td>
<td>45.6(^bc) (1.80)</td>
<td>25.8(^ac) (1.14)</td>
<td>326.78(^d) (17.928)</td>
<td></td>
</tr>
</tbody>
</table>

Means within rows with different letters are significantly different, (P< 0.05).

rumen microbial growth and digestion.

4.6.3 Voluntary intake of nutrients

Least square means and standard errors of daily intake of DM, OM, N, cellulose, NDF, ADF and gross energy (GE) for lambs fed the six diets are presented in Table 4.5. The intake of nutrients was expressed as a function of metabolic body weight (kgBW^{0.75}).

A significantly (P< 0.05) higher DM intake was observed for animals fed alfalfa–based diets compared to those on AWR2–based diets. Mean dry matter intake by animals on the 100 % alfalfa diet was 102.1g/kgBW^{0.75} per day compared with 83.4g/kgBW^{0.75} for 100 % AWR2 diet. Intake of DM by sheep on A+AWR1 and A+TWG diets were 95.4 g/kgBW^{0.75} and 88.8g/kgBW^{0.75} respectively. The corresponding figures for AWR2+AWR1
and AWR2+TWG diets were 73.8g/kgBW^{0.75} and 75.5g/kgBW^{0.75}. These figures indicate that the addition of alfalfa to AWR1 or TWG (legume–grass mixture) promoted greater intake of DM than the corresponding addition of AWR2 to AWR1 or TWG (grass–grass mixture). The legume–grass mixture therefore exhibited a positive associative effect. Other researchers have investigated the occurrence of interactions between legumes and grasses in feeding trials. Results from such trials have, however, been conflicting (Minson and Milford, 1967; Mosely and Jones, 1979; Hunt et al., 1985; Ndlovu and Buchanan-Smith, 1985). Minson and Milford (1967) investigated the effects of including different proportions of alfalfa and white clover (*Trifolium repens* L.) in a diet of mature pangolagrass (*Digitaria decumbens* Stent) fed to sheep. Increasing the level of legume increased intake and DM and crude protein digestibility, and reduced body weight losses. The authors considered that the effects were due to the legume overcoming a protein deficiency (3.6 %) in the grass. All the diets in the present study had crude protein contents above 10 % so a true protein deficiency at the tissue level is unlikely during the short term of this trial.

Soofi *et al.* (1982) noted either positive or negative associative effects when low and high quality forages were blended and used as the sole source of nutrients. Ndlovu and Buchanan-Smith (1985) attributed the beneficial effects of alfalfa supplementation in low quality forage diets (barley straw, bromegrass hay and corn cobs) fed to sheep to increased ruminal concentrations of ammonia and volatile fatty acids, resulting in increased rates of fiber digestion and rates of passage of undigested material. In the present study the difference in DM intake between A+AWR1 and A+TWG diets was not significant. This indicates that the stimulatory effect of alfalfa on DM intake of the two forages was independent of forage type. The probable reason for this may be because AWR1 and TWG straws had similar chemical compositions.

It therefore appears that responses by animals to inclusion of legumes in forage diets
Table 4.6: Least square means and standard errors of intake of digestible nutrients (g/kgBW\(^{0.75}\)/day) of diets

<table>
<thead>
<tr>
<th>Item</th>
<th>100 % Alfalfa</th>
<th>60 % Alfalfa + 40 % AWR1</th>
<th>60 % Alfalfa + 40 % TWG</th>
<th>100 % AWR2</th>
<th>60 % AWR2 + 40 % AWR1</th>
<th>60 % AWR2 + 40% TWG</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DDM</td>
<td>62.1(^a)</td>
<td>53.4(^b)</td>
<td>48.1(^bc)</td>
<td>54.6(^b)</td>
<td>46.5(^c)</td>
<td>42.3(^c)</td>
</tr>
<tr>
<td></td>
<td>(2.59)</td>
<td>(2.39)</td>
<td>(2.59)</td>
<td>(2.59)</td>
<td>(2.39)</td>
<td>(2.59)</td>
</tr>
<tr>
<td>DOM</td>
<td>56.8(^a)</td>
<td>48.0</td>
<td>43.1</td>
<td>52.3</td>
<td>44.6</td>
<td>41.2</td>
</tr>
<tr>
<td></td>
<td>(2.36)</td>
<td>(2.18)</td>
<td>(2.36)</td>
<td>(2.36)</td>
<td>(2.18)</td>
<td>(2.36)</td>
</tr>
<tr>
<td>DN</td>
<td>1.87</td>
<td>1.19</td>
<td>0.99</td>
<td>1.67</td>
<td>1.25</td>
<td>0.91</td>
</tr>
<tr>
<td></td>
<td>(0.070)</td>
<td>(0.061)</td>
<td>(0.070)</td>
<td>(0.070)</td>
<td>(0.061)</td>
<td>(0.070)</td>
</tr>
<tr>
<td>DCELL</td>
<td>14.7(^a)</td>
<td>18.8(^b)</td>
<td>15.1(^bc)</td>
<td>18.1(^bd)</td>
<td>16.8(^de)</td>
<td>15.7(^de)</td>
</tr>
<tr>
<td></td>
<td>(0.76)</td>
<td>(0.70)</td>
<td>(0.76)</td>
<td>(0.76)</td>
<td>(0.70)</td>
<td>(0.76)</td>
</tr>
<tr>
<td>DNDF</td>
<td>13.5(^a)</td>
<td>26.1(^b)</td>
<td>19.1(^c)</td>
<td>31.8(^d)</td>
<td>30.7(^de)</td>
<td>27.6(^bc)</td>
</tr>
<tr>
<td></td>
<td>(1.18)</td>
<td>(1.09)</td>
<td>(1.18)</td>
<td>(1.18)</td>
<td>(1.09)</td>
<td>(1.18)</td>
</tr>
<tr>
<td>DADF</td>
<td>9.9(^a)</td>
<td>16.0(^b)</td>
<td>13.0(^c)</td>
<td>16.6(^b)</td>
<td>16.2(^b)</td>
<td>14.9(^bc)</td>
</tr>
<tr>
<td></td>
<td>(0.70)</td>
<td>(0.65)</td>
<td>(0.70)</td>
<td>(0.70)</td>
<td>(0.65)</td>
<td>(0.70)</td>
</tr>
<tr>
<td>DE</td>
<td>268.24(^a)</td>
<td>230.51(^b)</td>
<td>206.76(^bc)</td>
<td>239.35(^b)</td>
<td>206.42(^bc)</td>
<td>187.87(^c)</td>
</tr>
</tbody>
</table>

\(^a,b,c,d,e\) Means within rows with different letters are significantly different (P < 0.05).

Daily intake of digestible nutrients are presented in Table 4.6. Intake of digestible dry matter is the product of intake of dry matter and digestibility of the dry matter. For this reason the intake of digestible dry matter was highly correlated with intake of dry matter (r = 0.92, P < 0.001) and slightly but significantly (P < 0.05) correlated with dry matter digestibility (r = 0.45). Daily digestible nitrogen intake varied from 0.91g/kgBW\(^{0.75}\) for AWR2 and TWG mixture to 1.87g/kgBW\(^{0.75}\) for 100 % alfalfa diet.

The differences in NDF contents of the diets were most likely responsible for the differences in intake of DM observed in the present study. The correlation coefficients between NDF and DM intake and NDF and energy intake were -0.65 and -0.64 respectively (Table 4.7). These correlation coefficients were all highly significant (P < 0.001).
Table 4.7: Simple correlation coefficients between voluntary intake of nutrients and chemical components of diets

<table>
<thead>
<tr>
<th>Chemical Component</th>
<th>Intake</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DM</td>
</tr>
<tr>
<td>OM (%)</td>
<td>-0.26</td>
</tr>
<tr>
<td>N (%)</td>
<td>0.11</td>
</tr>
<tr>
<td>Cellulose (%)</td>
<td>-0.66a</td>
</tr>
<tr>
<td>NDF (%)</td>
<td>-0.65a</td>
</tr>
<tr>
<td>ADF (%)</td>
<td>-0.54a</td>
</tr>
<tr>
<td>GE (Mcal/kg)</td>
<td>-0.10</td>
</tr>
</tbody>
</table>

a P< 0.001; b P< 0.01; c P< 0.05

These results are in agreement with those reported by Van Soest (1965) but lower than the -0.91 reported by Seoane (1983). The correlation between cellulose and DM intake and cellulose and energy intake were also highly significant (r = -0.66 in both cases, P< 0.001). Welch (1967) indicated that the primary factor affecting DM intake is fiber mass of forage rather than forage digestibility. Van Soest (1964) had earlier found that cell wall components (NDF), which represents the total fibrous fraction of the forage, is the primary factor which limits voluntary intake when present in concentrations greater than 55–60 % of DM. The NDF fractions of the alfalfa containing diets were lower than those containing AWR2 which had NDF values within the 55–60 % range. Conrad et al. (1964) found that for high forage diets with DMD below 66 %, voluntary intake was limited by physical factors such as rumen fill.

The importance of cell walls as determinants of voluntary intake was demonstrated by Mertens (1973), who reported that sheep eat a fairly constant quantity of cell walls, which is approximately 40g/kgBW^{0.75} per day. This may be because the proportion of cell walls in the plant varies inversely with the time the animal spends chewing and ruminating (Welch, 1982). This in turn may be related to the rate of clearance of digesta from the
reticulo-rumen. What this implies is that forages with low cell wall components have faster clearance rates from the reticulo-rumen. Animals on such forages will consume more dry matter because of the reduction in the 'filling effect'. Mean daily cell wall (NDF) intake varied from 34.2 to 49.3 g/kgBW$^{0.75}$, with values for four out of the six diets falling between 42.2 and 45.6 g/kgBW$^{0.75}$ (Table 4.5). This is in agreement with the findings of Seoane (1983) but slightly higher than the values reported by Mertens (1973).

Digestible energy content of forages has also been found to influence DM intake. Weston and Poppi (1987) reported that with long or coarsely chopped forages, voluntary consumption decreases with a decrease in DE content - generally a reflection of increasing fiber content in the forage. A look at Table 4.1 shows that even though the fiber fractions in the AWR2 based diets were higher than those in the alfalfa diets, the former had higher DE levels but animals on those diets still had significantly (P< 0.05) lower intakes.

It can be inferred from above that differences in voluntary intake by sheep of dry matter and nutrients cannot be adequately explained or attributed to differences in single factors such as digestibility or nutrient content of the diets.

4.7 NUTRITIVE VALUE OF THE DIETS

Digestibility and intake are two basic components of a forage that provide a measure of forage quality. Crampton et al. (1960) hypothesized that the effective nutritive value of a forage is determined jointly by (1) the level of maximum voluntary intake when the forage constitutes the entire diet and (2) the ultimate yield of digestible energy from the forage. An acceptable numerical index of the nutritive value of a forage must therefore include some expression of each of these factors (Soofi et al., 1982). Therefore, in this experiment nutritive value was expressed as digestible energy intake.
Daily digestible energy intake varied from 187.9 kcal/kgBW^{0.75} for AWR2 and TWG mixture to 268.2 kcal/kgBW^{0.75} for 100 % alfalfa diet (Table 4.6). Of the chemical components in the diets, cellulose, NDF and ADF were the fractions most highly correlated with daily digestible energy intake ($r = -0.71$, -0.53 and -0.61 respectively, $P< 0.001$). It is pertinent to note that all the correlations were negative, this is indicative of the fact that intake of digestible energy falls with increasing amounts of cell wall fractions in a diet.

When nutritive values of the diets were compared on the basis of intake of digestible energy per day, the 100 % alfalfa and 100 % AWR2 diets were not significantly different (Table 4.6). The differences between their respective mixtures with AWR1 and TWG straws were also not significantly different.

4.8 Conclusion

The intake of digestible nutrients (especially DE) is an important consideration in raising animals on an all forage diet. This study supports the hypothesis that voluntary intake is a much more important component determining the intake of digestible nutrients than digestibility. This implies that in situations where digestibility is used as the primary criterion for forage selection, differences in animal performance should be expected.

The results of this study also indicates that AWR2 harvested at the prebloom stage can be used as a substitute for alfalfa in supplementing AWR1 and TWG for winter feeding of sheep. This is because intake of digestible energy by sheep on alfalfa supplemented diets was not significantly different from that of sheep on AWR2 supplemented diets.

The relationships between cell wall fractions, digestibility and voluntary intake reported here provide useful practical indeces for predicting voluntary intake. They are indeces that must, however, be used with caution as they cannot be assumed to be valid.
for comparing different plant varieties or species. This is because specific differences in the organization of structural carbohydrates and lignin in the maturing cell wall may be as important as the content of these fractions in affecting both the rate of digestion and the size and shape of the disintegrated digesta particles (Troelsen and Campbell, 1968). These differences may well affect voluntary intake without changing the digestibility coefficient. The significantly higher intake by sheep on the alfalfa-based diets inspite of the fact that those diets were less digestible compared with the AWR2-based diets underscores this point. Also the results of this study has reaffirmed the theory of Van Soest (1965) that fiber mass inhibits intake in forages with a high cell wall content.
PARTICLE SIZE DISTRIBUTION EXPERIMENT

5.1 INTRODUCTION

The physical reduction in particle size of the structural components of forages by ruminants is an integral part of the ruminant digestive process. It exposes internal plant structures and increases the surface area available for attack by rumen microorganisms and digestive enzymes (Pond et al., 1984). Although the importance of this process has been recognized, quantification of particle size and description of its distribution in digesta have been difficult (Kennedy, 1984). The interest in particle size distribution of digesta arises from its possible role in determining rumen fill and thereby regulating feed intake (Moseley, 1984).

Various methods have been used to measure particle size distributions of digesta samples. The popular methods are wet-sieving (Evans et al., 1973; Allen et al., 1984) and dry-sieving (Ehle et al., 1982; Santini et al., 1983). Despite variations in methodology, the raw data generated have been expressed in a similar form i.e. proportion of total particles retained on each sieve. The subsequent manipulation of this data, however, vary greatly and is often of limited value. Presentation of the data in graphical form for example (Poppi et al., 1980; Moseley and Jones, 1984) is awkward and makes it difficult for more detailed analysis of physical breakdown. Other methods, such as modulus of fineness, although providing a single value, do not contain all the information necessary to define the distribution (Moseley, 1984). Waldo et al. (1971) suggested that forage
digesta particle sizes can be adequately described using a log normal distribution. These authors proposed an analytical procedure by which a log₁₀ mean ($\mu$) and log₁₀ standard deviation ($\delta$) were calculated from the regression of standard normal deviates of cumulative weight undersize on log₁₀ sieve size. This procedure has been reported to be adequate by some investigators (Ehle, 1984; Smith and Waldo, 1969) but inappropriate by others (Mertens et al., 1984; Moseley, 1984; Gates et al., 1988). The latter group of researchers have reported that digesta particle size distribution is more appropriately described by moment analysis. Considering the importance of digesta particle size distribution, there is a paucity of information on comparisons between different methods of describing the distributions in terms of their ability to relate to ruminant digestive function and voluntary feed intake. This study was conducted to provide information on such comparisons between different methods. The main objectives were:

1. to measure the rate of particle size reduction and distribution in the reticulo-rumen, omasum and abomasum of sheep fed alfalfa (legume) and secondcut Altai wild ryegrass (grass) and their combinations with tall wheatgrass or Altai wild ryegrass straws;

2. to determine an appropriate index to describe particle size distribution in the reticulo-rumen, omasum and abomasum of sheep; and

3. to determine the relationships, if any, between particle size distributions in the three sampling sites, voluntary feed intakes and digestibilities of different forage diets.
5.2 MATERIALS AND METHODS

5.2.1 Experimental protocol

Seventy-two Romanov x Western Whiteface wethers were used in this study (average weight 21kg). They were randomly allocated to the following dietary treatments:

1. 100 % alfalfa hay,

2. 60 % alfalfa hay + 40 % tall wheatgrass hay (TWG),

3. 60 % alfalfa hay + 40 % Altai wild ryegrass straw (AWR1),

4. 100 % secondcut Altai wild ryegrass hay (AWR2),

5. 60 % AWR2 + 40 % AWR1, and

6. 60 % AWR2 + 40 % TWG.

Preparation of diets, feeding and management of animals were as described in Materials and Methods section under experiment one. All animals were fed their respective diets for forty-five days before the commencement of slaughter. Three animals from each dietary treatment were randomly selected and slaughtered at 12, 24, 36 and 48 hours after feed removal. The digestive organs were removed within minutes and the contents of the reticulo-rumen, omasum and abomasum emptied into buckets. Samples of digesta from the three organs were taken and stored at -10°C.

5.2.2 Sieving procedure

After thawing and thorough mixing, digesta samples containing about 20g DM were taken and analysed for particle size distribution by a wet sieving procedure similar to that used to determine water-stable aggregates in soils (Bourgat and Kemp, 1957). The
samples were sieved for 12 hours through nests of five sieves arranged in descending order; 4.75, 2.00, 1.00, 0.50, and 0.25mm.

Basically the procedure involved suspending the stack of five sieves in a tank of clean water and oscillating it through a vertical plane. At the end of the downward stroke water flowed into the top sieve which had the largest sieve size. On the upward stroke water flowed through the mesh carrying the particles downwards.

After sieving, the sieves with all material left on them were oven dried at 105°C for 24 hours and weighed. The dry matter retained on each sieve was then determined.

5.2.3 Methods of expressing particle size distribution data

The methods of expressing particle size distribution in this study were based on simple proportions of particulate fractions using the critical size concept of 1mm as a cut off point between 'large' and 'small' particles and the soluble dry matter content as a proportion of total dry matter or combinations of these two. This consideration of particles in terms of 'large' and 'small' emphasizes the objective of this research and is based on the hypothesis of Mertens et al. (1984) that it is the characterization of the distribution of particles and not the mean size which is critical to research in particle size methodology and kinetics.

The material passing through the 0.25mm sieve was grouped together with the dissolved dry matter and classified as soluble dry matter (SDM). The soluble dry matter was calculated by difference. Dissolved dry matter, very fine particulate dry matter passing through the 0.25mm sieve and microbial dry matter comprise this fraction. No attempt was made to determine the relative contribution of each of these to the SDM fraction. It was assumed that SDM was the potentially soluble fraction. Particulate data was expressed as a proportion of the total dry matter collected on each sieve.
5.2.4 Calculations

1. Proportion of total particles less than 1mm (PIP) based on the critical particle size suggested by Poppi et al., (1980). This was calculated as the sum of the dry weight of material retained on the 0.50 and 0.25mm sieves divided by the total weight of material on all sieves.

2. Proportion of soluble DM in total DM (PSDM), calculated as the difference between the total dry matter (TM) and the total weight of material retained on all sieves (TS) divided by the total dry matter, i.e.

PSDM = (TM - TS)/TM.

3. Particle breakdown index (PBI) calculated by adding together (1) and (2) as suggested by Moseley (1984).

4. Proportion of coarse particles (PCTP) i.e. proportion of total particles retained on the 1mm sieve and those above it.

5. Proportion of total DM less than 1mm (DMLOMM).

5.2.5 Statistical analysis

Analysis of variance was performed using the GLM Procedure of SAS (1985) for determining least square means with unequal sample sizes. The statistical analysis was based on least square means because of imbalances in the number of observations recorded for the different sampling sites. Least square means of the effects were separated using the protected LSD test (SAS, 1985) and, when significant (P < 0.05), main effects or interactions were detected with probability levels consistent with the significance of the effects in the model.
The following model was used in the analysis of all the data generated from the above calculations:

\[ X_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + (\alpha\gamma)_{ik} + (\beta\gamma)_{jk} + \epsilon_{ijk} \]

where;
\[ X = \text{observation}, \]
\[ \mu = \text{overall mean}, \]
\[ \alpha = \text{effect of diet}, \]
\[ \beta = \text{effect of period}, \]
\[ \gamma = \text{effect of location}, \]
\[ \epsilon = \text{overall error}, \]
\[ i = 1, 2, \ldots, 6 \]
\[ j = 1, 2, \ldots, 4 \]
\[ k = 1, 2, 3. \]
5.3 RESULTS AND DISCUSSION

5.3.1 PARTICLE SIZE DISTRIBUTION IN THE RETICULO-RUMEN, OMASUM AND ABOMASUM

The effect of period after feed removal on particle size distribution in the reticulo-rumen, omasum and abomasum of animals on all diets was generally not significant. Because of this it was not possible to calculate the rate of particle size reduction for each diet or sampling site. The failure to detect differences between sampling periods could be due to the fact that the interval between last feeding and first sampling (24 hours) was sufficiently long to ensure that essentially all large particles had been reduced to the point that no further significant reduction in size occurred after that period. The effect of depriving the animals access to feed for such a long period may have exhausted the supply of nutrients and changed conditions in the rumen. Sutherland (1986) reported that digestion of feed consisting mainly of stalk material was complete by 24 hours, with no further change in digestibility or particle size distribution detectable at 48 hours.

The distribution of particles in the reticulo-rumen, omasum and abomasum followed a similar pattern irrespective of period or treatment effect. To illustrate the distribution, data for the periods and treatments were pooled and plotted against sieve size (Figure 1). The significant aspect of Figure 1 is the virtual absence of particles on the 4.75 and 2mm sieves from reticulo-ruminal and abomasal digesta and the retention of a relatively high amount of dry matter on the 2mm sieve from digesta of omasal origin. Abomasal digesta contained less dry matter on the 1mm sieve while ruminal and omasal digesta had about equal amounts. There was little difference between compartments in terms of dry matter retained on either 0.5 or
Figure 5.1: Percent dry matter retained on different sieve sizes of reticulo-ruminal, omasal and abomasal digesta (pooled data—all diets and periods)
0.25mm sieves. However, abomasal digesta contained a higher proportion of dry matter less than 0.25mm (70% of total dry matter) followed by reticulo-ruminal digesta (54%) and omasal digesta (42%).

The relatively high concentration of small particles in the reticulo-rumen observed in the present study is expected. Other researchers have noted that although particle size is a prerequisite for passage through the reticulo-omasal orifice, the material present in the reticulo-rumen at any time is predominantly below the threshold size (Evans et al., 1973; and Poppi et al., 1981b). Martz and Belyea (1986) and Sutherland (1986) postulated that the failure of particles which have been reduced below the threshold size to reach the reticulo-omasal orifice was due to entrapment in the ruminal mass of long fibrous material which acts as a filter bed. Their passage is only promoted when the large particles have been reduced in size and the mat is destroyed. Shaver et al. (1988) also deduced from their experiments that the effect large particles have on average retention time of dry matter in the rumen could be through their effect on rumen mat formation, and subsequent entrapment of small particles, as opposed to longer retention time of the large particles themselves. Ulyatt et al. (1984) found that during the latter part of a feeding cycle there was a considerable decline in the total volume of rumen contents and a reduction in effectiveness of the raft. This presumably brings about greater passage of dry matter in the latter period as a result of increased concentration of particles available for passage from the ventral reticulum to the omasum.

The higher proportion of particles greater than 1mm found in omasal digesta compared to abomasal and reticulo-omasal digesta appears to be a deviation from what has been observed by other workers. Waghorn et al. (1986), Ulyatt (1983), Uden
and Van Soest (1982) and Poppi et al. (1980) have all shown that very little material greater than 1mm in length escapes from the reticulo-rumen into the omasum over a range of different forage feeds. Most estimates place the value at less than 1% of the total dry matter passing. This has led to the concept that in sheep the reticulo-rumen allows the selective passage of particles which are smaller than 1mm and retain those which are greater. This size has therefore been taken as a biological particle size for materials flowing through the rumen. This is the basis of the critical particle size concept which has been used in the development of models for digesta flow. This concept divides rumen particles into two pools; a large particle pool which cannot pass out of the rumen easily, and a small particle pool which can leave the rumen rapidly. This implies that dietary residues must be reduced in particle size before they can escape the reticulo-rumen. As stated earlier the results from the present study are apparently not in consonance with this concept. This discrepancy may be more apparent than real. The reason for saying this is that the critical particle size cannot be expected to be a precise cut off because of the inevitable passage through the reticulo-omasal orifice of some large particles as a result of end-on delivery. The findings of McBride et al. (1984) support this view. They used endoscopy to study the movement of particles through the reticulo-omasal orifice and found that the reticulo-omasal orifice did not constitute a barrier to the passage of even large particles. They therefore concluded that the low passage of particles larger than 1mm is due to the failure of those particles to reach the reticulo-omasal orifice. Their work also established that liquid flows in both directions through the reticulo-omasal orifice, with a normal pulse of digesta leaving the reticulum with the second reticula contraction and intermittent return of material from the omasum to the reticulum. Such a two-way flow according to Sutherland (1986), opens up the possibility of an active sorting operation within


the omasum in which large particles are strained off and held within the omasum while small particles in suspension are pumped into the abomasum. Later, the backflow could gather the accumulated large particles and return them to the reticulum where they can be further reduced in size. The difference in particle size distribution between the omasum and abomasum points to the possibility of the operation of such a mechanism. Weston and Cantle (1984), have provided evidence for the first part of the mechanism in demonstrating differential passage of particles through the omasum, with larger particles having lower fractional clearances. It therefore appears that the high proportion of large particles in the omasum is the result of the accumulation of such particles after they get through the reticulo-omasal orifice. It may also be said that very little particle size reduction occurs in the omasum so the selective passage of smaller particles into the abomasum and/or absorption of solutes, (Bost, 1970) could have also contributed to the accumulation of the large particles in the omasum.

5.3.2 Effect of diet on particle size distribution in the reticulo-rumen of sheep

Particle size distribution of reticulo-rumen digesta of sheep fed the six diets is presented in Table 5.8.

The reticulo-rumen of sheep on diets containing grass generally contained higher proportions of coarse particles and lower amounts of dry matter less than 1mm. This may be related to the fibrous nature of the grasses. The 100 % AWR2 diet had the highest proportion of soluble dry matter than all the other diets. Diets containing AWR2, therefore had higher proportions of soluble dry matter compared to those containing alfalfa. Treolsen and Campbell (1968) observed that reduction
Table 5.8: Particle size distribution expressed by different methods in reticulo-rumen of sheep on different diets

<table>
<thead>
<tr>
<th>Diet</th>
<th>1Method of expression</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PCTP</td>
</tr>
<tr>
<td>100% Alfalfa</td>
<td>0.105&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>60% Alfalfa + 40% AWR1</td>
<td>0.202&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>60% Alfalfa + 40% TWG</td>
<td>0.363&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>100% AWR2</td>
<td>0.209&lt;sup&gt;ac&lt;/sup&gt;</td>
</tr>
<tr>
<td>60% AWR2 + 40% AWR1</td>
<td>0.290&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
<tr>
<td>60% AWR2 + 40% TWG</td>
<td>0.321&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a,b,c,d</sup> Means within columns with different letters are significantly different (P < 0.05).
1AWR1 = Altai wild ryegrass straw; AWR2 = prebloom second-cut Altai wild ryegrass hay; TWG = tall wheatgrass straw.
2PDSM = Proportion of soluble dry matter in total dry matter.
PBI = Particle breakdown index.
PCTP = Proportion of coarse particles in total particulate material.
DMLOMM = Proportion of dry matter less than 1mm.
in particle size of alfalfa diets resulted in more or less cuboidal particles which had a greater tendency to escape from the reticulo-rumen as opposed to the cylindrical particles which resulted from the breakdown of grass diets. The implication of this is that grass diets will stay in the reticulo-rumen longer and be subjected to a greater degree of rumination with the concomitant reduction in particle size and the release of a greater proportion of soluble fractions.

5.4 CORRELATION OF PARTICLE SIZE DISTRIBUTION WITH DIGESTIBILITY COEFFICIENTS AND VOLUNTARY INTAKE

Tables 5.9, 5.10 and 5.11 give the correlation coefficients between each of the methods for describing particle size distribution in the reticulo-rumen, omasum and abomasum and digestibility coefficients of nutrients.

The proportion of soluble dry matter (PSDM) in the reticulo-rumen 12 hours after feed removal was the best predictor of DM digestibility. The correlation between PSDM and dry matter digestibility was significant (\( r = 0.84, P < 0.05 \)). PSDM in RR 24 hours after feed removal was also significantly correlated with CD, ADFD and NDFD (\( r = 0.81 \) in each case, \( P < 0.05 \)), Table 5.9.

Proportion of particles less than 1mm in the total particulate material (PIP), particle breakdown index(PBI), proportion of coarse particles i.e. particles greater than 1mm (PCTP) and dry matter less than 1mm (DMLOMM) in omasal digesta 12 hours after feed removal were all significantly correlated with digestibility of one or more proximate fractions (Table 5.10).

Both PIP and PCTP gave the highest significant correlations with OM and GE digestibility, (\( r = 0.90, P < 0.01; \) and \( 0.87, P < 0.05 \) for OM and GE digestibility
Chapter 5. PARTICLE SIZE DISTRIBUTION EXPERIMENT

Table 5.9: Simple correlation coefficients of particle size distribution in reticulo-rumen of sheep at different times after feeding with digestibility coefficients of proximate fractions

<table>
<thead>
<tr>
<th>Time after feeding (Hrs)</th>
<th>Method of particle size description</th>
<th>DMD</th>
<th>OMD</th>
<th>CD</th>
<th>NDFD</th>
<th>ADFD</th>
<th>GED</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
<td>PIP</td>
<td>0.17</td>
<td>-0.07</td>
<td>-0.29</td>
<td>-0.49</td>
<td>-0.46</td>
<td>0.01</td>
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<tr>
<td></td>
<td>PSDM</td>
<td>0.84</td>
<td>0.74</td>
<td>0.79</td>
<td>0.61</td>
<td>0.62</td>
<td>0.76</td>
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<tr>
<td></td>
<td>PBI</td>
<td>0.43</td>
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<td>0.03</td>
<td>-0.20</td>
<td>-0.17</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>PCTP</td>
<td>-0.17</td>
<td>0.07</td>
<td>0.29</td>
<td>0.49</td>
<td>0.46</td>
<td>-0.01</td>
</tr>
<tr>
<td></td>
<td>DMLOMM</td>
<td>0.32</td>
<td>0.08</td>
<td>-0.11</td>
<td>-0.32</td>
<td>-0.29</td>
<td>0.16</td>
</tr>
<tr>
<td>24</td>
<td>PIP</td>
<td>0.65</td>
<td>0.61</td>
<td>0.25</td>
<td>0.01</td>
<td>0.02</td>
<td>0.64</td>
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<td></td>
<td>PSDM</td>
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<td>PBI</td>
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<td>0.34</td>
<td>0.76</td>
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<tr>
<td></td>
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<td>-0.65</td>
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<td>0.02</td>
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<tr>
<td></td>
<td>DMLOMM</td>
<td>0.62</td>
<td>0.60</td>
<td>0.30</td>
<td>0.09</td>
<td>0.07</td>
<td>0.62</td>
</tr>
</tbody>
</table>

c P < 0.05.

1 PIP = Proportion of particles less than 1mm in total particulate material.
PSDM = Proportion of soluble dry matter in total dry matter.
PBI = Particle breakdown index.
PCTP = Proportion of coarse particles in total particulate material.
DMLOMM = Proportion of dry matter less than 1mm.
Table 5.10: Simple correlation coefficients of particle size distribution in omasum of sheep at different times after feeding with digestibility coefficients of proximate fractions

<table>
<thead>
<tr>
<th>Time after feeding (Hrs)</th>
<th>Method of particle size description</th>
<th>DMD</th>
<th>OMD</th>
<th>CD</th>
<th>NDFD</th>
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<tr>
<td>12</td>
<td>PIP</td>
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<td>-0.77</td>
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<td>-0.21</td>
<td>-0.20</td>
<td>-0.49</td>
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<tr>
<td></td>
<td>PBI</td>
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<td>-0.84</td>
<td>-0.69</td>
<td>-0.62</td>
<td>-0.60</td>
<td>-0.80</td>
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<td></td>
<td>PCTP</td>
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<td>0.90</td>
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<td>0.77</td>
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<td>DMLOMM</td>
<td>-0.67</td>
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<td>-0.68</td>
<td>-0.66</td>
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<tr>
<td>24</td>
<td>PIP</td>
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<td>0.64</td>
<td>0.57</td>
<td>0.59</td>
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<td>0.91</td>
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<td>0.78</td>
<td>0.57</td>
<td>0.58</td>
<td>0.86</td>
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<tr>
<td></td>
<td>PCTP</td>
<td>-0.55</td>
<td>-0.49</td>
<td>-0.64</td>
<td>-0.57</td>
<td>-0.59</td>
<td>-0.50</td>
</tr>
<tr>
<td></td>
<td>DMLOMM</td>
<td>0.93</td>
<td>0.84</td>
<td>0.75</td>
<td>0.53</td>
<td>0.54</td>
<td>0.86</td>
</tr>
</tbody>
</table>

a P< 0.001; b P< 0.01; c P< 0.05.

1PIP = Proportion of particles less than 1mm in total particulate material.
PSDM = Proportion of soluble dry matter in total dry matter.
PBI = Particle breakdown index.
PCTP = Proportion of coarse particles in total particulate material.
DMLOMM = Proportion of dry matter less than 1mm.
Table 5.11: Simple correlation coefficients of particle size distribution in abomasum of sheep at different times after feeding with digestibility coefficients of proximate fractions

<table>
<thead>
<tr>
<th>Time after feeding (Hrs)</th>
<th>Method of particle size description</th>
<th>DMD</th>
<th>OMD</th>
<th>CD</th>
<th>NDFD</th>
<th>ADFD</th>
<th>GED</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PIP</td>
<td>-0.22</td>
<td>-0.27</td>
<td>-0.34</td>
<td>-0.31</td>
<td>-0.28</td>
<td>-0.24</td>
</tr>
<tr>
<td></td>
<td>PSDM</td>
<td>0.49</td>
<td>0.51</td>
<td>0.78</td>
<td>0.80</td>
<td>0.82c</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>PBI</td>
<td>0.22</td>
<td>0.21</td>
<td>0.35</td>
<td>0.39</td>
<td>0.42</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>PCTP</td>
<td>0.22</td>
<td>0.27</td>
<td>0.34</td>
<td>0.31</td>
<td>0.28</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>DMLOMM</td>
<td>-0.19</td>
<td>-0.22</td>
<td>-0.08</td>
<td>0.01</td>
<td>0.03</td>
<td>-0.21</td>
</tr>
<tr>
<td>12</td>
<td>PIP</td>
<td>-0.60</td>
<td>-0.64</td>
<td>-0.32</td>
<td>-0.12</td>
<td>-0.10</td>
<td>-0.66</td>
</tr>
<tr>
<td></td>
<td>PSDM</td>
<td>0.72</td>
<td>0.79</td>
<td>0.99a</td>
<td>0.97a</td>
<td>0.97a</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>PBI</td>
<td>0.63</td>
<td>0.68</td>
<td>0.94b</td>
<td>0.96b</td>
<td>0.97b</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>PCTP</td>
<td>0.60</td>
<td>0.64</td>
<td>0.32</td>
<td>0.12</td>
<td>0.09</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>DMLOMM</td>
<td>0.17</td>
<td>0.21</td>
<td>0.61</td>
<td>0.75</td>
<td>0.78</td>
<td>0.16</td>
</tr>
<tr>
<td>24</td>
<td>PIP</td>
<td>-0.60</td>
<td>-0.64</td>
<td>-0.32</td>
<td>-0.12</td>
<td>-0.10</td>
<td>-0.66</td>
</tr>
<tr>
<td></td>
<td>PSDM</td>
<td>0.72</td>
<td>0.79</td>
<td>0.99a</td>
<td>0.97a</td>
<td>0.97a</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>PBI</td>
<td>0.63</td>
<td>0.68</td>
<td>0.94b</td>
<td>0.96b</td>
<td>0.97b</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>PCTP</td>
<td>0.60</td>
<td>0.64</td>
<td>0.32</td>
<td>0.12</td>
<td>0.09</td>
<td>0.66</td>
</tr>
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<td></td>
<td>DMLOMM</td>
<td>0.17</td>
<td>0.21</td>
<td>0.61</td>
<td>0.75</td>
<td>0.78</td>
<td>0.16</td>
</tr>
</tbody>
</table>

a P< 0.001; b P< 0.01; c P< 0.05.

1 PIP = Proportion of particles less than 1mm in total particulate material.
PSDM = Proportion of soluble dry matter in total dry matter.
PBI = Particle breakdown index.
PCTP = Proportion of coarse particles in total particulate material.
DMLOMM = Proportion of dry matter less than 1mm.

respectively for both methods). PSDM in omasal digesta 24 hours after feed removal was also highly correlated with DMD (r = 0.97, P< 0.001).

The correlations between PSDM in abomasal digesta (24 hours) and digestibility of cellulose, NDF and ADF digestibility were all highly significant, (r =0.99, 0.97 and 0.97, respectively, P< 0.001), Table 5.11. This fraction turned out to be the best predictor of apparent digestibility coefficients of cell wall components (Table 5.12).

The degree of correlations between the distribution of particles in the three compartments and intake of nutrients were not as high as those observed for digestibility. The only significant correlations were observed for PIP and PCTP in the
Table 5.12: Simple regression equations that estimate apparent digestibility coefficients of some proximate fractions

<table>
<thead>
<tr>
<th>Fraction</th>
<th>$R^2$</th>
<th>Regression equation</th>
<th>$SE_a$</th>
<th>$SE_b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>DMD$^1$</td>
<td>0.94$^a$</td>
<td>$Y = 49.04 + 25.22X$</td>
<td>1.385</td>
<td>3.221</td>
</tr>
<tr>
<td>OMD$^2$</td>
<td>0.81$^b$</td>
<td>$Y = 84.09 - 44.73X$</td>
<td>5.304</td>
<td>10.688</td>
</tr>
<tr>
<td>CD$^3$</td>
<td>0.97$^a$</td>
<td>$Y = 23.44 + 56.04X$</td>
<td>3.335</td>
<td>4.642</td>
</tr>
<tr>
<td>NDFD$^3$</td>
<td>0.93$^b$</td>
<td>$Y = -13.68 + 98.07X$</td>
<td>9.344</td>
<td>13.004</td>
</tr>
<tr>
<td>ADFD$^3$</td>
<td>0.94$^a$</td>
<td>$Y = -11.29 + 91.96X$</td>
<td>8.236</td>
<td>11.462</td>
</tr>
<tr>
<td>GED$^1$</td>
<td>0.83$^b$</td>
<td>$Y = 49.63 + 23.36X$</td>
<td>2.253</td>
<td>5.240</td>
</tr>
</tbody>
</table>

$a P< 0.001; b P< 0.01.$

$SE_a$ Standard error of intercept;

$SE_b$ Standard error of slope.

$^1$Estimates of $Y$ from proportion of soluble dry matter (PSDM) in omasal digesta 24 hours after feed removal.

$^2$Estimate of $Y$ from proportion of particles less than 1mm to total particles in (PIP) omasal digesta 12 hours after feed removal.

$^3$Estimates of $Y$ from PSDM in abomasal digesta 24 hours after feed removal.

RR 24 hours after feed removal and intake of digestible organic matter ($r = 0.86, P< 0.05$). The correlation between PBI in abomasal digesta 24 hours after feed removal and intake of digestible neutral detergent fiber was highly significant ($r = 0.93, P< 0.01$).

Table 5.12 gives the best regression equations for estimating the digestibility coefficients of some feed fractions.

The negative slope obtained in the regression of PIP in omasal digesta (12 hours after feed removal) on in vivo OMD is consistent with expected biological function. An increase in the proportion of particles less than 1mm in omasal digesta within the 12-hour period indicates a faster rate of escape of such particles from
the reticulo-rumen, a site that accounts for 60–65% of organic matter digestibility (Church, 1976). The diets used in this experiment were all of low digestibility (OMD < 70%). Such diets generally contain less soluble components and less digestible cell walls (Moseley, 1984). One way by which the animal can increase the digestibility of such diets is by increasing the retention time in the rumen. Thus the greater the rate of passage of such particles the less digestible the OM fraction will be.

The positive association between PSDM and digestibility of the nutrients in the feed appears to contradict the concept that reduction of particle size of feeds is associated with reduced digestibility of the nutrients in the feed. That is based on the observation that reduction of particle size promotes faster rate of passage and therefore reduces the retention time of feed in the digestive tract, (Mertens et al., 1984). In the present experiment increases in the PSDM were brought about as a result of reduction in particle size in the reticulo-rumen so that any increase in PSDM is generally the result of longer retention time in the rumen giving the microbes and the digestive enzymes enough time to digest the nutrients. In the competition between passage and digestion of nutrients, slow digesting nutrients will have larger depressions in digestibility with smaller particles and increased rates of passage. This may partly explain the low digestibility coefficients observed in the alfalfa–based diets. The higher lignin content in alfalfa compared with AWR2 (Knipfel, 1978) may have reduced the rate of digestion of the alfalfa and coupled to its high rate of passage could have subsequently resulted in the reduced digestibility of the nutrients observed in this study.
5.4.1 Conclusion

The higher proportion of coarse particles in omasal digesta compared to reticulo-ruminal digesta was unexpected. However, this finding is in agreement with the hypothesis of McBride et al., (1984) which suggests that the reticulo-omasal orifice does not prevent the passage of large particles into the omasum. Also the large proportion of particles below the threshold particle size in the reticulo-rumen has reaffirmed the hypothesis that reduction of particle size below the threshold size is not the rate-limiting factor for passage of such particles.

The effect of NDF intake on particle size distribution has reaffirmed the importance of plant cell walls, as measured by NDF, as the most fundamental feed characteristic determining feeding value of forages. The significantly high correlations between particle size distribution and apparent digestibility coefficients as opposed to voluntary intake has also demonstrated that particle size is much more closely related to the former than to the latter.

In conclusion it is worthy to note that the failure to detect differences between sampling periods may have been due to the long intervals between periods. It is suggested that intervals between sampling periods be considerably shortened in any future work of this nature.
Chapter 6

GENERAL CONCLUSION

A number of investigators have demonstrated the importance that feed particle size reduction has on digestion (Kennedy, 1984 and Moseley, 1984). Others have shown that the efficiency with which forage feed particles are broken down by the animal is dependent on forage type and that this subsequently affects digestion (Moseley and Jones, 1984). One major implication of the above findings is that some measure of particle size distribution of feed or digesta would provide an indication of the feed material for subsequent digestion or the extent of digestion. In order to relate particle breakdown to other processes of digestion, it is important that the description of particle size distribution contain those features pertinent to particular events in the rumen e.g. both the degree of fineness of particles and the proportion of soluble matter made available must be considered. This study has shown that the description of digesta particle size distribution in terms of large, small and soluble fractions is physiologically justified.

The importance of particle size distribution versus mean particle size as a criterion for particle size description is based on physiological considerations. The mean particle size in feed or rumen has no unique physiological function or attribute. While large particles require and stimulate rumination and small particles escape the rumen, the mean particle has no clear-cut function (Mertens et al., 1984). Therefore unless the mean is extremely small or large it provides little information about the
condition of the feed or digesta. The results from this experiment indicate that the proper description of particle size distribution is an important consideration if one wants to establish relationships between particle size and ruminant digestive function.

The strong relationships between digestibility and digesta particle size (especially abomasal digesta), established in this study could be of practical importance in predicting digestibility of grazed forages. This is based on the fact that distribution of particles in the abomasum is similar, if not the same, as that in feces. This implies that analysis of particle size distribution in feces of grazing animals could be used to predict the digestibility of the grazed forage. It must, however, be recognized that the precision of the equations developed could be improved by testing a larger number of forages at different stages of growth. This is because the magnitude of the constants in each equation may probably differ between forages at different stages of growth. It is also important to appreciate the fact that the equations developed in this study apply mainly to growing sheep. However, the fundamental relationships established between particle size distribution and apparent digestibility coefficients of forages should apply to ruminants in general.

The results of this study have demonstrated that digestibility per se is not the major factor determining the voluntary intake of forages. This is based on the observation that even though the diets containing AWR2 were more digestible than the alfalfa diets the latter were eaten in greater quantities. The important determinant could be clearance of digesta from the reticulo-rumen which in turn was related to the total amount of cell wall components ingested. The higher retention time in reticulo-rumen of the more fibrous diets ensures that they are subjected to a longer period of microbial and enzymatic attack. This may explain
the higher digestibility coefficients of the proximate fractions observed in those diets.

Finally, this study has also shown that AWR2 harvested at the prebloom stage is comparable to alfalfa in terms of intake of daily digestible energy by growing lambs. As such it can substitute for alfalfa in an all-forage diet for lambs.
Bibliography


