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Nutrition of the grazing ruminant

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ABSTRACT

Ruminants grazing pasture rarely approach their genetic potential for meat, milk or wool production. There are wide differences also between plant species and between leaf, stem and inflorescence fractions in their capacity to sustain animal production. The relatively low productivity of grazing ruminants and the differences between plant components in nutritional value can be explained from an understanding of the factors that determine nutrient supply to the animal's tissues and the efficiency of metabolism. Nutrient supply to the tissues depends on (i) the nutrient contents of the forage available, which varies between plant species, their component parts, their stage of maturity and the growing conditions; (ii) the pasture components actually selected by the animal which are influenced by ease of eating, taste, odour and tactile characteristics of the plant material available, its water content, the structure of the sward, the dimensions of the animal's incisor arcade and its previous experience; (iii) the amount of each selected component eaten, which is influenced by the potential of the animal to utilize nutrients, the capacity of the reticulo-rumen and factors that affect the rate of digestion and outflow of organic matter from the rumen, and the time spent in eating and ruminating activities; (iv) modifications of consumed nutrients by rumen microbes, particularly the extent of breakdown of plant protein and the relative proportions of volatile fatty acids produced; (v) the efficiency of biochemical reactions metabolising the absorbed nutrients. Although a great deal is known about the way each of these factors influence nutrient supply to grazing animals, the complexity of the interactions between them often makes it extremely difficult to identify the specific reasons for reduced performance in any particular situation. However, by integrating current concepts and knowledge using computer simulation techniques, the factors limiting nutrient supply to the animal's tissues can be determined and the value of alternative management strategies for improving animal productivity assessed.

Keywords Grazing ruminant, pasture composition, diet selection, feed intake, rumen function, nutrient metabolism, computer simulation.

INTRODUCTION

Rarely do animals grazing pasture approach their genetic potential for meat, milk or wool production. For example, lambs fed reconstituted cow's milk under ideal environmental conditions are known to grow at rates in excess of 500 g/d (Hodge, 1974), but seldom do grazing lambs achieve growth rates over 330 - 350 g/d (Ulyatt, 1981). Furthermore, individual pasture species and plant components all vary widely in their capacity to support animal production. Ulyatt (1981) observed that lambs eating white clover (*Trifolium repens*) grew at 330 g/d, whereas animals consuming perennial ryegrass (*Lolium perenne*) grew at only 227 g/d. Irrigated summer pasture containing predominantly paspalum (*Paspalum dilatatum*) supports lamb growth rates as low as 60 g/d (Black *et al.*, 1979). Annual pastures that sustain growth rates of 200 - 300 g/d in their vegetative phase, often are unable to maintain live weight when mature (Purser, 1981). The leaf component of grasses and legumes is eaten in greater amounts

and sustains a higher rate of animal performance than the stem fraction (Minson, 1981).

The differences between plant components in their capacity to sustain animal performance and the relatively low productivity of grazing animals arise because the nutrients available to the animal's tissues vary widely and are less than required for maximum production. Nevertheless, the nutritional value of pasture plants can be improved, for example, by fertiliser application to the soil (Ozanne *et al.*, 1976; Rees and Minson, 1978), by physical or chemical treatment (Thomson and Beever, 1980) and by the provision of supplements such as protein or amino acids (Black *et al.*, 1979; Barry, 1981; Dove *et al.*, 1985), urea (Stephenson and Hopkins, 1985) or trace minerals (Panggabean *et al.*, 1985). The purpose of this paper is to identify the factors responsible for differences between plant components in their ability to provide nutrients to grazing ruminants so that ways of improving the nutritional value of pasture plants for animals may be developed.

FACTORS AFFECTING NUTRIENT SUPPLY AND UTILISATION

Most pastures contain a range of plant species and, within each species, the proportions and chemical composition of leaf, stem and inflorescence vary widely with season. The supply of nutrients to the tissues of a ruminant grazing these pastures and the efficiency with which the nutrients are utilised for body functions depend on (i) the nutrient contents of the forage components available, (ii) the actual components selected by the animal, (iii) the amount of each selected component eaten, (iv) modifications to consumed nutrients by rumen microbes, and (v) the efficiency of biochemical reactions metabolising the absorbed nutrients within the animal. A great deal is understood about many of these processes, but some areas require further clarification.

NUTRIENT CONTENT OF FORAGE COMPONENTS

The chemical composition of pasture plant material varies widely between species and their component parts such as leaf, stem, flower and seed. The composition of each component within a species can change markedly as the plant matures, and composition also varies with growing conditions. Some of these differences are illustrated in Table 1. Clovers tend to have less cell wall constituents than grasses at the same stage of maturity, but they have greater proportions of storage and soluble carbohydrate, protein and lipid. Leaves contain considerably less total cell wall material, particularly lignin, than stem from the same plant and this is compensated for by greater proportions of other carbohydrates, protein and lipid. Similar changes occur within individual leaves as they mature and senesce as is illustrated by the *Danthonia linkii* example in Table

TABLE 1 Effect of species, plant component and maturity on the chemical composition of pasture (% dry matter).

Plant material	CWC ^a	Lignin	Pectin	Soluble Carbohydrates	True Protein	Non-protein Nitrogen	Lipid	Ash
Whole plant: vegetative^b								
White clover	38.8	8.2	7.1	7.9	22.0	0.62	9.3	10.3
Perennial ryegrass	44.8	6.8	1.4	12.6	17.4	0.49	6.6	12.7
Plant components^c								
White clover: flowering								
green leaf	21.8	6.1	10.6	6.3	29.5	0.99	5.6	9.9
stem	39.9	18.9	7.8	6.8	13.8	0.87	3.2	9.3
flower	45.4	16.4	9.7	3.8	19.9	0.99	2.7	8.0
Stage of maturity^c								
<i>Danthonia linkii</i> : vegetative								
green leaf	58.1	3.2	2.5	8.1	11.1	0.20	2.7	9.4
stem	69.1	5.3	2.2	10.9	5.2	0.24	1.0	6.5
<i>Danthonia linkii</i> : flowering								
green leaf	69.4	6.0	1.1	2.3	11.2	0.15	2.8	9.1
dead leaf	74.0	8.4	0.9	0.7	3.8	0.11	2.3	9.3
stem	84.6	9.6	0.7	2.3	1.8	0.09	0.8	5.1
flower/seed	59.4	5.2	0.1	0.15	8.0	0.20	2.0	4.8

^a Cell wall constituents

^b Black *et al.*, (1982)

^c W.F. Colebrook, G.J. Faichney, J.L. Black unpublished analyses by methods of Faichney & White (1983).

1. Nitrogenous fertilizers increase the protein and non-protein nitrogen content of the plant, usually at the expense of water soluble carbohydrates. Fertilizers containing phosphorus, potassium, sulphur and trace elements generally increase the concentration of these elements in the plant material and improved growth is often associated with increased cell wall constituents (Rees and Minson, 1978). Weather can also affect plant composition. Low light intensity reduces the soluble carbohydrate content of plant cells and increases the non-protein nitrogen, water and ash content (Deinum, 1966). Plants grown under shade contain less cell wall constituents than those grown in full sun and some grass species produce increased proportions of leaf when grown under these conditions (Samarakoon *et al.*, 1990). Thus, within any pasture, there is normally a large range in the chemical composition of individual plant components available to a grazing animal for selection.

FORAGE COMPONENTS SELECTED

Sheep and cattle grazing pastures often select a diet that bears little resemblance to the overall composition of the feed available (Leigh and Mulham, 1966; Dudzinski and Arnold, 1973; L'Huillier *et al.*, 1986; Lascano and Thomas, 1988). At the extreme, Leigh and Mulham (1966) observed that 80% of the diet selected by sheep grazing a semi-arid grassland was derived from material that comprised only 5% of the total herbage available. Selection also occurs in temperate pastures which have less variation in the forage on offer. Barthram and Grant (1984) observed that sheep selectively grazed the leaf horizon at the top of a vegetative ryegrass sward and rarely penetrated to the lower levels containing pseudostems and dead material. Similarly, L'Huillier *et al.* (1986) found that sheep grazing a ryegrass - white clover pasture during summer in New Zealand largely bypassed the surface horizon containing predominantly dead reproductive stem to graze green material near the base of the sward. In general, sheep tend to select a diet containing a higher proportion of green leaf and less stem and dead material than is in the pasture (Ratray and Clark, 1984). A similar, but less pronounced, pattern exists with cattle (Forbes and Hodgson, 1985). Although there are many reports describing the diet selected by animals in different environments, most provide little basis for understanding why particular

plant components were selected. Neither gross chemical composition (Arnold, 1981) nor *in vitro* digestibility (Kenney and Black, 1984) of a forage are particularly suitable for predicting its selection by sheep.

A series of studies was undertaken in our laboratory to identify and quantify some of the factors that determine the selection of forage components by sheep. These experiments showed that at least four factors influence diet selection; namely, (i) ease of eating, measured as potential intake rate when a forage is offered alone to trained animals for short periods, (ii) sensory factors relating to taste, odour and tactile stimulation, (iii) water content of the forage and (iv) the quantity and spacial distribution of components within a sward. Animal experience is also important as indicated by the increased consumption of grain in animals previously exposed to cereals (Mottershead *et al.*, 1985) and the reduced consumption of a feed by lambs when experiencing gastro-intestinal illness after it was first ingested (Burritt and Provenza, 1989).

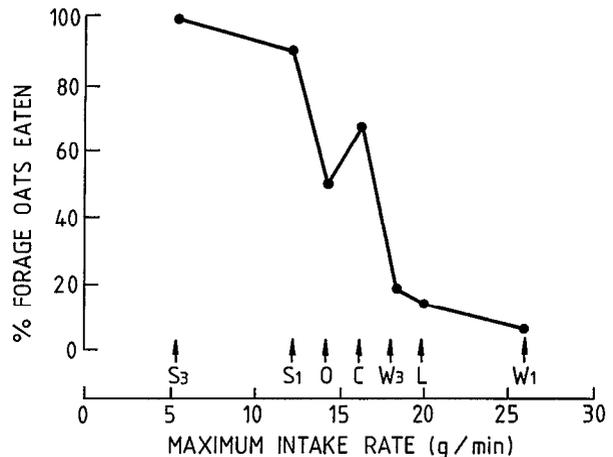


FIG 1 Relationship between preference for forage oats (O) when it was offered in pairs with other forage having different potential intake rates. S₃, wheaten straw 0 mm long; S₁, wheaten straw 10 mm long; O, dried vegetative forage oats; C, dried clover pasture; W₃, wheaten hay 24 mm long; L, lucerne hay; W₁, wheaten hay 10 mm long (from Kenney and Black, 1984).

Ease of Eating

Kenney and Black (1984) showed that, when sheep

were given a choice between two dried forages, they preferred, with few exceptions, the one that could be eaten at a faster rate. The preference for dried forage oats when offered with several other forages varying widely in nutritional value and potential intake rate is shown in Figure 1. Preference was defined as the intake of forage oats expressed as a percentage of the total intake of both forages on offer; a value of 50% means that preference for the two forages was equal. Forage oats was preferred when it was offered with a forage with a lower potential intake rate and, except for a dried clover dominant pasture, the reverse occurred when it was offered with a forage having a higher intake rate.

The same response was observed when potential intake rate of a single forage was altered by chopping it to different lengths. Colebrook *et al.* (1987) found that the intake rate of a wheaten hay increased from 7 to 25 g/min as the length of particles decreased from 30 to 4 mm (Figure 2a).

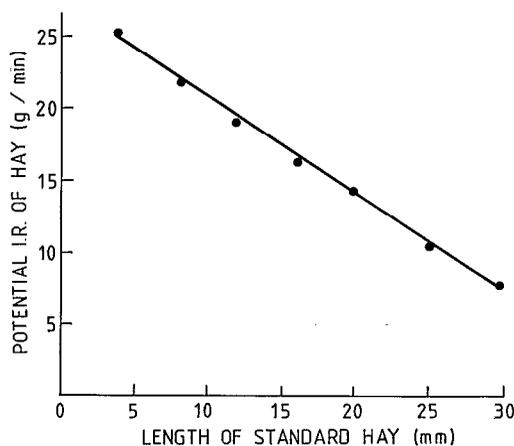


FIG 2a Relationship between potential intake rate and particle length for a wheaten hay (from Colebrook *et al.*, 1987).

When 12 mm hay was offered with one of a series of other lengths of the same hay, sheep consistently preferred the shorter hay that could be eaten at a faster rate (Figure 2b).

Similar observations have been made for several other forages including lucerne hay, dried forage oats and wheaten straw (W.F. Colebrook and J.L. Black, unpublished). Each of these experiments showed that sheep select strongly for forages that can be eaten at a faster rate and confirmed the earlier observations by

Kenney and Black (1984) that the degree of discrimination between forages with the same difference in intake rate declined as the mean intake rate of the forages increased.

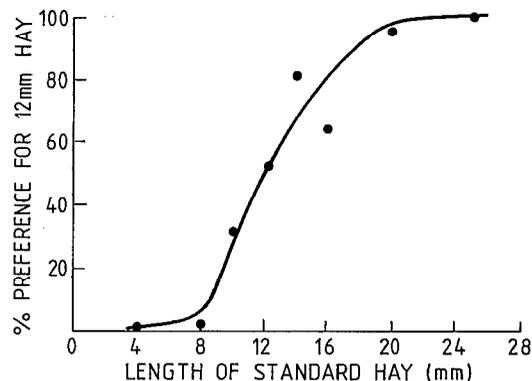


FIG 2b Relationship between preference for 12 mm particles compared with the same hay cut to other lengths (from Colebrook *et al.*, 1987).

Sensory Factors

When the results of all comparisons made by Kenney and Black (1984) were examined, preference was shown to be closely related to potential intake rate for all forages except the dried clover pasture. Further experiments in which small quantities of ground clover pasture were added to other forages showed that it was rejected because of sensory factors such as taste and odour. Sheep are known to respond both positively and negatively to the addition of various chemicals to either feed or water because of alterations to taste and odour (Arnold *et al.*, 1980; Gherardi and Black, 1986; Grovum and Chapman, 1988).

Although the importance of sensory factors in determining diet preference has been recognised for many years (Arnold, 1966), a simple comparison between two feeds does not necessarily give a quantitative measure of the difference in preference, particularly when one is strongly preferred. Each feed would need to be fed with every other feed to establish a relative preference ranking for a group of feeds. However, the

influence of sensory factors can be quantified by comparing the preference for any forage with that of a standard forage chopped to different lengths to vary its potential intake rate (Colebrook *et al.*, 1985). If the effects of sensory factors were similar, equal amounts would be selected when the test forage was offered with a standard forage having the same potential intake rate. By establishing a regression between preference for the test forage (e.g. *Themeda*, Figure 3) and the intake rate of different lengths of the standard forage with which it was offered, the intake rate of the standard hay with equal preference can be determined. If the intake rate of the standard hay that has equal preference to the test forage is greater than the potential intake rate of the test forage, the test forage is preferred relative to the standard. Conversely, if the intake rate of the standard forage with equal preference to the test forage is less than that of the test forage, the test forage is disliked relative to the standard forage. The difference in potential intake rate of the test forage when it is fed alone and the intake rate of the standard forage with equal preference to the test forage was called IR (Colebrook *et al.*, 1985) and is a quantitative measure of how much the test forage is liked or disliked relative to the standard forage.

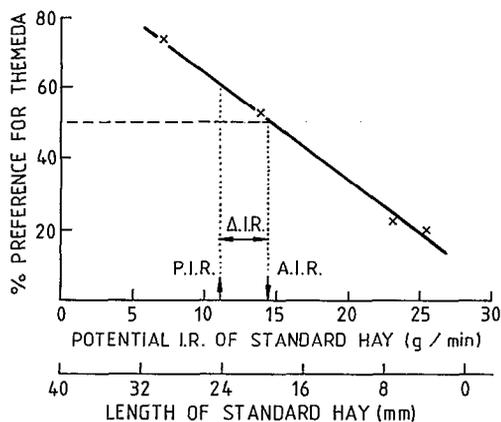


FIG 3 Relationship between preference for *Themeda* over a standard hay of different lengths. P.I.R. is potential intake rate of the test forage and A.I.R. is the intake of standard hay with equal preference to the test forage. IR is a quantitative measure (g/min) of the effect of sensory factors on the preference of the test forage relative to the standard hay (from Colebrook *et al.*, 1985).

Colebrook *et al.* (1985; 1990) examined the preference by sheep for 23 forages relative to a standard wheaten hay and showed that a difference in IR of 2 g/min between two forages resulted in almost complete preference for the forage with the higher IR. The IR values ranged from + 7.6 g/min for young leaves of *Danthonia linkii*, indicating that it was strongly preferred, to - 8.4 for preflowering white clover (*Trifolium repens*) indicating that it was strongly disliked. Colebrook *et al.* (1990) showed that a ranking of preference between forages on the basis of differences in IR was virtually the same as obtained when each forage was tested against every other forage. When the preference between many forages is to be determined, the IR procedure is much quicker.

The experiments of Colebrook *et al.* (1985; 1990) suggest that over the range of potential intake rates from 11 to 20 g/min for the forages examined, sensory factors have a greater influence on preference than does ease of eating. The relative importance of the two factors is currently being studied; preliminary results indicate that differences in ease of eating may be the more important determinant of preference for forages with low potential intake rates, whereas sensory factors form the predominant influence for forages that have a high potential intake rate and are easy to eat.

Water Content of Forage

Kenney *et al.* (1984) showed that the rate of intake of fresh forage increased as its water content increased, but the rate of dry matter intake declined once the dry matter content of the forage fell below 40% (Figure 4).

Limited preference tests with vegetative kikuyu grass (*Pennisetum clandestinum*) containing either 15 or 90% dry matter, indicated that water content had little effect on preference. However, more extensive studies covering a wide range of dry matter contents showed that water content of a forage has a major effect on preference (Black *et al.*, 1987). Preference for grass containing a range of dry matter contents was determined in tests with grass containing 11, 36 or 95% dry matter. Results of comparisons with grass containing 11 and 36% dry matter are given in Figure 5 and show that sheep select strongly for grass with the higher dry matter content.

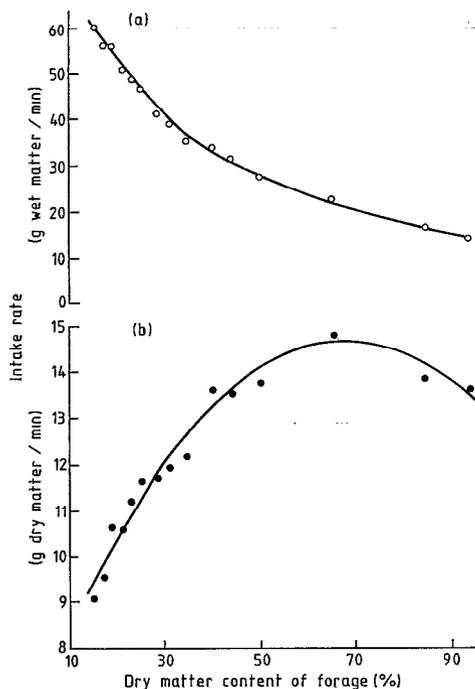


FIG 4 Relationship between dry matter content of kikuyu grass and the intake rate of (a) wet matter and (b) dry matter (from Kenney *et al.*, 1984).

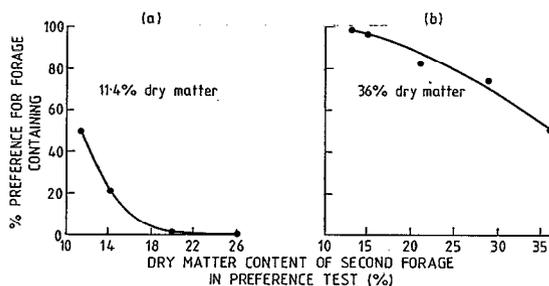


FIG 5 Relationship between preference for a forage containing either (a) 11.4% or (b) 36% dry matter and the same forage with other dry matter contents (from Black *et al.*, 1987).

Similar results were obtained when the water content of dried forage oats was increased by rehydration. These results show that sheep select material with lower

water content when other forage characteristics are identical and that the degree of discrimination for the drier forage decreases as the dry matter content of the forage increases. A 1% increase in dry matter content of forages containing 10, 20, 35 or 95% dry matter was estimated to increase preference by 10, 7, 3 and 0.3%, respectively. Further studies are required to identify the consequences of interactions between water content of a forage and its potential intake rate.

Sward Characteristics

Sward structure can have a major influence on the rate of pasture consumption (Hodgson, 1985; Forbes, 1988). In order to isolate the components of sward structure that determine intake rate and preference, Black and Kenney (1984) constructed a series of artificial pastures in which height and density were varied independently by placing tillers from vegetative ryegrass in holes at different spacings in pressed hardwood sheets. The rate of intake by sheep grazing these pastures increased with both the height and density of pasture and was best described by herbage mass per unit area effectively covered by one bite. Intake rate of dry matter ranged from about 0.5 to 6 g/min and the maximum occurred when pasture availability was a little under 1 t/ha dry matter. However, subsequent studies (Kenney and Black, 1986) showed that both intake rate and the pasture availability at maximum intake rate depended greatly on the distribution of plant material within the pasture horizons. When sheep grazed artificial pastures of vegetative subterranean clover where most plant material was in the lamina at the top of the sward, intake rate was less affected by pasture height than for grass and maximum intake rate approached 27 g/min dry matter when pasture availability was between 2 and 3 t/ha dry matter.

Comparisons between artificial pastures varying in height and density confirmed earlier observations that sheep prefer pastures that can be eaten at a fast rate except for the extremely dense pasture 120 mm high. Further comparisons with artificial pastures have been made to determine the effect on intake rate and preference by sheep of the distribution within a pasture of components that are either strongly preferred or strongly rejected (Black *et al.*, 1989). Pastures were constructed with different proportions and groupings of either se-

nescent or young vegetative Wimmera ryegrass (*Lolium rigidum*) grass material. Sheep selected strongly for the young grass and the rate at which the young grass was eaten declined substantially as the number of tillers in a group decreased and it became more difficult to select (Figure 6).

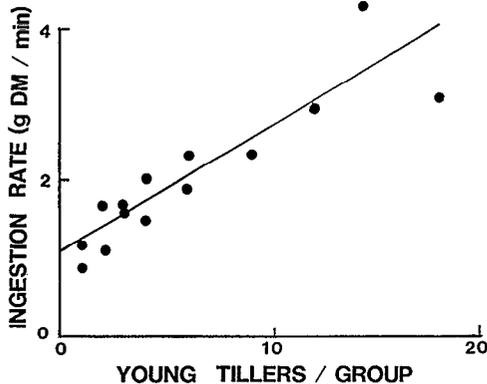


FIG 6 Relationship between ingestion rate of vegetative Wimmera ryegrass and the number of tillers in a group when interspersed with mature, senescent grass tillers (from Black *et al.*, 1989).

In addition, sheep had difficulty discriminating between the components when they were closer than 20 mm from one another. There were some differences between animals; sheep that ate at a slower rate were better able to select the vegetative tillers that were in close proximity to the mature tillers than were fast eaters. Taylor *et al.* (1987) suggested that incisor arcade breadth influences the amount of forage ingested per bite, the minimum distance between components for effective discrimination and maximum eating rate. This could explain largely why cattle are less able to discriminate between forage components than sheep (Forbes and Hodgson, 1985).

AMOUNT OF FORAGE CONSUMED

The amount of feed consumed by grazing ruminants has been estimated by Ulyatt (1984) to account for 50 to 70% of the variation between pastures in their capacity to sustain animal productivity. Intake is closely correlated with both the amount of pasture available per animal per day (pasture allowance, Rattray and Clark,

1984) and the digestibility of the forage selected (Minson, 1982). However, there are large differences in intake between forages and their components when either pasture allowance or digestibility are similar. For example, the intake of white clover by grazing lambs is almost twice that of perennial ryegrass at the same pasture allowance (Rattray and Clark, 1984). Similarly, the intake of legumes offered to penned sheep is greater than grasses with the same digestibility (Demarquilly and Weiss, 1970). There is also a large range in the intake of individual legume and grass species that have the same digestibility (Minson, 1982). The intake of grass leaf is substantially greater than that of stem with the same digestibility (Laredo and Minson, 1973) as is the intake of ground and pelleted forage compared with the same forage when chopped (Minson, 1982). Although intake can be correlated with certain pasture characteristics, this approach accounts for a relatively small amount of the variance between pastures (Minson, 1982) and does not explain the reason for the differences.

There is now strong evidence that the voluntary intake of a grazing ruminant may be limited by (i) the potential of the animal to use nutrients, (ii) the amount of digesta that can accumulate in the reticulo-rumen (hereafter called the rumen), (iii) the rate of removal of digesta from the rumen through digestion and outflow to the lower gut, and (iv) the time available for eating and ruminating activities (Black, 1984; Weston, 1985). The actual intake of an animal depends on its genotype and physiological state and the pasture components selected during grazing.

Potential to Use Nutrients

The upper limit to feed intake by ruminants is thought to be determined by the amount of energy required for biochemical reactions that fully satisfy the potential for all body functions including the maintenance of body temperature (Weston, 1982; Black, 1984; Weston and Poppi, 1987). It is likely that intake is ultimately controlled by "set points" in the feeding and satiety centres of the hypothalamus where peripheral and central nervous system signals are integrated and appropriate responses for either feeding or the cessation of feeding are generated (Della-Fera and Baile, 1984). Although the frequency and duration of eating periods by rumi-

nants can be altered substantially through various stimuli and management procedures, intake over a longer term for animals under optimal conditions appears to be controlled by the capacity of the animal to utilise energy (Weston and Poppi, 1987). Thus, maximum feed intake in growing animals differs between species, strain, sex and stage of maturity and is a summation of the energy needed for the net deposition of compounds in the body and integument, and for the animal's maintenance requirements. Consequently, feed intake is greater in fast growing than in slow growing animals (Black, 1984). During pregnancy and lactation feed intake generally increases, but often not to the extent expected by the increase in energy demand associated with the growth of conceptus and milk synthesis. Weston and Poppi (1987) postulate that this is because hormonal changes occurring in the animal during these physiological processes result in a reduced capacity for adipose tissue synthesis and an increased rate of lipolysis causing a depression in the energy requirement for potential body tissue deposition.

There is evidence that feed intake is depressed when the capacity of the animal to metabolise nutrients is reduced. Deficiencies of essential nutrients including amino acids, minerals and vitamins in the diet are consistently associated with sub-optimal feed intake because they reduce the rate at which the body can use energy (Black, 1984). Deficiencies in availability to the animal of either amino acids or minerals are likely to limit the feed intake of ruminants grazing pastures in many situations.

Limits to intake due to gastro-intestinal tract capacity

The feed intake required to satisfy total energy demand of grazing ruminants commonly may not be reached because of limitations due to gastro-intestinal tract capacity. Grovum (1987) presents evidence suggesting that this limit is in the capacity of the reticulum and rumen and not the intestines or abomasum. Thus, when the rumen limits feed intake, either dietary or animal factors that alter the amount of material that can accumulate in the rumen or its rate of disappearance from the rumen will affect voluntary feed intake. The magnitude of the effect of these factors on voluntary feed intake is difficult to determine experimentally, but Black *et al.*

(1982b), using computer simulation techniques, showed that changes to the intake of sheep were particularly sensitive to the fractional outflow rate from the rumen of structural carbohydrate, its potential degradability within the rumen and to the amount of organic matter accumulation in the rumen (Table 2).

TABLE 2 Predicted effect on voluntary feed intake by a 40 kg sheep given ryegrass of a 10% increase in several components known to affect feed intake when it is limited by rumen capacity.

Component changed by 10%	Predicted increase ^a in feed intake (g/d)
Fractional outflow rate of plant fibre	70
Potential degradability of plant fibre	65
Limit to accumulation of material in rumen	40
Proportion of fibre in forage	8
Rate of degradation of plant fibre	7
Fractional outflow rate of water	5

^a Basal intake was 1298 g/d dry matter. Adapted from Black *et al.* (1982b).

Intake appeared to be less sensitive to the fractional rate of digestion and the fractional rate of outflow from the rumen of water and solutes.

Upper limit to rumen digesta load

It is probable that the upper limit to rumen digesta load is affected by the live weight, genotype and physiological state of an animal. Black (1984) postulated that the maximum rumen digesta load of sheep increased with body weight in a pattern similar to that for changes in rumen weight with the highest value occurring at about 50 kg body weight. However, no experiments have been conducted to define this relationship in different genotypes. Weston (1982) and Weston and Cattle (1982) observed that rumen digesta load was lower during pregnancy and higher during lactation and in weaners than in adult wethers. From these results,

Weston (1985) suggested that rumen digesta load was positively related to the difference between the capacity of the animal to use energy and the energy supplied from the diet; that is, the energy deficit of the animal. These conclusions were confirmed by Gherardi and Black (1989) who showed that rumen organic matter content in 30 kg lambs fed a poor quality wheaten hay decreased linearly as the amount of energy available to the animals was increased by infusing a balanced mixture of nutrients into the abomasum (Figure 7).

matter (OM) per unit digesta free body weight (EBW) (from Gherardi and Black, 1989).

Thus, animals in poor condition, which have a higher energy demand than animals in good condition, eat more of a forage largely because of an increase in the amount of digesta accumulated in the rumen (Djajanegara and Doyle, 1989).

The amount of digesta that can accumulate in the rumen is also affected by the packing density of the forage. Plant materials that contain large quantities of cell wall constituents tend to accumulate less material in a given space (Van Soest, 1975), whereas the grinding and pelleting of the stem fraction of forage is associated with a three-fold increase in settling volume when dry (Laredo and Minson, 1975). Similarly, the treatment of cereal straw with alkali has been shown to increase by 40% the amount of dry matter accumulating in the rumen of sheep fed ad libitum (Dunlop, 1984). There is also evidence that the leaf fraction of grass has a higher packing density than the stem fraction (Laredo and Minson, 1975) and that legumes pack more densely than grasses (Thornton and Minson, 1973). Gherardi (1989) showed that rumen digesta load in sheep is strongly associated with the concentration of organic matter in rumen digesta.

Weston (1985) suggested that palatability of a forage also affects rumen digesta load, but recent experiments (Gherardi *et al.*, 1990), in which the prefer-

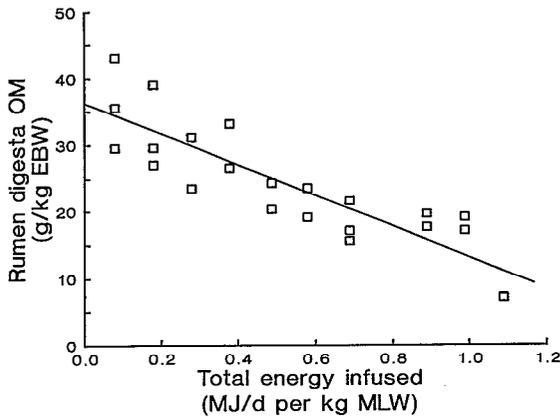


FIG 7 Effect of energy infused into the abomasum per unit metabolic live weight ($\text{kg}^{0.75}$, MLW) on the content of rumen organic

TABLE 3 Relative contribution of digestion, eating and rumination to dry matter (DM) clearance from the rumen of sheep fed three fresh forages and two hays at 950 g/d.

	Perennial ryegrass	Red clover	Lucerne	Lucerne hay	Meadow hay
Rumen DM pool (g)	387	341	264	554	530
DM digested (g/d)	569	586	525	352	468
DM outflow (g/d)	381	364	427	594	475
Contribution of eating to outflow (g DM/d)	189	184	200	208	129
Contribution of rumination to outflow (g DM/d)	192	180	227	386	346
DM fractional clearance rates (d^{-1})					
digestion	1.47	1.72	1.99	0.64	0.88
outflow	0.99	1.07	1.62	1.08	0.89
eating	0.49	0.54	0.76	0.38	0.24
rumination	0.50	0.53	0.86	0.70	0.65

Weston and Davis, 1986; Doyle, 1988). Interpretation of these studies could be confounded by other dietary or animal factors. In many cases, different forages were compared so that the differences in intake are just as likely to be the result of differences in factors that are known to affect voluntary feed intake such as organic matter digestibility, rates of outflow from the rumen or packing density of digesta in the rumen. Other studies with intra-ruminal feeding techniques are unable to account for the possibility that a low intake rate of the forage presumed to be unpalatable was due to insufficient time for ingestive and ruminating activities.

The effect of palatability per se on long-term intake has been studied in our laboratory by using a single forage and altering its acceptability through the addition of chemicals that have minimal effect on rumen function or animal metabolism (Gherardi, 1989; Gherardi and Black, 1990; Gherardi *et al.*, 1990). The addition of chemicals that either increase or decrease the preference for the forage was shown to have little effect on feed intake when either the treated or control diets were fed alone. However, when sheep were given a choice between treated and untreated forage over several weeks there was strong preference for the more palatable forage. These results suggest that the intake of a forage is little affected by palatability per se when only one feed is available but, when there is a choice between forage components with equal accessibility, sheep will eat a greater proportion of the more palatable material.

MODIFICATION OF CONSUMED NUTRIENTS BY RUMEN MICRO-ORGANISMS

Rumen microbes are necessary for the breakdown of plant structural carbohydrates, but they result in a less efficient use of many other dietary constituents than in simple stomached animals. Carbohydrates, proteins, pectins and organic acids in the forage consumed are converted to volatile fatty acids (VFA), which are the main energy source for the ruminant animal, carbon dioxide and methane with the loss of heat. From 10 to 15% of the energy from feed digested in the rumen is lost as methane and heat (Black, 1971). The relative proportions of the different VFAs produced vary widely depending on the chemical components degraded and

the pH within the rumen (Murphy *et al.*, 1982). Higher proportions of propionate are produced from the degradation of hemicellulose than cellulose, whereas the degradation of plant starch and sugars tends to produce VFA patterns high in both propionate and acetate and low in butyrate. In contrast, the degradation of cereal starch produces high concentrations of propionate. Thus, acetate production tends to be higher with forage than with concentrate diets. Typical molar proportions of VFAs produced when animals consume forage diets are 73:20:7 (acetate:propionate:butyrate) compared with 60:30:10 for forage-concentrate mixtures (Sutton and Morant, 1978). With sheep fed solely grain diets, VFA proportions of 50:40:10 have been observed (Judson *et al.*, 1968). The proportions of VFA produced also vary with the forage species eaten and its stage of maturity. Milford and Minson (1965) observed higher proportions of acetate and lower proportions of propionate in the rumens of sheep fed cocksfoot (*Dactylus glomerata*) compared with perennial ryegrass. Similarly, the rumen of sheep fed clovers tends to yield lower proportions of acetate and higher proportions of propionate than when grasses are eaten; Johns (1962) measured VFA molar proportions of 74:21:5 in sheep consuming short rotation ryegrass and 62:25:12 in sheep eating a perennial ryegrass-white clover mixture. Because the synthesis of propionate utilises hydrogen, less methane is produced and more digested energy is available to the animal when the propionate proportion is high as is observed when sheep eat clovers (Graham, 1969).

The amino acids available to ruminants for metabolism often bear little relation to those eaten. Protein flow to the intestine is of both dietary and microbial origin and the amount depends on the extent to which dietary protein is degraded and on the growth and outflow from the rumen of micro-organisms (Faichney and Black, 1979). With proteins that are rapidly and extensively degraded in the rumen, little dietary amino acid is absorbed from the intestine, whereas with other proteins less susceptible to microbial attack, significant proportions of dietary amino acid can be absorbed (Barry and Manley, 1984). The extent and rate of breakdown of forage protein are highly variable and depend on the nature of the protein, the plant tannin content and whether the protein is associated with structural carbohydrates in the cell walls. The procedure described by Gordon *et al.* (1987) indicates that the potential degradability of protein in

mass, species and pH within the rumen, by nutrients limiting the growth of the rumen microbial population and by the outflow rate of microbes from the rumen (Beever *et al.*, 1980-81).

Potential degradability within the rumen of plant fibre and protein affects the amount likely to remain in the rumen that has to be removed by outflow alone. The potential degradability of plant cell wall constituents ranges at least from 39 to 92% (Smith *et al.*, 1972). Black *et al.* (1982b) predicted that a difference of this magnitude would reduce the intake of perennial ryegrass by about 45%. The decline in potential degradability is normally associated with increasing fibre content and maturity of a forage. There is evidence that the potential degradability of structural carbohydrate in leaves is higher than that in stems with similar fibre concentrations (Poppi *et al.*, 1981), and that legumes have lower values than grasses (Smith *et al.*, 1972).

Relative importance of digestion, eating and ruminating: Presented in Table 3 is an estimate of the relative importance of digestion, eating and ruminating to the removal of dry matter from the rumen of sheep fed three fresh forages and two hays calculated from the results of Ulyatt *et al.* (1986) by Gherardi (1989). For the fresh forages, digestion contributed significantly more than outflow to the fractional rate of dry matter removal from the rumen, because of the high proportion of solubles released following comminution of the forage during eating. By contrast, outflow was more important than digestion for lucerne hay, whereas both processes were equally important for meadow hay. The relative contribution of eating and ruminating to outflow was similar for the fresh forages, but ruminating contributed two to three-times more to outflow with the hays.

Time for Eating and Ruminating Activities

The intake of pasture may be limited by the time available for eating and ruminating when the rate of dry matter intake is low. Sheep generally spend from 6 to 10 hours a day grazing, but the actual duration depends on pasture availability, day length and ambient temperature (Arnold, 1981). Even under conditions of severe pasture shortage, sheep and cattle rarely graze for more than 13 and 15 hours per day, respectively

(Arnold, 1981). Several different factors can cause the rate of forage intake to be so low that neither the animal's potential to utilise nutrients nor its rumen capacity are satisfied. These include pastures with low availability or herbage allowance, mature forages that are difficult to eat and young pastures high in water content. Black and Kenney (1984) measured over short periods of time the intake rate of vegetative ryegrass from artificially constructed pastures and found that it changed from 6 to less than 1 g/min dry matter as pasture availability decreased from around 1 t/ha to 0.1 t/ha. Thus, even when non-eating periods are not accounted for, the maximum intake of sheep eating at a rate of 1 g/min would be only 780 g/d. This is substantially less than the 1142 g/d dry matter reported by Ulyatt (1971) for young Romney Marsh wethers. Gherardi (1989) showed that the intake rate of chopped forage measured over short periods was three to four-fold greater than the mean intake rate during eating periods over a whole day. Curl and Davidson (1983) have reported feed intakes as low as 0.46 g dry matter/min for sheep grazing sparse pasture. Similarly, feed intake has been shown to be closely related to pasture allowance in New Zealand grazing systems (Ratray and Clark, 1984).

There is also evidence that the intake of pasture with high water content is limited by the rate of dry matter intake and not rumen capacity. John and Ulyatt (1987) found that the intake of wet forage changed little as the dry matter content increased from 12 to 25%, but the intake of dry matter increased linearly. The presence of a balloon containing 1.5 l water in the rumen did not alter the intake of forage high in water content, suggesting that the limit to intake was not due to feedback from excessive bulk in the rumen.

Effect of Forage Palatability on Feed Intake

Results from studies examining the effect of palatability of forage on long-term intake are equivocal (Greenhalgh and Reid, 1971; Minson and Bray, 1986; Weston and Davis, 1986; Burns *et al.*, 1987; Doyle, 1988). In some studies, little relationship was observed between preference for a forage and intake (Minson and Bray, 1986; Burns *et al.*, 1987), whereas in others, palatability was inferred to be responsible for observed differences in intake (Greenhalgh and Reid, 1971;

ence for a single forage was changed by adding chemicals that either increase or decrease preference, showed that rumen digesta load of sheep fed ad libitum was unaffected by forage palatability.

Rate of removal of digesta from the rumen

Material can be removed from the rumen both by outflow to the lower gut and by digestion. The component of digesta most limiting the intake of pasture and forages by ruminants is structural carbohydrate.

Outflow of digesta: Flow of material from the rumen is determined by the frequency and amplitude of rumen contractions and the size and density of particles within the rumen (Kennedy and Murphy, 1988). Many stimuli increase rumen motility including the physical properties of the diet, the degree of rumen distention, osmolality of rumen digesta, physiological state of the animal and climatic stress (Kennedy and Murphy, 1988). Increasing the amount of fibre in a diet generally results in a faster rate of passage from the rumen (Warner, 1981). This may be due to direct stimulation of the rumen wall affecting motility or it could be associated with increased salivary flow resulting from longer eating and ruminating times and the effect of increased osmolality on the outflow rate of solutes (Harrison *et al.*, 1975).

There are large differences between forages and their components in the rate of outflow of structural carbohydrate from the rumen. For example, the fractional outflow rate of lignin in the leaves of tropical grasses was 20% higher than for the stems (Poppi *et al.*, 1981) and that of the leaves of tropical legumes 44% higher than for stems (Hendricksen *et al.*, 1981). Similarly, Moseley (1981) observed that the passage of particulate matter during the first three hours after feeding was faster when sheep were given white clover than when they were fed perennial ryegrass.

The rate of outflow of structural carbohydrates depends primarily on the rate of breakdown of particles to sizes that have a high probability of passage through the reticulo-omasal orifice (Egan and Doyle, 1984; Poppi *et al.*, 1985) and on its density (Kennedy and Murphy, 1988). In the studies both of Hendricksen *et al.* (1981) and Moseley (1981), the material flowing faster from the rumen was observed to be broken down to smaller particles during eating. It is likely that the

morphological structure of plants differs in such a way as to cause differences in tensile and shearing strength (Evans, 1967)

The effectiveness of eating, as measured by the proportion of large feed particles reduced to small particles that will pass through a sieve with a pore size of 1 mm, varies widely between feeds and animals (Lee and Pearce, 1984; Ulyatt *et al.*, 1986). It is greater for leaves than stems, for legumes than grasses and for fresh forage than hays. There are also substantial differences between individual grass species. Ulyatt (1985) found that individual sheep with slow eating rates were more effective in reducing particle size than were fast eaters.

Rate and extent of digestion: The rate of digestion of a forage and the potential degradability within the rumen of its components can have a considerable effect on feed intake. Because soluble carbohydrates are degraded by rumen micro-organisms about 150 times faster and storage carbohydrates about five times faster than structural carbohydrates (Maeng and Baldwin, 1976), the relative proportions of these constituents in a plant can affect its rate of removal from the rumen and its intake. For example, Black *et al.* (1982b) predicted that approximately 5% of the difference in feed intake between sheep eating white clover and perennial ryegrass could be attributed to differences in the chemical composition assuming the rate of fibre digestion was the same. However, the rate of digestion of cell wall constituents has been observed to vary by as much as eight-fold across plant materials, although variations of three- to four-fold are more common within a species as it matures (Smith *et al.*, 1972). A three-fold change in the rate of degradation of structural carbohydrate in ryegrass was predicted to alter voluntary feed intake by 15% (Black *et al.*, 1982b). The results of Smith *et al.* (1972) also indicate that the rate of cell wall digestion in legumes is greater than that of grasses but, with both forage classes, the rate of digestion was positively related to the soluble dry matter content of the plant. Despite the observations of Smith *et al.* (1972), differences have not been shown in the rate of structural carbohydrate digestion between leaf and stem fractions of tropical grasses and legumes (Poppi *et al.*, 1981; Hendricksen *et al.*, 1981). The rate of digestion of forage components is also affected by the microbial

both perennial ryegrass and white clover is similar after prolonged incubation in rumen fluid, but the rate of degradation is much slower for clover (Figure 8).

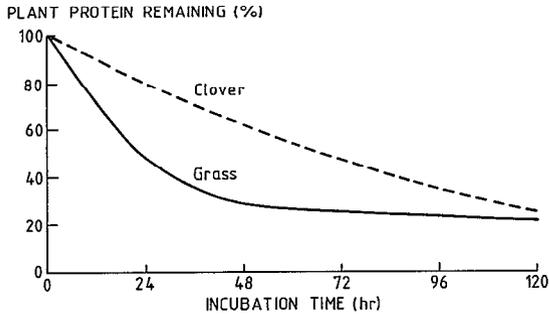


FIG 8 Degradation of plant protein in ryegrass and white clover following an *in vitro* incubation with rumen fluid. The plant material was in a young vegetative state, frozen within one minute of harvest to -20°C and freeze dried. Plant protein remaining was determined by the method of Gordon *et al.*, (1987).

This would allow more protein to flow from the rumen intact for sheep eating white clover than ryegrass as was observed by MacRae and Ulyatt (1974). Jarrige (1989) summarises estimates for the degradability of protein in feeds measured by placing samples in nylon bags and incubating them within the rumen for 48 hours; values for some feeds are given in Table 4.

This summary confirms that there is little difference between many temperate grasses and legumes in potential protein degradability when in a vegetative state. However, potential degradability declines in more mature forage cured as hay and in some forms of silage made from mature plant material. There was a substantial range in potential degradability for cereal grains, with low values for the tannin-containing sorghum, and for oilseeds with low values in extruded meals.

Condensed tannins that are found in some plants such as *Lotus* species and sainfoin (*Onobrychis viciifolia*) bind with plant proteins during mastication and reduce their degradation by rumen micro-organisms. A strong positive correlation has been observed between the tannin content of these plants and the proportion of dietary protein digested post-ruminally (Barry and Manley, 1984). Condensed tannins vary in molecular weight from 7,700 for *Lotus pedunculatus* to

22,000 for sainfoin. The low molecular weight tannins precipitate plant protein but also inactivate bacterial enzymes in the rumen, whereas the high molecular weight molecules precipitate plant proteins but do not affect microbial enzymes. Because of the effect on microbial enzymes, the low molecular weight tannins reduce the digestion of cellulose and hemicellulose (Barry and Manley, 1984) and reduce feed intake (Barry and Duncan, 1984).

TABLE 4 Mean values for the potential degradability of crude protein measured by suspending the feed in nylon bags in the rumen of cattle for 48 hours (after Jarrige, 1989).

Feed	Potential degradability (g/g)
Fresh Forage	
Grasses	0.73
Legumes	0.73
Roughages	
Grasses	0.66
Legumes	0.66
Straws	0.60
Silages	
Grasses	0.78
Legumes	0.78
Maize, whole plant	0.72
Maize, ears	0.55
Cereal grains	
Oats	0.78
Maize	0.42
Barley	0.74
Sorghum	0.40
Oil Seeds	
Rapeseed	0.90
Linseed	0.80
Pea	0.90
Soyabean, extruded	0.49

The amount of microbial protein flowing to the intestine depends on the availability for microbial growth of energy as adenosine triphosphate derived from the degradation of substrates in the rumen and on the supply of ammonia and sulphur. The efficiency of microbial protein supply may be reduced when large numbers of protozoa are present in the rumen because

of they can engulf and digest bacteria and recycle protein within the rumen pool with a net loss of amino acids (Bird and Leng, 1984). The relative proportions of amino acids in the major species of rumen bacteria and protozoa are similar and are little affected by the diet eaten (Purser and Buechler, 1966; Chamberlain *et al.*, 1986).

Because soluble carbohydrates are rapidly degraded by rumen micro-organisms, virtually no glucose is absorbed by ruminants eating forage diets (Huntington, 1984). However, when some concentrates high in starch, particularly maize starch, are eaten, substantial amounts of glucose may be absorbed (Tucker *et al.*, 1968).

Lipids generally constitute from 3 to 10% of plant dry matter. They are hydrolysed in the rumen where the fatty acids are saturated. Microbes contain up to 15% lipid so that the amount of lipid absorbed by sheep can be greater than the amount eaten (Outen *et al.*, 1974). In addition, rumen microbes synthesise many of the water-soluble vitamins required by the host animal.

EFFICIENCY OF NUTRIENT UTILISATION

Utilisation of Energy-Yielding Nutrients

The efficiency of utilisation of metabolisable energy for growth and fattening (k_f) in ruminants is commonly well below that observed in non-ruminants and varies from less than 0.2 to over 0.7 (Agricultural Research Council, 1980). It is negatively related to the metabolizability (metabolizable energy/gross energy) and fibre content of the diet. However, even with forages having similar metabolizability, values of 0.44 and 0.33 have been observed for spring and autumn cuts of the same grass (Corbett *et al.*, 1966) and of 0.51 and 0.33 for white clover and perennial ryegrass (Rattray and Joyce, 1974).

The consequences on animal performance of varying k_f of a diet from 0.23 to 0.46 are illustrated in Table 5 for a 20 kg weaner lamb eating 1000 g/d dry matter from white clover using the simulation model described by Black (1984). Clearly, variation in k_f of the magnitude commonly observed has a major effect on animal productivity. The variation in k_f between diets results from differences in the particular nutrients metabolised and the energetic efficiency of the compet-

ing biochemical pathways.

TABLE 5 Predicted effect on animal performance of changing k_f from 0.23 to 0.46 in a 20 kg weaner sheep eating 1000 g/d white clover.

k_f	0.23	0.35	0.46
Liveweight gain (g/d)	180	245	335
Fat deposition (g/d)	48	73	98
Protein deposition (g/d)	23	33	42

Blaxter (1962) attempted to explain the negative relationship between k_f and the fibre content of diets through the greater proportional production of acetate and its less efficient use by the animal. However, Tyrrell *et al.*, (1979) found that the efficiency of acetate utilisation depended upon the basal diet fed. Higher efficiencies resulted when acetate was infused into the rumen of cattle eating hay and concentrates than cattle eating only hay. MacRae and Lobley (1982) suggested that the efficiency of acetate utilisation is influenced by the production of the co-factor NADPH₂ which is needed for the biosynthesis of fatty acids from acetate. They argued that, when the supply of glucose or its precursors, propionate and amino acids, was insufficient to produce the NADPH₂ required for this reaction as would occur with animals fed forage diets, energy was lost as heat through inefficient substrate cycles. Limited experimental evidence supports this contention. A computer model that simulates the metabolism of absorbed nutrients in sheep also indicates that this explanation is tenable (Black *et al.*, 1987a). Investigations with this model of variations in the pattern of absorbed nutrients and in the proportion of energy deposited in the body as either protein or fat, indicate that the efficiency of utilization of absorbed energy is a function of both the biochemical efficiency of utilization of absorbed nutrients for specific body functions and the inefficient use of adenosine triphosphate through substrate cycles when its concentration rises to unphysiological levels, such as occurs when the utilisation of acetate is inhibited by inadequate NADPH₂ supply.

Absorbed lipid was predicted to be used with the highest efficiency, varying from 0.69 to 0.74, de-

pending on the ratio of other nutrients (Black *et al.*, 1987b). These values are similar to experimental observations that range from 0.61 to 0.84 (Czerskanski *et al.*, 1966; Garrett *et al.*, 1976). Amino acids were predicted to be used with an efficiency of from 0.24 to 0.47 depending largely on the proportion that was either incorporated into body protein or catabolized. Additional acetate was predicted to be used with an efficiency of 0.57 to 0.70 depending on the supply of other nutrients when NADPH_2 was not limiting the conversion of acetyl-CoA to fatty acids. Tyrrell *et al.* (1979) measured an efficiency of 0.69 in cattle fed hay and concentrates. However, when NADPH_2 was predicted to be limiting acetate utilization, the k_f of additional acetate was predicted to be as low as 0.16 which is comparable with 0.10 observed by Hovell *et al.* (1976). This value was predicted to increase substantially when the proportion of energy derived from propionate, glucose or amino acids was increased (Black *et al.*, 1987a).

When the effects of increasing energy absorption from whole diets was simulated, the ratio of VFA and glucose had little effect on k_f for intakes near maintenance with predicted values ranging from 0.61 to 0.64. However, the k_f at higher intakes declined from 0.55 for a diet providing VFAs in the proportion 60:30:10 (acetate:propionate:butyrate) and 10% of the absorbed energy as glucose to 0.32 when VFA were in the proportions 73:20:7 and 1% of the absorbed energy was from glucose. These predictions indicate that the efficiency of utilization of energy from some forages, when consumed at high rates, may be limited by the availability of NADPH_2 . Hence an increase in the absorption of glucose and other soluble carbohydrates, propionate or amino acids may result in an improved efficiency of energy utilisation of ruminants grazing poorer quality forages.

The investigations using the simulation model indicate that the efficiency of utilisation of absorbed energy by ruminants is a function of both the biochemical efficiency of utilisation of absorbed nutrients for specific body functions and the inefficient use of adenosine triphosphate through substrate cycles such as the acetate - acetyl-CoA cycle when the utilisation of acetate is limited by insufficient NADPH_2 . Collation of the predictions from all simulations (Figure 9) shows a strong negative dependence of k_f on adenosine triphosphate utilisation through the degradation path-

way. Apart from the low values associated with amino acid supplementation of protein deficient diets, all values less than 0.5 were associated with a flux of at least 1 mole/d through the degradation pathway.

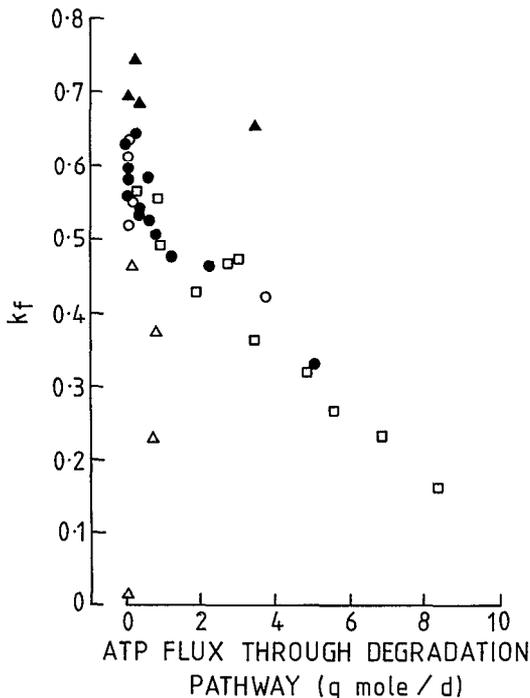


FIG 9 Relationship between predicted k_f and mean degradation of adenosine triphosphate through substrate cycles for a variety of conditions; o, variation in propensity for protein synthesis; •, variation in protein glucose and lipid content of absorbed nutrients; Δ , supplements of amino acids; \blacktriangle , supplements of lipid; \square , supplements of acetate. (from Black *et al.*, 1987b).

Utilization of Protein and Amino Acids

The efficiency of utilisation of absorbed amino acids depends on the amount absorbed in relation to the energy available to the animal, and on the match between the proportions of amino acid absorbed and those required for all body functions. There appears to be a wide range of pasture situations where animal performance is limited because of insufficient amino acids absorbed relative to the energy available. Improvements in animal performance have been observed with increased absorption of protein or amino acids in young sheep eating a variety of grass-based pastures in their

vegetative state (Black *et al.*, 1979; Barry, 1981; Poppi *et al.*, 1988) or mature annual pasture (Black and Mulholland, 1983), in pregnant (Barry and Manley, 1985) and lactating sheep (Dove *et al.*, 1985), in beef cattle eating tropical grasses (Hennessy, 1981) and in dairy cows either grazing temperate pastures (Rogers *et al.*, 1980) or eating pasture based silage (Rogers *et al.*, 1979).

Black *et al.* (1976) suggested that approximately half of the difference in performance between lambs eating either white clover or perennial ryegrass could be attributed to a difference in amino acid absorption with the more rapid microbial degradation of grass proteins resulting in insufficient amino acid supply despite the grass containing over 20% crude protein. This explanation for inadequate amino acid absorption contrasts with that occurring when young sheep graze mature annual pastures. Computer predictions for young sheep grazing summer pastures in Southern Australia suggest that insufficient dietary inorganic sulphur limited microbial growth in the rumen and, with only 6% true protein in the forage, total amino acid flow from the rumen was insufficient to maximize body growth for the energy available from the consumed forage (Black and Mulholland, 1983).

The performance of grazing animals can be improved sometimes by the supply of a single amino acid, a clear example being the response in wool growth to sulphur-containing amino acids (Langlands, 1970; Reis, 1979). The molar proportions of absorbed amino acids required by an animal depend on the relative contributions of different body functions to total amino acid needs. By comparing the molar proportions of essential amino acids and the combinations of cystine plus methionine and of tyrosine plus phenylalanine absorbed from different diets with requirements for different body functions it is possible to predict the probable maximum efficiency of absorbed protein use and the order in which amino acids are limiting. Predictions of this type suggest that the maximum efficiency of amino acid use for a sheep maintaining weight while consuming ryegrass would be around 0.5 with the order of the first four limiting amino acids being cystine plus methionine, threonine, leucine and lysine (Black *et al.*, 1982a). However, if the animal were to grow at a rate of 400 g/d, the efficiency of amino acid use would increase to 0.82 with lysine and then the sulphur-

containing amino acids, threonine and histidine being the first to fourth most limiting amino acids. Storm and Ørskov (1984) estimated from experiments that the limiting order of amino acids in microbial protein for the growth of Suffolk-cross lambs was methionine, lysine, arginine and histidine. For lactating ewes consuming ryegrass, the maximum efficiency of absorbed protein use was predicted to range from 0.82 to 0.88 depending on amount of milk produced and the limiting order of amino acids was leucine, lysine, histidine and valine (Black *et al.*, 1982a). Isoleucine, lysine and valine have been estimated to be the first limiting amino acids for dairy cattle (Oldham, 1981).

A deficiency in protein supply is most likely to occur in ruminants grazing grass-based pastures when growth rates are high, particularly with sheep, during lactation, in animals with high wool growth potentials and when body protein loss is enhanced during severe infestation with internal parasites. Studies by MacRae *et al.* (1982) indicate that energy expenditure is affected little by internal parasites, but severe infestation with *Trichostrongylus colubriformis* resulted in over 20 g/d extra protein loss in the form of sloughed cells and mucins passing to the ileum (Poppi *et al.*, 1986).

IMPROVING THE PERFORMANCE OF GRAZING RUMINANTS

It is clear from the above discussion that a great deal is known about many of the factors that limit the performance of grazing ruminants. Each of the improvements to the nutritional value of pasture plants mentioned in the introduction to this paper, including supplements of protein, urea and minerals, grinding and pelleting or alkali treatment of forage, and the replacement of grass with legumes or the provision of a more leafy pasture, can be explained by one or more of the factors described. Thus, available knowledge provides enormous scope for adopting management procedures that should improve the performance of animals in particular situations.

Role of Computer Simulation Models

It is clear also that the amounts and relative proportions of nutrients absorbed by different classes of animal grazing the same pasture can vary and that the nutrient requirements of these animal differ depending on their

genotype, physiological state and environmental factors such as the weather and parasite burden. Thus, a management strategy that will improve performance in one situation may not work in another. For a producer to assess whether an economic advantage can be achieved through adopting a new procedure, he must know for the particular situation the factors limiting animal performance, the pattern of response to a change in these factors and the methods for making these changes. The complexity of the interactions between the animal, its physiological state, the pasture and the weather makes it extremely difficult for the human mind alone to assess, for any specific situation, the actual factors limiting animal performance and the most appropriate strategy for improving productivity. However, by integrating the fundamental concepts and knowledge about ruminant nutrition and physiology that has been generated over decades of research into computer programs that simulate animal function, it will be possible to improve the precision of the decision making process (Black *et al.*, 1990). Already such programs have given valuable insights into ways of improving animal productivity through changed management practices (Black *et al.*, 1979; Black and Bottomley, 1980; Black and Mulholland, 1983) and through identifying plant characteristics that could be changed to improve their nutritional value (Black, 1987).

Before computer programs are widely adopted by producers and their advisors, they must be easy to use and cover adequately the major components of an enterprise that determine profitability. Development of such a computer system is a major task and requires effective co-ordination between experts from different fields and dedication by both the scientists involved and the research funding organisations. Although the enormous amount of research that has gone into understanding the physiological processes of grazing animals and their interactions with pastures allows the development of effective simulation models, the principles derived cannot be applied satisfactorily in industry unless the situations being simulated are accurately described. Currently, much of the information needed is unavailable. A major challenge for both animal scientists and managers of production enterprises is to obtain satisfactory descriptions of the chemical and physical characteristics of pasture plants and their components, of the growth and production characteristics of both pastures

and different strains and sexes of animals, and of other climate and environmental conditions that affect productivity. For example, less than 1% of the analyses of animal feed collated by the Australian Feed Information Centre contained all the information required to predict rumen function and amino acid absorption. Research is currently being undertaken to describe these characteristics for feeds consumed by ruminants in Australia. Until all the characteristics of pastures that affect animal productivity are described for each forage eaten by grazing ruminants, current knowledge of the principles discussed in this paper cannot be effectively applied. Unfortunately, collection of such data is regarded as unattractive by many research scientists and funding organisations, but it is essential for the effective application of much existing knowledge.

REFERENCES

- Agricultural Research Council. 1980. *The Nutrient Requirements of Ruminants*. Commonwealth Agricultural Bureaux, Farnham Royal.
- Arnold, G.W. 1966. The special senses in grazing animals. II. Smell, taste and touch and dietary habits in sheep. *Australian Journal of Agricultural Research* 17: 531-542.
- Arnold G.W. 1981. Grazing behaviour. In: *Grazing Animals*. World Animal Science B1. Ed. F.H.W. Morley, Elsevier, Amsterdam, pp. 79-104.
- Arnold G.W.; de Boer E.S.; Boundy C.A.P. 1980. The influence of odour and taste on the food preferences and food intake of sheep. *Australian Journal of Agricultural Research*. 31: 571-587.
- Barry T.N. 1981. Protein metabolism in growing lambs fed on fresh ryegrass (*Lolium perenne*) - clover (*Trifolium repens*) pasture *ad lib*. 1. Protein and energy deposition in response to abomasal infusion of casein and methionine. *British Journal of Nutrition*. 46: 521-532.
- Barry T.N.; Duncan S.J. 1984. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 1. Voluntary intake. *British Journal of Nutrition* 51: 485-491.
- Barry T.N.; Manley T.R. 1984. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 2. Quantitative digestion of carbohydrates and proteins. *British Journal of Nutrition* 51: 493-504.
- Barry T.N.; Manley T.R. 1985. Glucose and protein metabolism during late pregnancy in triplet-bearing ewes given fresh forages *ad lib*. 1. Voluntary intake and birth weight. *British Journal of Nutrition* 54: 521-533.
- Barthram G.T.; Grant S.A. 1984. Defoliation of ryegrass-dominated swards by sheep. *Grass and Forage Science* 39: 211-219.
- Beever D.E.; Black J.L.; Faichney G.J. 1980-81. Simulation of the effects of rumen function on the flow of nutrients from the stomach of sheep: Part 2 - Assessment of computer predictions. *Agricultural Systems* 6: 221-241.

- Bird S.H.; Leng. R.A. 1984. Further studies on the effect of the presence or absence of protozoa in the rumen on live-weight gain and wool growth of sheep. *British Journal of Nutrition* 52: 607-611.
- Black J.L. 1971. A theoretical consideration of the effect of preventing rumen fermentation on the efficiency of utilization of dietary energy and protein in lambs. *British Journal of Nutrition* 25: 31-55.
- Black J.L. 1984. The integration of data for predicting feed intake, nutrient requirements and animal performance. In: *Herbivore Nutrition in the Subtropics and Tropics*. Eds. F.M.C. Gilchrist and R.I. Mackie, Science Press, Craighall, South Africa, pp. 648-671.
- Black J.L. 1987. Nutritional criteria for forage nutritive value. In: *Improving the Nutritive Value of Forage*. Ed. K.J. Hutchinson. Standing Committee on Agriculture, Canberra, *Technical Report Series* 20: 29-43.
- Black J.L.; Bottomley. G.A. 1980. Effects of shearing and lambing dates on the predicted pasture requirements of sheep in two Tasmanian locations. *Australian Journal of Experimental Agriculture and Animal Husbandry* 20: 654-661.
- Black J.L.; Colebrook W.F.; Gherardi S.G.; Kenney P.A. 1989. Diet selection and the effect of palatability on voluntary feed intake by sheep. *Proceedings of the Minnesota Nutrition Conference*. 50: 139-151.
- Black J.L.; Dawe S.T.; Colebrook W.F.; James K.J. 1979. Protein deficiency in young lambs grazing irrigated summer pasture. *Proceedings of the Nutrition Society of Australia* 4: 126.
- Black J.L.; Faichney G.J.; Beever D.E.; Howarth B.R. 1982a. Alternative systems for assessing the nitrogen value of feeds for ruminants. In: *Forage Protein in Ruminant Animal Production*. Ed. Thomson D.J., D.E. Beever D.E. and R.G. Gunn. Occasional Publication; *British Society of Animal Production* 6: 107-118.
- Black J.L.; Faichney G.J.; Sinclair R.E. 1982b. Role of computer simulation in overcoming limitations to animal production from pastures. In: *Nutritional Limits to Animal Production from Pastures*. Ed. J.B. Hacker. Commonwealth Agricultural Bureaux, Farnham Royal. pp 473-493.
- Black J.L.; Fleming J.F.; Davies G.T. 1990. Future for whole animal prediction models. In *Modelling Digestion and Metabolism in Farm Animals*. Ed. A.B. Robson and D.P. Poppi. Lincoln University, Canterbury, New Zealand. (In Press).
- Black J.L.; Gill M.; Beever D.E.; Thornley J.H.M.; Oldham J.D. 1987a. Simulation of the metabolism of absorbed energy-yielding nutrients in young sheep: efficiency of utilisation of acetate. *Journal of Nutrition* 117: 105-115.
- Black J.L.; Gill M.; Thornley J.H.M.; Beever D.E.; Oldham J.D. 1987b. Simulation of the metabolism of absorbed energy-yielding nutrients in young sheep: efficiency of utilisation of lipid and amino acid. *Journal of Nutrition* 117: 116-128.
- Black J.L.; Graham N.McC.; Faichney G.J. 1976. Simulation of protein and energy utilisation in sheep. In *From Plant to Animal Protein*. Ed. Sutherland T.M., J.R. McWilliam and R.A. Leng. University of New England, Armidale. pp 161-166.
- Black J.L.; Kenney P.A. 1984. Factors affecting diet selection by sheep. II. Height and density of pasture. *Australian Journal of Agricultural Research* 35: 565-578.
- Black J.L.; Kenney P.A.; Colebrook W.F. 1987. Diet selection by sheep. In *Temperate Pastures; Their Production, Use and Management*. Eds. J.L. Wheeler, C.J. Pearson and G.E. Robards. Australian Wool Corporation/CSIRO, Melbourne, pp.331-334.
- Black J.L.; Mulholland J.G. 1983. Application of information on the chemical composition of feeds to the management of sheep. In *Feed Information and Animal Production*. Ed. G.E. Robards and R.G. Packham. Commonwealth Agricultural Bureaux, Farnham Royal. pp. 357-360.
- Blaxter K.L. 1962. *The Energy Metabolism of Ruminants*. Hutchinson, London.
- Burns J.C.; Fisher D.S.; Morrison W.H. III. 1987. Comparison of steer preferences among Panicum accessions in short-term grazing and stall fed forage. In: *Second International Symposium on the Nutrition of Herbivores*. Occasional Publication of the Australian Society of Animal Production. pp 95-96.
- Burritt E.A.; Provenza F.D. 1989. Food aversion learning: conditioning lambs to avoid a palatable shrub (*Cercocarpus montanus*). *Journal of Animal Science*. 67: 650-653.
- Chamberlain D.G.; Thomas P.C.; Qiuq J. 1986. Utilization of silage nitrogen in sheep and cows: amino acid composition of duodenal digesta and rumen microbes. *Grass and Forage Science*. 41: 31-38.
- Colebrook W.F.; Black J.L.; Kenney P.A. 1985. Effect of sensory factors on diet selection by sheep. *Proceedings of the Nutrition Society of Australia* 10: 99-102.
- Colebrook W.F.; Black J.L.; Kenney P.A. 1987. A study of factors influencing diet selection by sheep. In: *Second International Symposium on the Nutrition of Herbivores*. Occasional Publication of the Australian Society of Animal Production. pp. 85-86.
- Colebrook W.F.; Black J.L.; Purser D.B.; Collins W.J.; Rossiter R.D. 1990. Observed and predicted preference by sheep for six cultivars of subterranean clover. *Australian Journal of Agricultural Research* (In Press).
- Corbett J.L.; Langlands J.P.; McDonald I.; Puller J.D. 1966. Comparison by direct animal calorimetry of the net energy values of an early and a late season growth of herbage. *Animal Production* 8: 13-27.
- Curl M.L.; Davidson J.L. 1983. Defoliation and productivity of a Phalaris - subterranean clover sward, and the influence of grazing experience on sheep intake. *Grass and Forage Science* 38: 159-167.
- Czerkawski J.W.; Blaxter K.L.; Wainman F.W. 1966. The metabolism of oleic, linoleic and linolenic acids by sheep with reference to their effects on methane production. *British Journal of Nutrition* 20: 349-362.
- Deinum B. 1966. Climate nitrogen and grass. Research into the influence of light intensity, temperature, water supply and nitrogen on the production and chemical composition of grass. *Mededelingen Landbouwhogeschool Wageningen* 66: 91.
- Della-Fera M.A.; Baile C.A. 1984. Control of feed intake in sheep. *Journal of Animal Science* 59: 1362-1368.
- Dermarquilly C.; Weiss P.H. 1970. Tableaux de la valeur alimentaires des fourrages. *Ministere de l'Agriculture Institut National de la Recherche Agronomique, Servier d'Experimentation*

- et d'Information I.N.R.A., Versailles.
- Djajaneaga A.; Doyle P.T. 1989. The intake and utilization of urea-treated rice straw by sheep differing in body condition. *Australian Journal of Agricultural Research*. **40**: 1037-1045.
- Dove H.; Milne J.A.; McCormack H.A.; Spence A.M. 1985. The effect of supplementation on non-ammonia nitrogen flows at the abomasum of lactating grazing ewes. *Proceedings of the Nutrition Society* **44**: 63A.
- Doyle P.T. 1988. Utilisation of clover diets by sheep. III. Palatability of a mature subterranean clover hay. *Australian Journal of Agricultural Research*. **39**: 891-898.
- Dudzinski M.L.; Arnold G.W. 1973. Comparison of diets of sheep and cattle grazing together on sown pastures on the Southern Tablelands of New South Wales by principal components analysis. *Australian Journal of Agricultural Research*. **24**: 899-912.
- Dunlop A. 1984. Factors affecting the intake and utilization of alkali-treated forages by sheep. *PhD Thesis*, University of Sydney, Australia.
- Egan J.K.; Doyle P.T. 1984. A comparison of particulate markers for the estimation of digesta flow from the abomasum of sheep offered oat hay. *Australian Journal of Agricultural Research* **35**: 279-291.
- Evans P.S. 1967. Leaf strength studies of pasture grasses. II Strength, cellulose content and sclerenchyma tissue proportions of eight grasses grown as single plants. *Journal of Agricultural Science (Cambridge)*. **69**: 175-181.
- Faichney G.J.; Black J.L. 1979. Factors affecting rumen function and the supply of nutrients. In *Physiological and Environmental Limitations to Wool Growth*. Ed. J.L. Black and P.J. Reis. University of New England Publishing Unit, Armidale. pp. 179-192.
- Faichney G.J.; White G.A. 1983. *Methods for the Analysis of Feeds Eaten by Ruminants*. CSIRO, Melbourne.
- Forbes T.D.A. 1988. Researching the plant-animal interface: the investigation of ingestive behaviour in grazing animals. *Journal of Animal Science*. **66**: 2369-2379.
- Forbes T.D.A.; Hodgson J. 1985. Comparative studies on the influence of sward conditions on the ingestive behaviour of cows and sheep. *Grass and Forage Science*. **40**: 69-77.
- Garrett W.N.; Yang Y.T.; Dunkley W.L.; Smith L.M. 1976. Energy utilization, feedlot performance and fatty acid composition of beef steers fed protein encapsulated tallow or vegetable oils. *Journal of Animal Science*. **42**: 1522-1533.
- Gherardi S.G. 1989. Evaluation of Factors Affecting Voluntary Feed Consumption by Sheep. *PhD Thesis*, University of Sydney, Sydney.
- Gherardi S.G.; Black J.L. 1989. Influence of post-rumen supply of nutrients on rumen digesta load and voluntary intake of roughage by sheep. *British Journal of Nutrition*. **62**: 589-599.
- Gherardi S.G.; Black J.L. 1990. Effect of palatability on voluntary feed intake by sheep. I. Identification of chemicals that alter the palatability of a forage. *Australian Journal of Agricultural Research* (In Press).
- Gherardi S.G.; Black J.L.; Colebrook W.F. 1990. Effect of palatability on voluntary feed intake by sheep. II. The effect of altering palatability of a wheaten hay on long-term intake and preference. *Australian Journal of Agricultural Research* (In Press).
- Gordon G.L.R.; McMahon G.R.; Black J.L. 1987. *In vitro* estimation of the potential degradability in the rumen of forage protein and fibre. In *Second International Symposium on the Nutrition of Herbivores*. Occasional Publication of the Australian Society of Animal Production. pp. 135-136.
- Graham N. McC. 1969. The net energy value of artificially dried subterranean clover harvested before flowering. *Australian Journal of Agricultural Research*. **20**: 365-373.
- Greenhalgh J.F.D.; Reid G.W. 1971. Relative palatability to sheep of straw, hay and dried grass. *British Journal of Nutrition*. **26**: 107-116.
- Grovum W.L. 1987. A new look at what is controlling food intake. In: *Feed Intake by Beef Cattle*. Ed. F.N. Owens. Oklahoma State University, Stillwater. pp 1-40.
- Grovum W.L.; Chapman H.W. 1988. Factors affecting the voluntary intake of food by sheep. 4. The effect of additives representing the primary tastes on sham intakes by oesophageal-fistulated sheep. *British Journal of Nutrition*. **59**: 63-72.
- Harrison D.G.; Beever D.E.; Thomson D.J.; Osbourn D.F. 1975. Manipulation of rumen fermentation in sheep by increasing the rate of flow of water from the rumen. *Journal of Agricultural Science, Cambridge*. **85**: 93-101.
- Hendricksen R.E.; Poppi D.P.; Minson D.J. 1981. The voluntary intake, digestibility and retention time by cattle and sheep of stem and leaf fractions of a tropical legume (*Lablab purpureus*). *Australian Journal of Agricultural Research* **32**: 389-398.
- Hennessy D.W. 1981. Responses of beef cattle to supplements of protein or non-protein nitrogen when grazing native pastures of the north coast of New South Wales. In *Recent Advances in Animal Nutrition in Australia 1981*. Ed. D.J. Farrell. University of New England Publishing Unit, Armidale. pp 74-81.
- Hodge R.W. 1974. Efficiency of food conversion and body composition of the preruminant lamb and the young pig. *British Journal of Nutrition*. **32**: 113-126.
- Hodgson J. 1985. The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society*. **44**: 339-346.
- Hovell F.D.deB.; Greenhalgh J.F.D.; Wainman F.W. 1976. The utilization of diets containing acetate salts by growing lambs as measured by comparative slaughter and respiration calorimetry together with rumen fermentation. *British Journal of Nutrition*. **35**: 343-363.
- Huntington G.B. 1984. Net absorption of glucose and nitrogenous compounds by lactating Holstein cows. *Journal of Dairy Science*. **67**: 1919-1927.
- Jarrige R. 1989. *Ruminant Nutrition: Recommended Allowances and Feed Tables*. Libbey Eurotext, Paris.
- John A.; Ulyatt. M.J. 1987. Importance of dry matter content to voluntary intake of fresh grass forage. *Proceedings of the New Zealand Society of Animal Production*. **47**: 13-16.
- Johns A.T. 1962. Some aspects of rumen metabolism influencing intake and production in sheep. *Proceedings of the New Zealand Society of Animal Production*. **22**: 88-98.
- Judson G.J.; Anderson E.; Luick J.R.; Leng R.A. 1968. The contribution of propionate to glucose synthesis in sheep given diets of different grain content. *British Journal of Nutrition*. **22**: 69-75.

- Kennedy P.M.; Murphy M.R. 1988. The nutritional implications of differential passage of particles through the ruminant alimentary tract. *Nutrition Research Reviews*. 1: 189-208.
- Kenney P.A.; Black J.L. 1984. Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. *Australian Journal of Agricultural Research*. 35: 551-563.
- Kenney P.A.; Black J.L. 1986. Effect of simulated sward structure on the rate of intake of subterranean clover by sheep. *Proceedings of the Australian Society of Animal Production*. 16: 251-254.
- Kenney P.A.; Black J.L.; Colebrook W.F. 1984. Factors affecting diet selection by sheep. III. Dry matter content and particle length of forage. *Australian Journal of Agricultural Research*. 35: 831-838.
- Langlands J.P. 1970. Efficiency of wool production of grazing sheep. 3. The use of sulphur-containing amino acids to stimulate wool growth. *Australian Journal of Experimental Agriculture and Animal Husbandry*. 10: 665-671.
- Laredo M.A.; Minson D.J. 1973. The voluntary intake, digestibility, and retention time by sheep of leaf and stem fractions of five grasses. *Australian Journal of Agricultural Research*. 24: 875-888.
- Laredo M.A.; Minson D.J. 1975. The effect of pelleting on the voluntary intake and digestibility of leaf and stem fractions of three grasses. *British Journal of Nutrition*. 33: 159-170.
- Lascano C.E.; Thomas D. 1988. Forage quality and animal selection of *Arachis pintoi* in association with tropical grasses in the eastern plains of Colombia. *Grass and Forage Science*. 43: 433-439.
- Lee J.A.; Pearce G.R. 1984. The effectiveness of chewing during eating on particle size reduction of roughages by cattle. *Australian Journal of Agricultural Research*. 35: 609-918.
- Leigh J.H.; Mulham W.E. 1966. Selection of diet by sheep grazing semi-arid pastures on the Riverine Plain. 2. A cotton bush (*Kochia aphylla*) - grassland (*Stipa variabilis* - *Danthonia caespitosa*) community. *Australian Journal of Experimental Agriculture and Animal Husbandry*. 6: 468-474.
- L'Huillier P.J.; Poppi D.P.; Fraser T.J. 1986. Influence of structure and composition of ryegrass and prairie grass- white clover swards on the grazed horizon and diet harvested by sheep. *Grass and Forage Science*. 41: 259-267.
- MacRae J.C.; Lobley G.E. 1982. Some factors which influence thermal energy losses during the metabolism of ruminants. *Livestock Production Science*. 9: 447-456.
- MacRae J.C.; Smith J.S.; Sharman G.A.M.; Corrigan W.; Coop R.L. 1982. Energy metabolism of lambs infected with *Trichostrongylus colubriformis*. *European Association of Animal Production*, Publication No. 29: 112-115.
- MacRae J.C.; Ulyatt M.J. 1974. Quantitative digestion of fresh herbage by sheep. II The sites of digestion of some nitrogenous constituents. *Journal of Agricultural Science (Cambridge)*. 82: 309-319.
- Maeng W.J.; Baldwin R.L. 1976. Factors influencing rumen microbial growth rates and yields: effects of urea and amino acids over time. *Journal of Dairy Science*. 59: 643-647.
- Milford R.; Minson D.J. 1965. The energy value of ryegrass and cocksfoot assessed by a slaughter technique with lambs. *British Journal of Nutrition*. 19: 373-382.
- Minson D.J. 1981. Nutritional differences between tropical and temperate pastures. In: *World Animal Science, B1. Grazing Animals*. Ed. F.H.W. Morley. Elsevier Publishing Company, Amsterdam. pp 143-157.
- Minson D.J. 1982. Effects of chemical and physical composition of herbage eaten upon intake. In: *Nutritional Limits to Animal Production from Pastures*. Ed. J.B. Hacker. Commonwealth Agricultural Bureaux, Farnham Royal, England. pp 167-182.
- Minson D.J.; Bray R.A. 1986. Voluntary intake and *in vivo* digestibility by sheep of five lines of *Cenchrus ciliaris* selected on the basis of preference rating. *Grass and Forage Science*. 41:47-52.
- Moseley G. 1981. Herbage quality and physical breakdown in the foregut of sheep. *Proceedings of the New Zealand Society of Animal Production*. 41: 142-151.
- Mottershead B.E.; Lynch J.J.; Elwin R.L.; Green G.C. 1985. A note on the acceptance of several types of cereal grain by young sheep with and without prior experience of wheat. *Animal Production*. 41: 257-259.
- Murphy M.R.; Baldwin R.L.; Koong L.J. 1982. Estimation of stoichiometric parameters for rumen fermentation of roughage and concentrate diets. *Journal of Animal Science*. 55: 411-421.
- Oldham J.D. 1981. Amino acid requirements for lactation in high-yielding dairy cows. In *Recent Advances in Animal Nutrition - 1980*. Ed. W. Haresign. Butterworths, London. pp 33-65.
- Outen G.E.; Beever D.E.; Osbourn D.F. 1974. Digestion and absorption of lipids by sheep fed chopped and ground dried grass. *Journal of the Science of Food and Agriculture*. 25: 981-987.
- Ozanne P.G.; Purser D.B.; Howes K.M.W.; Southey I. 1976. Influence of phosphorus content on feed intake and weight gain in sheep. *Australian Journal of Experimental Agriculture and Animal Husbandry*. 16: 353-360.
- Panggabean T.; Moir R.J.; Purser D.B.; Laby R. 1985. Multi-element effects in sheep. In *Ruminant Physiology: Concepts and Consequences*. Ed. S.K. Baker, J.M. Gawthorne, J.B. Mackintosh and D.B. Purser. University of Western Australia, Perth. pp 347-355.
- Poppi D.P.; Cruickshank G.J.; Sykes A.R. 1988. Fish meal and amino acid supplementation of early-weaned lambs grazing Roatall fescue (*Festuca arundinacea*) or Huia white clover (*Trifolium repens*). *Animal Production* 46: 491.
- Poppi D.P.; Hendrickson R.E.; Minson D.J. 1985. The relative resistance to escape of leaf and stem particles from the rumen of cattle and sheep. *Journal of Agricultural Science (Cambridge)*. 105: 9-14.
- Poppi D.P.; MacRae J.C.; Brewer A.; Coop R.L. 1986. Nitrogen transactions in the digestive tract of lambs exposed to the intestinal parasite, *Trichostrongylus colubriformis*. *British Journal of Nutrition*. 55: 593-602.
- Poppi D.P.; Minson D.J.; Ternouth J.H. 1981. Studies of cattle and sheep eating leaf and stem fractions of grasses. II Factors controlling the retention of feed in the reticulo-rumen. *Australian Journal of Agricultural Research*. 32: 109-121.
- Purser D.B. 1981. Nutritional value of Mediterranean pastures. In: *World Animal Science, B1. Grazing Animals*. Ed. F.H.W. Morley. Elsevier Publishing Company, Amsterdam. pp 159-

- 180.
- Purser D.B.; Buechler S.M. 1966. Amino acid composition of rumen organisms. *Journal of Dairy Science*. **49**: 81-84.
- Rattray P.V.; Clark D.A. 1984. Factors affecting the intake of pasture. *New Zealand Agricultural Science*. **18**: 141-146.
- Rattray P.V.; Joyce J.P. 1974. Nutritive value of white clover and perennial ryegrass. IV. Utilisation of dietary energy. *New Zealand Journal of Agricultural Research*. **17**: 401-406.
- Rees M.C.; Minson D.J. 1978. Fertiliser sulphur as a factor affecting voluntary intake, digestibility and retention time of pangola grass (*Digitaria decumbens*) by sheep. *British Journal of Nutrition*. **39**: 5-11.
- Reis P.J. 1979. Effects of amino acids on the growth and properties of wool. In: *Physiological and Environmental Limitations to Wool Growth*. Ed. J.L. Black and Reis P.J. University of New England Publishing Unit, Armidale. pp. 223-242.
- Rogers G.L.; Bryant A.M.; McLeay L.M. 1979. Silage and dairy cow production. III Abomasal infusion of casein, methionine and glucose, and milk yield and composition. *New Zealand Journal of Agricultural Research*. **22**: 533-541.
- Rogers G.L.; Porter R.H.D.; Clarke T.; Stewart J.A. 1980. Effect of protected casein supplements on pasture intake, milk yield and composition of cows in early lactation. *Australian Journal of Agricultural Research*. **31**: 1147-1152.
- Samarakoon S.P.; Shelton H.M.; Wilson J.R. 1990. Voluntary feed intake by sheep and digestibility of shaded *Stenotaphrum secundatum* and *Pennisetum clandestinum* herbage. *Journal of Agricultural Science (Cambridge)* **114**: 143-150.
- Smith L.W.; Goering H.K.; Gordon C.H. 1972. Relationships of forage composition with rates of cell wall digestion and indigestibility of cell walls. *Journal of Dairy Science*. **55**: 1140-1147.
- Stephenson R.G.A.; Hopkins P.S. 1985. Water medication to improve the husbandry of grazing sheep and cattle. In: *Recent Advances in Animal Nutrition in Australia in 1985*. R.B. Cumming. University of New England Publishing Unit, Armidale, Australia. pp 2.1-2.9.
- Storm E.; Ørskov E.R. 1984. The nutritive value of rumen micro-organisms in ruminants. 4. The limiting amino acids of microbial protein in growing sheep determined by a new approach. *British Journal of Nutrition*. **52**: 613-620.
- Sutton J.D.; Morant S.V. 1978. Measurement of the rate of volatile fatty acid production in the rumen. In: *Ruminant Digestion and Feed Evaluation*. Ed. D.F. Osbourn, D.E. Beever and D.J. Thomson. Agricultural Research Council, London. pp 7.1-7.10.
- Taylor St. C.S.; Murray J.I.; Ilius A.W. 1987. Relative growth of incisor arcade breadth and eating rate in cattle and sheep. *Animal Production*. **45**: 453-458.
- Thomson D.J.; Beever D.E. 1980. The effect of conservation and processing on the digestion of forages by ruminants. In *Ruminant Digestion and Feed Evaluation*. Ed. Y. Ruckebusch and P. Thivend. M.T.P. Press, Lancaster. pp 291-308.
- Thomson R.F.; Minson D.J. 1973. The relationship between apparent retention time in the rumen, voluntary intake, and apparent digestibility of legume and grass diets in sheep. *Australian Journal of Agricultural Research*. **24**: 889-898.
- Tucker R.E.; Mitchell G.E.; Little C.O. 1968. Ruminal and post-ruminal starch digestion in sheep. *Journal of Animal Science*. **27**: 824-826.
- Tyrell H.F.; Reynolds P.J.; Moe P.W. 1979. Effect of diet on partial efficiency of acetate use for body tissue synthesis by mature cattle. *Journal of Animal Science*. **48**: 598-606.
- Ulyatt M.J. 1971. Studies on the causes of the differences in pasture quality between perennial ryegrass, short-rotation ryegrass and white clover. *New Zealand Journal of Agricultural Research*. **14**: 352-367.
- Ulyatt M.J. 1981. The feeding value of temperate pastures. In: *World Animal Science*, B1. Grazing Animals. Ed. F.H.W. Morley. Elsevier Publishing Company, Amsterdam. pp 125-141.
- Ulyatt M.J. 1984. Determinants of voluntary feed consumption. In: *Plant Breeding and Feeding Value of Pastures and Forages*. Ed. M.J. Ulyatt and J.L. Black. DSIR, Palmerston North.
- Ulyatt M.J. 1985. Pasture composition and animal production. In: *Ruminant Physiology: Concepts and Consequences*. Ed. S.K. Baker, J.M. Gawthorne, J.B. Mackintosh and D.B. Purser. University of Western Australia, Perth. pp 195-203.
- Ulyatt M.J.; Dellow D.W.; John A.; Reid C.S.W.; Waghorn G.C. 1986. Contribution of chewing during eating and rumination to the clearance of digesta from the ruminoreticulum. In *Control of Digestion and Metabolism in Ruminants*. Ed. L.P. Milligan, W.L. Grovum and A. Dobson. Reston, Prentice Hall, New Jersey. pp 498-515.
- Van Soest P.J. 1975. Physico-chemical aspects of fibre digestion. In: *Digestion and Metabolism in the Ruminant*. Ed. I.W. McDonald and A.C.I. Warner. University of New England Publishing Unit, Armidale. pp 351-365.
- Warner A.C.I. 1981. Rate of passage of digesta through the gut of mammals and birds. *Nutrition Abstracts and Reviews*. **51(B)**: 789-820.
- Weston R.H. 1982. Animal factors affecting feed intake. In: *Nutritional Limits to Animal Production from Pastures*. Ed. J.B. Hacker. Commonwealth Agricultural Bureaux, Farnham Royal, England. pp 183-198.
- Weston R.H. 1985. The regulation of feed intake in herbage-fed ruminants. *Proceedings of the Nutrition Society of Australia*. **10**: 55-62.
- Weston R.H.; Cattle J.A. 1982. Voluntary roughage consumption in growing and lactating sheep. *Proceedings of the Nutrition Society of Australia*. **7**: 147.
- Weston R.H.; Davis P. 1986. Low palatability as a constraint to the intake of a wheat straw diet by sheep. *Proceedings of the Nutrition Society of Australia* **11**: 172-175.
- Weston R.H.; Poppi D.P. 1987. Comparative aspects of food intake. In: *The Nutrition of Herbivores*. Ed. J.B. Hacker and J.H. Temouth Academic Press, Sydney. pp 133-161.