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STUDIES ON THE NUTRITION OF GRAZING RUMINANTS
COLLECTED PAPERS

BY

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PREFACE

The majority of the world's cattle and sheep obtain most of their feed by grazing, yet studies on housed ruminants and experiments on the growth of grassland herbage that exclude grazing animals outnumber direct investigations of animal production from pasture. Such studies are a legitimate approach towards, and make necessary contributions to, an understanding of the processes involved in pastoral systems, but in themselves they are not sufficient to gain a full appreciation of these processes which entail complex interactions between climate, soil, plant and animal.

Interactions between components of pastoral systems.

Research on the nutritional value of cut herbage and on the nutrient requirements of housed animals yields essential basic information but however detailed the results may be, they cannot be combined so as to allow the precise definition or prediction, establishment or amendment, of the nutrient intake or productive performance of a grazing animal. The animal's needs, the amount and quality of the feed that it chooses to eat, and even the use made of the energy and nutrients gained will vary with the type of feed available, the ease with which it is acquired, and with the ever-changing climatic conditions. The feed on a pasture that is available for consumption comprises the herbage that the animal has not eaten on previous occasions plus the gains by growth and minus the losses due to senescence and decay. The gains and losses and animal demand will very rarely, if ever, be in balance. Moreover, in what manner and to what extent the animal does eat at any particular time determines, often to a large extent, what it shall have to eat and so how it shall perform in the future. Grazing animals will exercise considerable freedom in their choice of diet even though restraints are

imposed by management, and the day to day changes in the pasture alter the range of the choice open to them. In selecting their feed the animals may eat more of one species than of another, or more of one part of a plant than of another. This behaviour, due to individual characteristics of the animals and plants and other causes, will be reflected in the botanical and morphological composition of the subsequent growth of herbage. The rate and extent of the subsequent growth as a whole, within the limits imposed by the supplies of solar energy, water and plant nutrients, will reflect the extent to which grazing has reduced the photosynthetic area of the plants and, consequentially, the extent of their root systems. Grazing may also render the plants more vulnerable to extremes of climate, and the exposure of bare ground may promote the erosion of soil by wind or water. All changes in the plant canopy will be accompanied and will in turn be modified by changes in the microclimate of the sward, and in the soil moisture and temperature regimes. Alterations will also occur in the direction or rate of change in populations of organisms both above and below the soil surface, including bacteria, fungi, and invertebrata such as helminths. All these effects, and their consequences for plant and animal production, will be further compounded with those due to the trampling of plant and soil by the grazing animals, and to the irregular redistribution of plant nutrients in their excreta.

Nature of an effective programme of pastoral research.

The dynamic interactions inherent in pastoral systems will be only partially understood and characterized if investigations are confined to studies of isolated components of the systems, of the biology of ruminants and, separately, of plant growth. Two mutually dependent approaches are necessary: synthesis must accompany analysis.

Investigations of an analytical nature stem initially from reports and observations of an anecdotal and descriptive type. One or more variables in the system being examined are isolated for study by holding other variables constant so far as this is possible within the limits set by the current state of knowledge. As analysis proceeds and detailed knowledge accumulates the precision and complexity of the experiments can increase, but it becomes increasingly necessary to test in a wider context the validity of conclusions drawn from them. Attempts must be made to construct from the detailed knowledge a model that describes a significant part of the system as a whole and which, as with analysis, has to be developed through a regenerating cycle of hypothesis and test. The results obtained as each model is put to the test will reveal the existence of interactions between variables that were previously unrecognized or whose significance was not appreciated; it may be found that other effects were accorded undue emphasis. Further analytical studies are then to be made, but now these are based on informed observation and not simply on anecdote and description. The information that they yield should in turn allow the construction of improved models.

Quantity and quality of herbage in relation to animal production.

The first paper in this thesis (1)* is an assessment, made at the beginning of 1966, of the state of knowledge at that time of the nutritional value of grassland herbage. In considering indexes of nutritional value, information was drawn from a wide range of closely controlled, analytical, experiments but wherever possible the significance

* Numbers in parentheses refer to the order in which the papers are presented as indicated on their top right-hand corners, and as shown in the list below.

of the indexes was assessed in a wider context and by appeal to the animal. For example, to what extent are the differences that are found between herbage species in digestibility, as between Lolium perenne and Dactylis glomerata, reflected in significant differences in the performances of animals that graze these species?

Information of this type even on much larger differences, such as those between pasture growth stages, was scanty in 1950 when I was appointed to the Rowett Research Institute to develop a programme of grassland research appropriate to the aims of the Institute, which were "the advancement of understanding of the energy and material requirements of animals of agricultural importance so as to enhance the quality and quantity of their production to meet the needs of man".* At this time it was generally assumed that data on the effects of various cutting regimes on the growth of ungrazed swards and on the nutritional value of the feed harvested were directly applicable to grazed swards. It was further assumed that management practices devised from such information would inevitably promote large increases in animal production. It was nevertheless recognized that production from British grasslands remained disappointingly low. When expressed as "utilized starch equivalent" the mean national output was estimated to be about 1900 kg/ha/year†, representing some 3500 kg of dry matter. In contrast, dry matter yields more than twice as great were commonly harvested by machine. It was

* Cuthbertson, D. P. (1963). - In: "Progress in Nutrition and Allied Sciences". Edinburgh : Oliver & Boyd.

† Report of the Committee on Grassland Utilization (1958). London: Her Majesty's Stationery Office, Cmnd. 547.

clearly necessary to account for the apparent wastage of over 50 per cent of herbage grown and to increase from this low level the utilization of British grasslands which provided, and continue to provide, 60 per cent or more of the total feed eaten by that country's cattle and sheep. Equally clearly, greater understanding of the processes affecting the efficiency of pasture utilization and of the resulting animal production could come only from a research programme that included detailed studies of animals at pasture.

The immediate difficulty was one that had for long hampered such work: how might the quantity and quality of the feed eaten by grazing animals be measured? In 1950, techniques for estimating the digestibility of grazed herbage from faecal composition, and for estimating faeces output from the dilution in faeces of inert reference substances administered to the animals, were of recent origin. Little was known about the precision and accuracy of the estimates of grazing intake that could be obtained by their use. I therefore defined as a prime objective of the research programme, the development and critical evaluation of such techniques.

Intake from a pasture had frequently been estimated by cutting sample areas before and after a period of grazing to determine the amount of herbage apparently removed by the animals. While the faecal index techniques were being examined, the cutting method was used in experiments on two problems that appeared to be of immediate importance. These were (a) the possibility that low animal production from pasture might be due to a qualitative defect in the diet as well as to a failure to utilize fully the herbage grown; and (b) that the annual production from an area of pasture, in any case, was determined largely by the production obtained during the normal grazing season, which often extended over no more than 6-8 months.

The herbage grown on intensively managed pastures usually provided lactating dairy cows, and other classes of livestock, with more than sufficient protein for their needs. It appeared likely that milk production by potentially high-yielding animals was limited primarily by the supply of dietary energy. Feeds of low protein content were therefore given to dairy cows grazing pastures where intake was not restricted by a low availability of herbage. It was found (2,3) that only small increases in milk yield were obtained because the consumption of these feeds was accompanied by a significant reduction in the amount of herbage eaten. It was concluded that additional feed could usefully increase production when pastures were so heavily stocked that there was insufficient herbage to meet the needs of the animals, but large amounts were used in Britain when good grazing was readily available and they were simply replacing a less costly feed, namely grazed herbage. It appeared that their use generally represented a mistaken attempt to adjust the notional value of the diet of the grazing cows so as to match estimates of their requirements calculated, inappropriately, from tables of feeding standards.

The highest costs in milk and beef production were incurred in winter, when the animals were often housed and hand-fed. It was possible that economies would be effected, especially during the rearing phase, if the grazing season could be extended through some or all of this period by saving the late-summer growth on suitably prepared pastures. The relative values of a number of herbage species for maintaining young dairy and beef cattle were examined in trials that continued throughout several winters, when it was found (4) that the species which gave the highest yields of cut herbage gave the poorest results in terms of animal performances. There were found to be several reasons for this apparently anomalous result. There was variation between species in the extent of wastage in the standing herbage during the winter, and in the acceptability

to the animals of what remained as shown by variation in their daily intakes and in the percentage of the available herbage that was consumed. These differences in the selectivity and intensity of grazing were reflected in the amount of damage done by trampling; moreover the types of herbage that were most susceptible to such damage were also less easily grazed when under snow.

It was recognized that if the pasture management on a farm was modified to permit late autumn and winter grazing, there would be repercussions that involved the long-term management and use of all grasslands on that farm. Appropriate methods for the integration of winter grazing in farming systems were therefore developed (5,7). They were based on information gained from experiments on the production of herbage to be saved for winter use (5) and on the performance of cattle grazing such herbage (6). This information also indicated means by which the grazing season could be usefully extended for fattening cattle and milking cows.

Both series of experiments, the feeding of grazing dairy cows and the extension of the grazing season, clearly demonstrated that the amount of animal product to be obtained from a pasture could not be determined reliably unless it was grazed, and that estimates of productivity based simply on measurements of the amount of feed harvested by machine could be seriously misleading.

The reasons for the differences between the treatments in animal performance would not have been made clear without the estimates of intake made by the cutting technique, but an examination of the technique showed (8) that it was not sufficiently precise and accurate for use in closely detailed studies of the intake and utilization of herbage by ruminants. Moreover, it could not usually be made to give estimates of the intake of

individual animals, but only of groups, and the intake of energy and nutrients could not be determined except by an unreliable process of calculation (1) based on the estimated chemical composition of the herbage thought to have been eaten. All these difficulties emphasized the need for dependable indicator techniques.

Development of techniques for estimating grazing intake.

Errors in indirect methods for estimating digestibility from faecal composition were identified and evaluated in a series of experiments where the excretion of nitrogen, plant pigments (chromogen), and later of material soluble in 0.2N HCl was studied (9,10,11,12). Continuous digestibility trial procedures were devised to assist this work (10,11), and nitrogen was shown to be the most generally satisfactory faecal index of digestibility (9,12).

To develop satisfactory methods for the estimation of faeces output, the passage of inert substances through the alimentary tract was studied. It was shown (13) that the water-insoluble substance chromium sesquioxide (Cr_2O_3) was excreted more evenly than the soluble polyethylene glycol because (14) the latter, in solution, moved more rapidly from the reticulo-rumen than feed residues. It appeared that Cr_2O_3 was the best chemical marker-substance available and reasons were sought for the variation in its concentration in faeces. It was found (15) that Cr_2O_3 , when administered in a concentrated form in a capsule, failed to mix adequately with the contents of the reticulo-rumen and passed from this organ in advance of the feed residues that it was intended to mark. A method of administration was required that would result in the Cr_2O_3 being carried well into the rumen, and there released slowly into the ingesta. To this end, Cr_2O_3 was incorporated in a specially made paper

and it was found (15,16) that compared with other methods of administration, variation in the excretion of Cr_2O_3 was significantly reduced when it was given as the paper. This finding was confirmed with grazing animals (17,18) in experiments where the errors associated with various regimes for sampling faeces were defined.

These studies of the faecal nitrogen and Cr_2O_3 techniques showed that if they were applied without a considerable knowledge of their limitations, they were likely to yield spurious results. Many of the errors associated with the sampling and analysis of faeces, and with the subsequent calculations of digestibility and faecal output, were found to be biasing and not simply random. It was shown that if precautions were taken to minimize these errors it was probable that the digestibility of the herbage grazed by a single animal over a period of a week could be estimated with a standard error of about $\pm 1\%$, and that an estimate of the mean daily intake of digestible organic matter would have a standard error as low as $\pm 6\%$ (8,19). These values, which were later supported by the results of an experiment with grazing dairy cows (23), indicated the numbers of animals that would be required for the detection, at the 5% level of significance, of differences in the digestibility and intake of herbage due to differences between pastures (10).

Intake and utilization of energy by grazing animals.

When the indicator methods for estimating grazing intake had been developed to the point where they could be used with reasonable confidence, special attention was paid to the intake and utilization of energy by grazing cattle and sheep for it was clear (1,2,3) that generally their productivity was determined by the amount of energy available to them rather than by the amount of protein or other nutrients in the diet.

It could be expected that the net efficiency with which an animal converted the metabolizable energy of a feed to, say, milk or meat would vary little whether that animal was given the feed in a stall or obtained it by grazing. The gross efficiency of conversion was likely to differ between the two circumstances because of variation in the amount of energy expended in maintenance activities. The magnitude of the increase in energy expenditure due to grazing was examined by statistical analysis of data on feed intake, and animal liveweight and production. It was shown (19) that imperfections in the techniques for measuring intake could cause very large errors in the values obtained for the expenditure. The improved techniques that had been developed were used for studies on dairy cows and sheep close-folded on pastures that promoted positive energy balances in the animals, and in this respect were typical of British low-land pastures. The method of statistical analysis was refined. For both species of animal it was found (20,22) that the expenditure of energy in maintenance under these grazing conditions was some 20 per cent greater than the expenditure that would be incurred in stall-feeding. In order to make such a comparison with sheep it was necessary to define the maintenance requirements of this species when kept indoors. This was done both by a calorimetric procedure and by determination of the amounts of feed required to hold liveweights constant (21). The two sets of estimates were in good agreement and showed that the British standard values then generally accepted were in error.

In the course of the experiments with the dairy cows it was found (23) that their herbage intake varied directly with the digestibility of the feed, as had been demonstrated with stall-fed animals. It was also found that intake at a given digestibility was lower at the end of the grazing season than at the beginning. This result shed some light on the common practical observation that "autumn" pastures did not appear to sustain animal production as well as earlier growths of herbage.

In a further examination of this phenomenon, calorimetric studies were made of the net energy values of an early and a late season growth of herbage (24). The difference that was found between the herbages appeared to be consistent with the differences between them in water-soluble carbohydrate content, the digestibility of cellulose, the molar proportions of volatile fatty acids produced in the rumen, and the proportion of the gross energy lost as methane.

In 1963 I joined the Pastoral Research Laboratory of the C.S.I.R.O., Division of Animal Physiology, at Armidale, N.S.W. The purpose of this Laboratory, in a country where some 160 million sheep and 19 million cattle graze the whole year round, is to increase understanding of the processes in soil, plant and animal that together determine the productivity of the land and of the animals it sustains. The objects of the programme of research that I initiated were to determine, in a variety of controlled long-term pastoral systems supported by detailed studies on penned animals: (i) what grazing animals eat; (ii) in what forms the feed consumed becomes available to them for metabolism; (iii) for what purposes and in what amounts the energy and nutrients of the feed are used; and (iv) to study in both the short- and long-term the extent to which various pastures meet or modify the needs of the animals. This work, as with the work of the whole Laboratory, was linked primarily with problems concerning the sheep industry, and especially with wool production.

Productivity of breeding ewes.

Since each year in Australia many millions of ewes are engaged in breeding and rearing a lamb, it was surprising that very little was known about the effects of pregnancy and lactation on wool growth. Most of the information available had been obtained from the fleece-

weights at shearing of ewes that had or had not reared a lamb. It was unsatisfactory because usually it did not distinguish the effects due to pregnancy from those due to lactation. In addition it had not been obtained in well defined nutritional conditions and so it did not show how the effects varied with feed intake. Studies were made on Merino ewes whose primary function was the production of wool and the breeding of replacement stock for wool-producing flocks. In an exploratory experiment (25) it was found that lactation caused a significant reduction in the amount of wool grown by ewes grazing good pastures although there was a large increase in feed intake. The effects of pregnancy as well as of lactation were then examined (26) with housed ewes given feed in constant amounts throughout the breeding cycle and it was found that the effects were not proportionately greater at one level of feeding rather than another. The reduction in wool growth was more marked than with the grazing ewes which could vary their feed intake as the physiological state changed but, as in the earlier experiment (25), it was noted that the average daily rate of wool growth increased rapidly when the lambs were weaned. This finding led to a study of the effects of variation in the length of lactation on the productivity of grazing ewes and, in consequence, on the immediate and long-term performances of their lambs which were weaned at various ages (26,27). To assist definition of the effects of treatments imposed on the ewes, and of their consequences in the nutrition of their lambs, a reliable technique for measuring the yield and composition of milk produced by grazing ewes was developed (28).

Stocking rate and production.

The effects of variation in the length of lactation on ewe and lamb were studied with ewes grazed continuously at three different stocking rates.

The effects of stocking rate on the production from a pasture are greater than any that will result from changes in the management of the grazing of a fixed number of animals. If a very low stocking rate is doubled, animal production per unit area may also be doubled if the feed supply is sufficient to maintain unimpaired the production per head, but in general each increase in stocking rate will be accompanied by a reduction in individual performance. The point at which this reduction is not at least compensated for by an increased production per unit area will almost certainly be higher if wool alone is to be produced than if the sheep are also to breed their replacements. With dairy cows, or in prime lamb and beef production, the optimum stocking rate may be well below the maximum attainable. It is possible that practices uneconomic at a low stocking rate, such as the provision of concentrate feeds for grazing dairy cows (2,3), may be worthwhile or necessary at the higher rates, but even if a high rate has a satisfactory outcome over a short period of time, it may be too high over a period of several years if it causes retrogressive changes in plant and soil which jeopardize continuing productivity. Effects of stocking rate have also to be studied over a long term so as to examine the effects of variation between years in climate. Difficulties associated with a high rate in drought might be acceptable if drought occurred on average, say, one year in ten.

The experiment on varying the length of lactation of grazing ewes provided a striking example of interaction between treatment and stocking rate (26,27). At the highest stocking rate of the ewes it was found that lambs might have to be weaned at an early age if they were even to survive, let alone grow satisfactorily. Quite different results were obtained at each of the other two stocking rates. In addition the patterns of lamb growth showed distinctive differences between years (27). Studies on the growth and on the development of rumen function in the young lamb were accompanied by studies on the onset of helminth

infestation. It was found (29) that the onset was significantly delayed if lambs were weaned at an early age on to pastures reserved for them, that is before they had the opportunity to ingest large numbers of infective larvae due to the consumption of large amounts of herbage contaminated by the ewes.

Calorimetry, and metabolism in the rumen.

At high stocking rates the availability of herbage may be reduced to the extent that the grazing animals have great physical difficulty in obtaining their feed. When the energy cost of grazing good pastures was estimated (20,22) it was realized that higher values might be obtained when feed was scarce. There were a number of reports to this effect, some indicating as much as a threefold increase in the amount of feed required by an animal to maintain a given liveweight in difficult grazing conditions, compared with the requirement on good grazing or in stall-feeding. Because of the considerable number of uncertainties attending the calculation of energy expenditure from data on feed intake and animal liveweight and production (1), it was desirable that additional estimates should be made by some other means. If a more direct method of estimation were available it would be possible to study more closely the causes of variation in the energy expenditure of grazing animals. Techniques were therefore developed for measuring the oxygen consumption and carbon dioxide production of grazing sheep and a satisfactory and thoroughly tested system is now available (30).

The determination of the quantity and quality of feed consumed by grazing animals (8,9,10,11,12,19), of the losses of energy and nutrients in their faeces (13,14,15,16,17,18) and of their heat production and losses of energy in gaseous products of digestion (30), yields

valuable information on efficiency of production. Knowledge must also be gained of processes intermediate between the consumption of feed and its outcome if causes of variation in efficiency are to be understood. A major part of the energy of the feed eaten by ruminant animals becomes available to them as the volatile fatty acids (VFA) acetic, propionic and butyric, and their rates of production in grazing sheep were measured by a technique in which radio-isotopes of the acids were infused into the rumen (31). It was found that the rate of production of each acid was significantly related to its concentration in the rumen for sheep grazing a variety of pastures, as well as for those given concentrate and roughage feeds. Further examination of the results showed that the amount of energy (kcal/day) supplied to a sheep as the three VFA could be predicted from the 24h mean value for the total VFA concentration as determined by steam distillation of ruminal liquor (30,31).

Conclusion and integrating summary.

The technique used for the measurement of VFA production, which disclosed the significance of ruminal concentration and so opened up a new line of attack on problems of the nutritional value of herbage and of animal productivity, is only one of the wide range of research techniques now used on confined animals. Many more must be applied to grazing animals, with modification as necessary, so that the effects of treatments can be fully assessed. If assessments are made only in terms of the amount of milk, meat or wool finally obtained, a procedure that should be no more acceptable in the field than it now is indoors, it is unlikely that the information gain can be widely applied because it is unlikely that general principles will be established; nor may it be seen that work done on one problem bears on another because it is not recognized that the problems have common roots.

Great care must be taken in defining the objectives of a grazing experiment and in its design, because the establishment and execution are likely to be very costly. In addition to material requirements, such as good fencing and the provision of suitable yards supplied with electric power etc., there will be heavy demands on labour for routine management as well as for experimental requirements. For example, it is considerably more difficult and time-consuming to maintain fistulated animals in good condition at pasture than it is indoors and the determination of feed intake, which may readily be achieved with housed animals, is a major undertaking in the field. Moreover, the large outlay may be wasted if insufficient thought has been given to the types of measurement that should be made and the techniques required have not been prepared, and if actions that would be taken to meet various contingencies were not clearly defined at the time the experiment was designed. For example, if the animals on one area of pasture became seriously short of feed, should the numbers be reduced on this area only and not on the others in the experiment, or should supplementary feed be given to that group or to all groups when either action is likely to cause major alterations in the nature of the comparisons being studied? If such problems have not been anticipated the original experiment may become no more than a test of ~~farming~~ ability.

Grazing experiments must also be supported by facilities for experiments of an analytical type so that problems they bring to notice can be examined and resolved appropriately. Thus the suitability for winter use of one type of pasture (4) led to a detailed study of methods of managing that pasture (5) and subsequently to the development of a satisfactory system for out-wintering cattle (6,7); uncertainty about the reliability of indicator techniques for estimating grazing intake led to detailed studies of relationships between feed digestibility and faecal indexes (9) and of the passage of inert materials through the alimentary tract (13,14), and then to improved techniques (10,15,16)

which were applied in several experiments (19,20,22,23) when opportunities for further studies were accepted (11,12,17,18,24); observations on the wool growth and feed intake by lactating ewes at pasture (25) were followed by the examination in well controlled conditions of effects of reproduction on wool growth (26), and led to investigations on the nutrition and growth of the young lamb (26,27,28,29); dissatisfaction with methods available for estimating the energy expenditure of grazing animals (20,22), stimulated the development of techniques of indirect calorimetry that can be used in the field to study this and many other problems (30,31).

The study in depth of a process followed by the application of the findings in a larger context should in turn promote further detailed research, and so on. This progressive cycle, once it is entered, will lead to a greater understanding, and will assist the management to greater advantage, of the complex events that follow the simple action of putting an animal on to a pasture to graze.

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I have been lucky to work in organizations where I could readily consult colleagues who were specialists in particular facets of my work. My thanks are due especially to Mr. I. McDonald of the Rowett Institute's Department of Biometry and to its Head, Mr. A. W. Boyne. Their expertise clarified many problems of experimental design and of the interpretation of results.

The tempo of the programme of research that I established at Aberdeen was much increased when Dr. J. F. D. Greenhalgh and Dr. J. P. Langlands joined my Section, for three-year periods from 1956 and 1959 respectively, to study for the degree of Ph.D.. Though I was officially their Supervisor, in practice their stays with me were most enjoyable and fruitful periods of collaboration, and the same is true of my present supervision of Mr. B. A. Young. I have received much help, in a variety of ways, from my colleagues in C.S.I.R.O. at Armidale, especially Mr. W. H. Southcott, and from Dr. R. A. Leng of the University of New England.

I am also most grateful for the help I have received from Technical Assistants, who are named in the papers submitted. The work often imposed a very heavy burden in the routine care and maintenance of the animals and pastures, as well as in the physical problems associated with experimental requirements. All discharged their responsibilities most conscientiously and with work of very high quality.

Finally, I would like to acknowledge my debt to my tutors, first at the University of Reading and then in post-graduate work at the (then) Massey Agricultural College. In particular, study under the supervision of Professor I. L. Campbell and his colleagues at Massey first stimulated my interest in pastoral research.

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PUBLICATIONS 1 - 31

THE NUTRITIONAL VALUE OF GRASSLAND HERBAGE.

by

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INTRODUCTION

It has been estimated that about one quarter of the earth's land surface is covered by grasslands.⁽¹⁾ In a natural state they vary from the treeless prairies, steppes and pampas of the temperate regions to the savannahs of the tropics and sub-tropics with their varying proportions of trees and shrubs. The vegetation and the innumerable wild animals of many species that they sustain have presumably acted as reciprocal factors in natural selection.⁽²⁾

Man has domesticated only a few of these species of animals and he has so far brought into cultivation only a few grasses; perhaps 40 of about 10,000 known species account for over 90 per cent of sown pastures⁽³⁾ but in the main their chemical composition, which is frequently used as an index of nutritional value, is not especially distinctive. When compared with many of the species they are intended to replace, the cultivated grasses do usually show a greater ability to respond by increased growth to an increase in soil fertility. They often provide qualitative as well as quantitative benefits to the animal in that maturation, seed-shed, senescence and decay may proceed less rapidly and may be delayed more readily by management.

Grassland communities are naturally dynamic. The balance of the species is determined by many factors - climatic, topographic, edaphic and biotic - and can be changed markedly by the type of management imposed.⁽⁴⁾ The persistence of the more productive grasses depends to a large extent upon a continued supply of plant nutrients. Legumes, as a result of their symbiotic relation with Rhizobia play a major role in improving the nitrogen status of soils^(5,6) They have therefore come to be an important constituent of grasslands and of the diet of grazing animals. Efforts to obtain legumes that can be established satisfactorily in tropical and sub-tropical pastures have only recently begun to meet with success.⁽⁷⁾

Many other plant species contribute to grassland communities. Dicotyledonous herbaceous plants, known collectively as forbs, often contain higher concentrations of minerals than associated grasses and legumes⁽⁸⁾ but produce lower yields of dry matter and may be less digestible.⁽⁹⁾ These species and the many woody 'browse' plants that make an important contribution to the feed supply of grazing animals in many areas will not be considered in this review. In addition, toxicoses and other disorders in livestock due to plant constituents or contaminants, such as alkaloids in Phalaris,⁽¹⁰⁾ oestrogenic substances,⁽¹¹⁾ and photosensitization caused by the fungus Pithomyces chartarum⁽¹²⁾ will not be discussed.

The botanical, chemical and morphological diversity of grassland vegetation is matched by the diversity of methods of utilization. These vary from highly capitalized systems of mechanical harvesting for the feeding of fresh or conserved herbage to confined animals, to pastoral systems where animals are wholly dependent on grazing throughout the year. Even in Britain and the U.S.A., where the grazing season may be short and there are large areas of arable crops, grasslands remain for economic reasons the chief source of feed for sheep and cattle and provide at least 60 per cent of their total annual feed requirements.^(13,14) At the other extreme Australia's 160 million sheep (about one-sixth of the world's total) and 19 million cattle obtain virtually all their feed from grazing.

Non-ruminants. - Some non-ruminant animals that utilize grassland herbage will be mentioned briefly here. Pigs and poultry are commonly held on pasture though sometimes the consumption of herbage, which may be as much as 2 kg of dry matter daily by sows⁽¹⁵⁾ and 20 g daily by laying hens,⁽¹⁶⁾ is incidental to other intended benefits such as the acquisition from the soil of iron and other nutrients. Dried herbage is used in large amounts in rations compounded for these animals and here the paramount considerations are low levels of structural carbohydrate, the concentration and the quality of the protein (see Chapter 18), and the concentrations

of vitamins and of minerals. The horse is able to utilize cellulosic material as a result of microbial digestion in its caecum and colon⁽¹⁷⁾ which may account for half the total capacity of the alimentary tract.⁽¹⁸⁾ The end products of this digestion include volatile fatty acids and newly synthesized water-soluble vitamins (cf. Chapters 3 and 4 - digestion in the ruminant). Microbial digestion is preceded by gastric digestion and the stomach of the horse accounts for only about one-eighth of the capacity of the alimentary tract. If the digestibility of the fodder eaten is low, so that the volume of indigestible residues is large, working animals especially may be in negative energy balance. The grazing behaviour of the horse tends to reduce the effective nutritional value of an area of pasture for this species.⁽¹⁹⁾ Where they defaecate they do not graze and mature herbage accumulates; conversely where they graze they do not defaecate, and may overgraze.

Documentation. - The references given in the text have been chosen for the reasons that they are the most recent of a number of appropriate reports, and that they bear particularly on the statements that are made. Whenever possible, reference is made to reviews.

CRITERIA OF NUTRITIONAL VALUE

The nutritional value of feeds for domestic livestock is expressed by the level of animal production of the desired type that is achieved and, unless the animal is killed at an early age for meat, by the length of productive life. It is a function not only of the proportion of the feed made available to the animal by digestion, and the suitability of the digested nutrients for the various metabolic processes but also, and most importantly, of the quantity consumed. Such information is obtained from biological measurements and data from chemical and other types of analyses can be interpreted only in their light.

The nutritional value of a feed is generally given in terms of the value per unit weight but that of grassland herbage has also to be viewed in a wider context. A far larger amount of herbage is harvested directly by animals themselves in grazing than is fed to them by hand. In grazing, the animal is directly subject to the climate and it gains a certain weight of herbage with more or less effort, and so with smaller or greater net benefit, according to the abundance, the pattern of distribution, and the quality of the herbage available. These characteristics of the pasture themselves reflect the climate, the previous activity of the animal, the net growth rate of the plant cover (actual growth less wastage by decay etc.), the condition of the soil and the complex interactions that ensue.

The nutritional value of grassland herbage, both fresh and conserved and whether grazed or hand-fed, is determined primarily by its ability to meet the requirements of the animal for energy and protein.⁽²⁰⁾ The caloric need can be regarded as the primary need to which the requirements for all nutrients are linked⁽²¹⁾ and in fact the grassland feeds of temperate zones do not usually have protein contents lower than those required by the animal at whatever level of production it attains in response to the amount of energy these feeds supply. Problems of protein supply are largely confined to the tropics and sub-tropics though even here the primary need is often for an increase in energy supply.⁽²⁶⁷⁾ There are no universal inadequacies (or excesses) of minerals, or deficiencies of those vitamins that the ruminant does not derive from microbial syntheses in its digestive tract; such problems are of a relatively local or temporary nature.

Energy value especially, and protein value, will be discussed in the following sections on voluntary feed intake, digestibility, the utilization of absorbed nutrients and feed evaluation. Specific nutrients, herbage conservation and various methods of feed preparation

will then be considered, and a final section will deal with nutritional consequences of grazing.

VOLUNTARY FEED INTAKE

The intake of feed in the long form only will be discussed in this section; processed feeds will be considered later.

The eating behaviour of higher animals, including the regulation of intake, appears ultimately to be subject to central nervous control,^(22,23) but of greater immediate importance is the nature of the stimuli that provoke the neural responses. A number of homeostatic mechanisms for quantitative regulation have been proposed,^(22,24,25) e.g., the stimulation of receptors sensitive to the concentrations of certain metabolites in blood, and in non-ruminant animals physical mechanisms appear to be of relatively less importance. In contrast the regulation of intake in ruminant animals can be described to a considerable extent, though not exclusively, in physical terms. Much evidence has accumulated that cattle and sheep tend to eat so that a certain degree of distention of the digestive tract, and in particular of the reticulo-rumen, with feed or with indigestible residues is maintained or restored.^(26,27,28) At this point appropriate physiological responses are presumably evoked by receptors sensitive to mechanical stimuli such as stretch.⁽²⁹⁾

The reticulo-rumen normally contains about three-quarters of the total contents of the gut.⁽¹⁸⁾ The more rapidly the breakdown and digestion of feed proceeds in this organ the faster can be the rate of passage of digesta onward through the small orifice leading to the omasum and, ultimately, the excretion of residues in faeces; hence the greater is the quantity of feed that must be eaten in a given period of time if a certain degree of "fill" is to be maintained. The amount of feed eaten

is thus a function of the rates of digestion in and of passage from the reticulo-rumen but these processes are the major steps in the degradation of feed in the alimentary tract of ruminants⁽³⁰⁾ and so it is found that they can be related to the extent of digestion as measured in digestibility trials.^(27,28,31) The general form of the relationship between the digestibility* and the voluntary intake of feed by cattle and sheep is shown diagrammatically in Figure 1.

(Figure 1 hereabouts)

In order to compare the feed intakes by animals differing widely in liveweight (W), they are often expressed in terms of metabolic body size ($W^{0.73}$ or $W^{0.75}$);^(31,32,33,125) $W^{0.75}$ has recently been recommended⁽²⁰⁴⁾ for general adoption. Intakes have also been related to $W^{1.00}$ ^(34,35,36) and some of the published exponents, ^(37,38,39,40) or those that can be calculated from the raw data given by some workers, ^(32,35,41) have fiducial limits that do not exclude either 0.73 or 1.00. Because of the frequent usage hitherto, $W^{0.73}$ will be used here.

When intakes are adjusted for differences in liveweight the values found for a feed of a given digestibility vary with the age, physiological state and other characteristics of the animal.^(42,76) For example, a lactating dairy cow might eat 120 g dry matter/kg $W^{0.73}$ /day, whereas a steer or wether sheep might eat no more than 80 g/kg $W^{0.73}$. Differences in intake are found between animals of a similar type; coefficients of variation ranging from 7 to 14 per cent have been reported.^(31,32,33,37,43)

* $\frac{\text{Feed} - \text{Faeces}}{\text{Feed}} \times 100$ Known as the apparent digestibility;
the faeces includes matter of endogenous origin as well as feed residues.

The abscissa in Figure 1 may be scaled in terms of the apparent digestibility of the feed dry matter, of the organic matter, or of the energy, and the actual values will range from a minimum of about 30 per cent to a maximum of about 85 per cent. In a certain range of digestibility, approximately 60 to 70 per cent, it has been found^(31,34,44,45) that there is an inflexion in the feed intake line. If the complement of this line is drawn,^{namely} that describing the change in faecal output, it is seen that as digestibility falls from the higher values the quantity of faeces excreted first increases^(37,45) and then becomes approximately constant,⁽⁴⁵⁾ but it will ultimately decrease. The finding that in the higher range of digestibility ruminant animals do not eat to the extent that they have to deal with feed residues as large as they evidently can excrete, implies that regulation of intake in this range is primarily physiological in type. Thermostatic or chemostatic mechanisms may then supervene at threshold levels determined by the metabolic activity of the animal, e.g., the level of milk production, so that intake will be adjusted to meet the physiological demand for energy.^(28,31,34,37,44,45,62) As feed quality falls physiological regulation becomes overshadowed, but certainly not superseded, by primarily physical effects to which most attention has been given in work done up to the present time.

In this discussion the chief interest lies in how the slope of the feed intake line, that is the change in intake per unit change in digestibility, and the position of the line, that is intake at a given digestibility, varies between feeds. Up to the present time, only a few publications have either given this information directly or provided data that are adequate in form and extent for re-calculation by regression analysis; available information is given in Table 1.

(Table 1 hereabouts)

The values for the regression coefficients will be considered first. Digestibilities of 70 per cent or more were, with few exceptions, found only with the temperate species. These species

were examined to determine if the regressions of intake on digestibility departed significantly from linearity in the manner illustrated in Fig. 1, but the observations were too few in number, or showed too much scatter, and no significant quadratic or higher terms were detected. The significant regression coefficients given in Table 1 show that for a change in digestibility of one unit in both temperate and tropical feeds, the corresponding change in intake varied between about 1.0 and 1.7 $\text{gDM/kgW}^{0.73}$. The effects that such a change in nutritional value will have upon animal production may be large. Blaxter⁽³¹⁾ has cited the example of two hays of 50 and 55 per cent digestibility respectively. If a sheep eats 62 $\text{g/kgW}^{0.73}$ of the former, and there is an increase in intake per unit of digestibility of 2 $\text{g/kgW}^{0.73}$, it will gain 28 per cent more energy in digested nutrients when offered the latter. This represents nearly a two-fold increase in the amount of energy available above maintenance needs, and so a 10 per cent increase in digestibility may promote nearly 100 per cent increase in liveweight gain. The particular importance of voluntary intake as a measure of the nutritional value of tropical roughages has been stressed by Milford.⁽⁴¹⁾ For a large part of the year the intake of many of these feeds may be below that required to meet the animals' needs.

The failure to obtain significant regression relationships for some of the feeds listed may reflect the variability between animals in intake performance and a paucity of data, but it is also possible that in these cases the rates of breakdown in the rumen were not adequately described by the digestibility data. Measurements of rates of breakdown or of rumen fill under steady state conditions⁽⁴⁸⁾ might resolve such anomalies unless a mechanism of intake regulation was involved other than through gut distension. This mechanism might involve humoral factors such as high concentrations of acetic acid in peripheral blood,^(49,50,51) or the nitrogen status of the animal.^(58,59)

The drastic reduction in intake and the low faecal excretion

when feed digestibility approaches the bottom of the range can still be explained fairly well in physical terms but also reflects the nutritional status of the animal and the state of the symbiotic "functional field"⁽⁵²⁾ of the rumen. Breakdown and digestion of feed in the rumen, though aided by the mechanical effects of mastication⁽⁵³⁾ and rumination,^(52,54) is mainly achieved by the activity of the resident micro-flora and -fauna. This activity profoundly affects the nutrition of the host (Chapter 3) but can also be regarded from another standpoint, that of the nutrition of the microbial population. Growth and activity of the population will be limited by, amongst other things, the supply of appropriate nutrients and it can be expected that variation in the supply will be reflected in the rates of processes in the rumen.⁽⁵⁵⁾ Roughages of low digestibility invariably contain low proportions of available nitrogen and there is evidence that a supply of nitrogen insufficient for the maintenance of an actively functional ruminal population is a major factor limiting the utilization of these feeds by ruminants.^(55,58,59) Shortages of some other nutrients for bacteria such as certain inorganic ions and branched chain fatty acids^(29,56) may also be associated with the limitation of intake when poor quality feeds are given.^(67,59)

There is a limited amount of direct information on the minimum level of dietary nitrogen necessary. Recycling of nitrogen, particularly of urea in saliva and by diffusion through the rumen epithelium, plays an important role in the nitrogen economy of the animal^(29,347) so that the effects of a change from a higher to a lower nitrogen ration may not immediately become apparent. In a long term trial with sheep given steadily decreasing amounts of nitrogen in the feed (800g dry matter per day), Moir and Harris⁽⁵⁵⁾ found that intakes started to fall when the nitrogen intake was below 7 g per day, that is about 0.8 per cent (5 per cent crude protein) in the feed that was used. Large changes were found within the rumen: the concentration of bacteria was greatly reduced as was the rate of digestion of cotton thread. In many

experiments where the nitrogen content of poor quality roughage diets has been raised by the addition of urea (see Chapter 27), the intake of these feeds has been increased and concomitant increases in the rates of digestion and passage have been observed.⁽⁶¹⁾ There have, however, been conflicting reports^(57,60) and recent work⁽⁵⁹⁾ suggests that increased nitrogen intakes, apart from any effects upon ruminal bacteria and the rates of digestion and passage of feed, may promote increases in voluntary intake because of an improvement in the nitrogen status of the animal. When casein was infused into the duodenum of sheep, their intakes of urea supplemented wheaten straw increased although there were no measurable changes in the rates of cotton thread digestion in the rumen, in dry matter digestibility, mean retention time of the feed in the alimentary tract, and the extent of rumination activity. Improvements in acetate and propionate tolerances were found suggesting that when dietary nitrogen levels and the nitrogen status of animals are low, intake is, at least in part, regulated chemostatically by the ability of the animal to cope with these (and probably other) metabolites.

Some other studies on the amounts of protein in feed associated with satisfactory consumption and efficient utilization have given results in general agreement with those of Moir and Harris.⁽⁵⁵⁾ Elliott and Topps⁽⁶³⁾ found that dry matter intake was positively related to crude protein content over the range 2.6 to 10 per cent; the data suggested that the effect was greater below rather than above 8 per cent. Blaxter and Wilson⁽⁶⁴⁾ suggested that a minimum level of 8.5 per cent was required and Milford and Minson⁽⁴⁷⁾ found that the intake of two sub-tropical herbage species declined significantly only when their crude protein content was 7 per cent or less. From a statistical study of a large volume of published data, Glover and Dougall⁽⁶⁵⁾ found that the digestibility of crude

fibre plus nitrogen free extractive began to fall markedly at crude protein levels below about 6 per cent.

All these reports suggest that improvement in the crude protein content of tropical and sub-tropical feeds, which is often well below even 6 per cent for long periods of the year, may be one of the important goals of the plant breeder in these areas. In temperate zones, conserved herbage and particularly hay may contain as little as 1 per cent of nitrogen because the material has been cut at a mature stage to obtain high yields per unit area, and may also have been badly processed. In these cases protein insufficiency is generally of less importance than the energy value, particularly if the feed forms only a part of the ration or is given for only part of the year when other feeds of higher protein content, such as fresh grass, are not available. If the herbage is cut at an earlier stage of growth in order to gain a conserved product of higher energy value then the protein content will also be higher.

The other feature of the data in Table 1 to be discussed is the variation in intake at a given digestibility which, with feeds that are not deficient in cobalt⁽¹⁹³⁾ or some other nutrient, reflects the subjective evaluation by the animal of its feed. For example, the intake by sheep of Setaria sphacelata at a digestibility of 55 per cent was barely two-thirds the intake of Sorghum alnum at the same digestibility by similar animals.⁽⁴⁷⁾ There appears to be greater variability of this type with tropical than with temperate feeds. In any case, significant relationships between digestibility and intake are more likely to be found within rather than between fodder species or varieties, and legumes, including lucerne (Medicago sativa) which is not very highly digestible (see Fig.2), tend to be eaten in greater amounts than are grasses.⁽³⁵¹⁾

Any understanding of the animal's subjective evaluation is necessarily limited and must stem from empirical observations on feed acceptability. These have been made in many trials where free choice of a number of different cut grasses or types of pasture^(66,67,68) has been allowed, but attempts to link the observations with objective measurements have so far met with little success. At the present state of knowledge animals appear to be fickle

in their choice; apart from differences due to their species, physiological state, experience and individuality the preferences of the same animal may vary at different times.^(69,70,71) The nature of the choice generally has little if any significance in the sense of self-regulatory nutritional "wisdom", i.e. the deliberate selection of a particular feed in an attempt to meet the need for a particular nutrient, though there are some exceptions as in the case of induced sodium deficiency.⁽¹²⁶⁾ The results of the choice may well be of importance from their effect on the amount of feed eaten and the resulting productivity of the animal. A striking illustration is provided by the syndrome of "ill thrift" in grazing lambs in New Zealand where it has been found that a major cause of poor growth during autumn is an abnormally low intake of herbage at this time.⁽⁷²⁾ A similar phenomenon, though smaller in magnitude, occurs elsewhere in the world.^(37,73) In wholly pastoral areas, relative unacceptability of some plants in a grazed community could be advantageous for these plants would then form a reserve of feed for use during periods of feed scarcity.⁽²⁶¹⁾

The senses of taste, smell, touch and sight are probably all involved in the determination of feed preferences.⁽⁷⁴⁾ Many characters of the plant that might perhaps affect the animal's choice such as hairiness or scent,⁽⁶⁹⁾ could be measured only with difficulty, if at all; the characters that were measured, say the degree of contamination with excreta, soil or fungi,⁽⁶⁸⁾ might be scaled in inappropriate units or their importance unduly weighted, whilst others contributing to the net assessment by the animal might be totally overlooked.

If part of the animal's response to a feed results from events occurring at the cellular level, e.g. in taste buds in the tongue, it is unlikely that chemical data expressed in such terms as crude fibre or

crude protein can be very useful indexes. Discrimination may be determined by the presence of an apparently novel constituent such as the unidentified substance(s) extracted from a cultivar of Phalaris arundinacea.⁽⁷⁵⁾ Of other plant constituents there is conflicting evidence on the importance of soluble carbohydrate level.^(67,77,78) This may be an imperfect index of acceptability because it is only one of a large number of associated variables in the feed. The same comment applies to observations made on the effects of the water content of a feed, both intra-cellular and on the surface as rain etc.^(76,79) The report by Arnold⁽⁸⁰⁾ that intake was directly related to water content in the range 14 to 28 per cent was based on measurements made on grazing animals during a period of active plant growth. The direct introduction of large volumes of water into the rumen, unless retained in a rubber bladder that physically reduces rumen volume, does not reduce intake by the animal.⁽⁸¹⁾

Much of the discussion on the effect of water stems from observations that the intake of silage increases with increasing dryness⁽⁸²⁾ but it is clear that water per se is not the causal factor.⁽⁸³⁾ Addition of water to or its removal from a silage does not alter voluntary intake which remains lower than the intake of hay made at the same time from the same type of herbage. Variation in the water content of silage is only one consequence of variation in the original material or in the ensiling processes; other constituents such as acetic acid^(49,50,51) and possibly some nitrogenous compounds,⁽⁸³⁾ but not histamine,⁽⁸⁴⁾ appear to have a metabolic effect that results in reduced intake.

It is well known that phosphorus deficient animals have depraved appetites⁽¹⁹⁰⁾ and that low feed intakes are characteristic in cobalt deficiency.⁽¹⁹³⁾ Some effects of major mineral fertilizers will be discussed in a later section.

DIGESTIBILITY

Probably the most useful single measure of the nutritional value of a grassland feed is its apparent digestibility. Apart from the effect on feed intake already discussed, the digestibility value is a measure of the largest and most variable single loss to the animal, by excretion, of energy and nutrients. For temperate grasses the minimum loss of energy in faeces represents about 15 per cent of intake and the maximum rarely exceeds 50 to 55 per cent; corresponding values for tropical materials are about 25 to 70 per cent respectively. In contrast the losses of energy in urine or as methane do not, in either case, usually exceed 8 to 10 per cent of gross energy intake.⁽²¹⁾

The digestibility values obtained for a feed using healthy ruminant animals have shown only small variation due to differences in species, breed, physiological state, age, activity and physical environment, provided that the feed is given to the animals at a standard level.^(86,87,88,92) Level of feeding can be assessed by reference to the quantity required to achieve zero energy retention (maintenance), and the effects of variation in level are illustrated by the results of a large number of trials reported by Blaxter.⁽⁸⁹⁾ An increase from a maintenance to a twice maintenance level in the intake of dried grasses and hays given in long form was accompanied by a fall in digestibility of 0.119 times the indigestibility at the lower level, the fall consequently being greater for feeds of lower rather than higher quality. An effect due to level of feeding was also found with fresh herbage that was preserved by freezing;⁽⁹⁰⁾ that it was not detected in another study⁽⁹¹⁾ probably reflects the difficulties of measuring dry matter intakes accurately when green material, which shows short-term changes in moisture content, is given.

The greatest differences in digestibility between feeds are

those due to differences in stage of growth, and as the plants mature their composition shows large changes. Some examples of the effect of age on the digestibility and composition of temperate herbage species are shown in Fig. 2A and Table 2.

(Fig. 2 and Table 2 hereabouts)

The general pattern of change is much the same for all species but there are some characteristic differences. Legumes as a class, with the notable exception of lucerne (Medicago sativa), maintain a place amongst the most digestible components of pasture herbage and this is also true of tropical legumes (Fig.2B). The digestibility of some of the temperate grasses such as ryegrass (Lolium perenne) and cocksfoot (Dactylis glomerata) remains roughly constant for some time after active growth has commenced in the spring.⁽⁹³⁾ At about the time of ear emergence digestibility starts to fall at a rate of 0.3 to 0.5 units daily, a change that occurs in timothy (Phleum pratense) from the start of growth. The digestibility of the cocksfoot varieties now in use is consistently lower than that of many other cultivated species though it may prove possible to breed improved varieties.⁽⁹⁴⁾

Chemical and botanical changes are exemplified by the detailed analyses of a ryegrass variety (Table 2). As with digestibility, the changes in temperate species conform to one general pattern though the absolute values for composition will vary. For example, the concentration of soluble carbohydrate tends to be lower in cocksfoot and timothy than in ryegrass,⁽²⁰⁸⁾ and legumes generally contain larger amounts of nitrogen and minerals than grasses. The earliest growth increments in spring are due to increases in leaf lamina and leaf sheath. These parts of the plant contain proportionately more nitrogen, lipid, carotene and minerals and less lignin, and are more digestible, than the stem which begins to elongate rapidly once the flowering head emerges.^(100,112) The leaf lamina then becomes a steadily smaller proportion of the whole plant.

To the animal the most important change is the progressive increase in structural constituents and especially lignin which, with a variety of other substances, contribute to the crude fibre fraction that is commonly determined (see Chapter 1). Even in the young plant, cellulose and hemicellulose comprise at least one-third of the dry matter, but are then highly digestible.^(97,101) As their concentration in the plant increases to 50 per cent or more, so their digestibility decreases. This may be due in part to physico-chemical changes, such as an increasing crystallinity^(97,102,103) or degree of polymerization of the cellulose, but is mainly due to increasing lignification. Lignin is virtually indigestible - the disappearance of small amounts in passage through the gut may be an artifact arising from difficulties in exact chemical determination^(104,105) - and it reduces the extent and the rate of breakdown of the structural carbohydrates by combining chemically with them to form materials that are resistant to enzymic degradation, as well as by forming physical barriers to digestion.^(97,102,105,106,348)

The increase in structural components is accompanied by a decrease in the crude protein (nitrogen x 6.25) content of the plant and lignification of cell walls will impede the digestion of this and other constituents. Values obtained for the apparent digestibility of the crude protein, however, reflect the large amounts of metabolic faecal nitrogen (M.F.N.) excreted by the animal.⁽³⁴⁹⁾ This excretion includes cellular detritus from the gut mucosa, glandular secretions such as mucoproteins and digestive enzymes and microbial protein, and can be related to the amount of feed eaten, about 0.4 g nitrogen being excreted per 100 g feed dry matter.^(107,108) As dietary crude protein levels fall from initially high values the M.F.N. becomes an increasingly large fraction of total faecal N. Apparent digestibility consequently declines with increasing rapidity from a maximum of 80 to 85 per cent until at a crude protein concentration in the dry matter of from

2 to 4 per cent, zero and negative values are found.^(109,110) Most of the nitrogen in the plant is organically combined though as much as 30 per cent may be in non-protein form. This fraction is soluble in water and normally includes some 5 to 10 per cent of inorganic nitrogenous compounds.^(111,112)

The water soluble carbohydrates can constitute from as little as 1 to more than 30 per cent of the plant dry matter and are wholly digestible. The concentration does not follow a readily definable pattern but reflects the balance between the rate of production by photosynthesis and the rates of utilization in energy metabolism, for the elaboration of polysaccharides and protein for growth, and for storage in root or seed, as determined by the physiological state of the plant.^(100,112)

Under many systems of management grassland herbage may be utilized almost as it grows, allowing little opportunity for large changes to occur in digestibility and composition due to maturation. When successive month-old regrowths of temperate grasses are examined it is generally found that they are not as digestible as the first growths in spring although in late summer the plants may consist almost entirely of leaf lamina and contain considerably more crude protein.^(99,113,114) Later growths of leaves have been found to contain greater amounts of structural carbohydrates than first growths⁽¹¹⁵⁾ and water soluble carbohydrate contents are usually low.⁽¹¹⁶⁾ If herbage left standing through the winter suffers frost damage and leaching the material remaining green can be of good quality but the digestibility of the entire plant falls appreciably.⁽¹¹⁷⁾

Tropical herbage plants are almost all adapted to a short growing season before flowering. Seasonality of rainfall and of adequate soil moisture often restricts growth to short period(s) of the year and though the first, vegetative, growth can be 75 per cent digestible and contain from 15 to 20 per cent of crude protein the rapid onset of flowering causes a rapid decline in quality.⁽¹¹⁸⁾ The crude protein content of the grasses becomes so low that negative apparent digestibilities and negative nitrogen balances in animals maintained on these feeds are common.⁽⁴¹⁾ If frost occurs in subtropical areas it kills the aerial growth of many of the legumes and of indigenous grasses; dry mature growths of cultivated grasses here and in tropical regions often decline in quality rather slowly during the dry season (0.05 to 0.15 units of digestibility per day - Fig. 2B) as do surviving legumes.⁽⁴⁷⁾ Analyses as detailed as those given in Table 2 have not been reported for tropical grasses but these plants do show similar changes in composition with age. Even young growths, however, rarely contain less than 30 per cent of crude fibre in the dry matter, later increasing to over 40 per cent when crude protein contents can fall to as low as 1 or 2 per cent.^(41,119,120)

UTILIZATION BY THE ANIMAL

Not all the energy of the apparently digested nutrients is available to the animal for cellular metabolism. The microbial digestion of cellulosic feeds results in the production of considerable volumes of methane and its removal by eructation, and the loss of energy from the rumen as heat of fermentation which is of no consequence to the animal in a thermo-neutral environment. By convention, the apparently digestible energy minus the methane energy, but not the heat of fermentation, and minus the gross energy of the urine is referred to as metabolizable energy.

At maintenance levels of feeding and above, the urine energy does not usually amount to more than 8 per cent of the gross energy of the feed. (89) The loss tends to decrease with increasing intake (98) but shows little relationship with feed digestibility. It is better described by the amount of carbon in the urine (89) than the amount of nitrogen (123,124) which reflects the nature of the diet. Herbage of high digestibility generally have a high nitrogen content and in excreting more nitrogen in the urine than from feeds of lower digestibility and nitrogen content, the animals lose a larger proportion of energy intake. (73,98) Only part of the nitrogen is excreted as urea with a calorific value of 5.45 kcal/g nitrogen. Large amounts of hippuric acid, the purine derivatives uric acid and allantoin, and detoxication products are excreted as well as xylose and other non-nitrogenous compounds, as in the special case of essential oils from some desert range plants. (21, 121) The excretion of all these substances is in part a consequence of ruminal digestion and the metabolic activity of the micro-organisms, (122) and may result in a heat of combustion as high as 35 kcal/g urinary nitrogen. (21)

In general the methane produced in the digestion of herbage represents about 8 per cent of total energy intake. The loss tends to decrease with decreasing apparent digestibility of the feed; again as a percentage of total intake, it tends to decrease as the level of feed intake rises. (89,98) These effects reflect changes in the extent of breakdown of holocellulose which chiefly determines the digestibility of the herbage diet as a whole. (97) Several workers have reported that around 4.7 g of methane are produced per 100 g digested carbohydrate. (125) These relationships are not entirely satisfactory perhaps because "digested carbohydrate" is determined only indirectly by the Weende system of summative analysis (see Chapter 1) and is the digested crude fibre plus digested nitrogen-free extractive. A better relationship would be expected with directly determined chemical entities as has

been found in one case where methane and digested cellulose were examined.⁽⁷³⁾ Wolin⁽¹²⁷⁾ has proposed a theoretical rumen fermentation balance which allows the estimation of methane production from the molar proportions of acetic, propionic and butyric acids in ruminal liquor; this approach has received some support from experimental observations.⁽¹²⁸⁾ Calculation from the balance equation of the heat production associated with cellulose fermentation gives a value of about 7 kcal/100 kcal cellulose digested which is in good agreement with that of 6 kcal obtained by Marston.⁽¹²⁹⁾ If methane is used as an index of fermentation heat Marston's data yield the relationship of 0.8 kcal/kcal methane which is the most generally accepted of the few estimates available.^(130,131)

The loss of up to 15 per cent of the gross energy of roughages as methane plus heat can be regarded as a price to be paid for the microbial digestion that permits the utilization of these feeds by the animals. Quantitatively, the most important end products of the digestion are the steam-volatile fatty acids (V.F.A.) acetic, propionic and n butyric and together they probably provide well over half the total energy supply of ruminants.^(132,133,134,262) The efficiency with which the energy of V.F.A. is utilized by the animals appears to vary with the molar proportions of the acids in the mixture and the purpose for which they are used. The efficiency of lipogenesis increased as the proportion of acetic acid fell,⁽¹³⁵⁾ though conflicting results have recently been reported.⁽³⁵²⁾ The efficiency of milk synthesis changes in a similar way unless the fall is very large, and the propionic acid levels are high; milk fat production then decreases markedly due to a change in the supply of acetate and β hydroxybutyrate precursors.⁽¹³⁶⁾ A marked decrease, to 2 per cent or less of fat in milk rarely occurs when cows are at pasture⁽¹³⁷⁾ unless the feed contains exceptionally low amounts of structural carbohydrate. It is also uncommon when rations, even those including large amounts of readily fermentable

carbohydrate feeds such as cooked maize, contain more than about 25 per cent of long roughage.⁽¹³⁸⁾ The efficiency of utilization of V.F.A. for maintenance also appears to vary inversely with the proportion of acetic acid but the range of the variation is much smaller than that shown when fat or other materials are synthesized.^(73,98,139)

Of the V.F.A. produced from herbage feeds, acetic acid normally constitutes from 50 to over 70 per cent of the ^{molar} total.⁽¹³⁴⁾ Many studies have now shown that a change from lower to higher values, and a corresponding reduction in the proportion of propionic plus butyric acids, accompanies increasing maturity and fibre content and decreasing digestibility of the feed.^(140,141) This change is also reflected in the performance of animals; the percentage utilization of the M.E. of the diet falls (see Table 2). Variation in the proportion of acetic acid is also related, inversely, to water-soluble carbohydrate which promotes the formation of propionic acid.^(134,140,142) Relationships between the composition or digestibility of the feed and the proportions of propionic or butyric acids have generally not been so precise as those with acetic acid. There appears to be a fine balance in the rumen between conditions that favour the relatively greater production of either the C₃ or the C₄ acid;⁽¹⁴⁰⁾ the outcome may depend in part upon the extent of acetate-butyrate interconversion.⁽¹⁴³⁾

As with digestibility values, V.F.A. proportions show some variation between herbage species. They show rather small changes with increasing maturity of pasture legumes and the acetic acid level tends to be higher when cocksfoot, rather than other temperate grass species, is eaten.⁽¹⁴⁰⁾ In addition, tropical herbages yield higher proportions of acetic acid than temperate feeds;⁽¹⁴⁴⁾ this would be expected from the difference in crude fibre contents.

There has been considerable discussion on the nutritional significance of the water-soluble carbohydrates⁽¹¹⁴⁾ which quite often constitute as much as one-quarter of the digestible dry matter of temperate herbage. Substances so reactive, and in such amounts, must have a considerable effect on the course of microbial digestion. It is known that ammonia concentration in the rumen falls when a readily available carbohydrate, starch, is added and there are probably effects on the nitrogen economy of the animal⁽¹⁴⁵⁾ (see Chapter 3). In addition, the production of V.F.A. containing a high proportion of propionic acid could be expected to improve animal performance but there is, as yet, little supporting evidence. Workers in New Zealand^(146,147) reported that carcass-weight gains by sheep at pasture could be related to the carbohydrate contents of the herbage but no measurements were made of the quantities eaten and these effects could well have been confounded with those due to differences in feed intake.⁽²⁷⁶⁾ More certain evidence was obtained in a calorimetric trial⁽⁷³⁾ where studies on two herbage of very similar chemical and botanical composition, apart from a difference in soluble carbohydrate content, and of the same digestibility, yielded a consistent series of observations. The cellulose of the herbage with the higher sugar content was digested to a significantly smaller extent and less methane was produced; the V.F.A. produced in the rumen included a significantly higher proportion of propionic acid, and the metabolizable energy of the feed was used by the animal more efficiently.

ASSESSMENT OF NUTRITIONAL VALUE

It is desirable that any feed can be described in terms of its nutritional worth in a particular set of circumstances so that the performance of individual animals can be predicted, or determined, with some precision.⁽²¹⁾ When confronted with the immense range of

feeds produced by grasslands the problem is to select one or more common characteristics that can be determined readily and will give reliable estimates of feeding value.⁽¹⁴⁸⁾

Biological Methods.

The ultimate test of a feed is animal performance and if this is measured in terms of energy and nitrogen retentions, uncertainties about the caloric and protein contents of liveweight gains etc. are largely resolved. Nitrogen retention can usually be measured at the cost of little extra analytical work when digestibility trials are made. On the other hand the measurement of energy retention involves much skilled but laborious and time consuming work⁽¹⁴⁹⁾ (see Chapters 30 and 31).

Feeding systems based on the net energy concept, which stems from the fundamental calorimetric work of Kellner and Armsby have, however, been used in practice in Europe for many years. The evaluation of feeds for these systems - starch equivalent (SE), Scandinavian Food Unit etc. - is based on measurements of digestibility as is the Total Digestible Nutrient (TDN) system of N. America. It is done by summing the quantities in the feed of the digestible nutrients determined as true or crude protein, crude fibre, nitrogen free extractive and crude fat with weightings that approximately represent their relative energy values. To calculate the SE of roughages the values obtained are then reduced by between 0.29 and 0.58 times the crude fibre content of the feed as used, depending upon the amount present. This has the apparently odd result that if the lower factor (0.29) is appropriate to a fresh herbage the higher factor will apply to the same material after it has been dried.^(150,151)

That a single feed may be assigned values which differ widely according to the method of assessment is due to inconsistent assumptions

about the efficiency with which the energy of digested nutrients is used by the animal; it also reflects the inherent but mistaken view that a unit of SE or TDN etc. has constant value to the animal regardless of the purpose for which it is used.⁽²¹⁾ Nevertheless, measurements of digestibility remain as a firm basis for the assessment of energy value. As Dijkstra⁽¹⁵¹⁾ has pointed out, the calculation of SE is essentially the application of the crude fibre "correction" to the digestible organic matter (DOM) content of the feed. The situation with TDN is similar. Swift⁽¹⁵⁾ has described its determination as a laborious, cumbersome, indirect and inaccurate effort to determine digestible energy. From a study of many roughages he found that the caloric value of the TDN was 4.41 ± 0.13 kcal/g. Very similar values, showing slightly larger variation, are commonly found for the energy value per g of the digestible dry matter (DDM) or DOM of grassland feeds. This result reflects the large contributions of cellulose (4.2 kcal/g) and other polysaccharides with varying, but smaller, amounts of protein (5.7 kcal/g) to the energy they supply. Crude fat is a relatively small part of this supply and a significant fraction of the ether-extractable material of herbage comprises plant pigments, fatty acids, nitrogenous substances and even some ash;⁽¹¹²⁾ consequently the standard value for the heat of combustion of fat, 9.5 kcal/g, is usually inappropriately high.

Measurements of the amounts of DDM or DOM consumed by cattle and sheep therefore provide good estimates of apparently digestible energy intake and may be obtained fairly readily. Measurements in terms of OM are often preferred to those on a DM basis because mineral matter, which as such has no energy value to the animal, is excluded and because the ash content of the feed, which is normally some 5 to 10 per cent of the dry matter, may be increased massively by contamination with soil. The calorific value of DOM, however, tends to be a little more variable than that of DDM,⁽¹⁵³⁾ probably because variation in the amount of

protein has a proportionately greater effect.

Moir⁽¹⁵⁴⁾ has shown that there is almost a 1 : 1 relationship between the per cent apparently digestible energy (Y) and per cent dry matter digestibility (X) over a range of X from 30 to 73. The regression equation that he obtained : $Y = 1.006 X - 2.013$ accounted for 99.6 per cent of the variation in Y. For a large number of feeds of different types (but apparently excluding oil-seeds which have high heats of combustion), of digestibilities (X) from 30 to 83, and given at various levels to both cattle and sheep, he found that 96.2 per cent of the variation in digestible energy kcal/gDM (Y^1) was accounted for in the equation $Y^1 = 0.0462 X - 0.158$. The range in Y^1 was from 1.24 to 3.65 kcal/g. A similar and precise relationship for sub-tropical herbage has been reported.⁽¹⁵³⁾

The determination of per cent apparently digestible energy (ADE), or of DM digestibility if a bomb calorimeter is not available, can also lead directly towards the evaluation of feeds for the feeding system proposed by Blaxter.^(21,155) In this system rations are devised so as to predict animal performance on the bases of the amount and concentration of metabolizable energy (ME) in the feed(s) to be supplied. The determination of ME requires the measurement of methane production as well as of energy losses in faeces and urine but only small errors accrue if ME is assumed to be 80 per cent of ADE.^(21,98,152)

The apparent digestibility (D) of the energy, DM or OM of a feed times its voluntary intake (I) gives the total digestible intake (DI). As has been seen (Fig.1), I and D are correlated and the question arises: which of the two is the more important in determining DI and thence the level of animal production? The data of Miller,⁽³⁵⁾ Milford,⁽⁴¹⁾ Minson,⁽³³⁾ and Conrad⁽³⁶⁾ were examined by the method of Henderson and Hayman⁽¹⁵⁶⁾ who showed that when a regression analysis of the type

$\log_{10} DI = \log_{10} I + \log_{10} D$ is made, the regression coefficient $b_{x_i y} = (\text{Cov}(y, x_i) / \text{var } y)$ represents the proportion of the variation in the dependent variable y that is attributable to variation in x_i .

It was found with both temperate and tropical herbage that from 60 to 75 per cent of the changes in DI were accounted for by changes in intake as such. Voluntary intake therefore appears to be a better measure of the value of a feed than its digestibility determined under the usual conditions of restricted, constant, daily intake. Measurements of digestibility, and thence of DI, can of course be obtained whilst voluntary intake is being studied but there is a practical difficulty. The variation in digestive efficiency between animals, expressed as a coefficient of variation, is generally found to be of the order of ± 2 per cent but the variation in intake is some five times greater. Thus if groups of three animals are used there would be a 90 per cent chance of showing a digestibility difference between two feeds of about 5 percentage units, or more, significant at $P = 0.05$ but there would be a similar chance of showing a significant difference in intakes only if the difference was as large as approximately 40 per cent. There may well not be the facilities available for groups of ten animals which are required if differences in intake of from 15 to 20 per cent are to be detected. (33,157)

If the voluntary intake of ADE can be measured it does predict quite closely the performances of similar animals given the feed ad libitum. Crampton and his colleagues⁽³²⁾ have devised a "nutritive value index" (NVI) which is essentially the ADE(kcal) consumed per kg liveweight^{0.75}; their index could more simply be expressed in these terms than by taking the further step of dividing by the arbitrary constant 80 (the "expected intake of Standard Forage" in $g/kg^{0.75}$) to obtain the NVI.⁽¹⁵³⁾ Correlations between NVI and liveweight change of from + 0.88 to + 0.94 have been reported when a change of 0.5 kg in

liveweight over a period of 11 days was found to reflect a change in NVI of about 8 units.⁽³²⁾

Digestibility values themselves certainly provide a good general index of the nutritional value of feeds but how meaningful is this index when differences in digestibility are small? For example, are the differences of about five percentage units between ryegrass and cocksfoot at similar stages of growth (Fig.2) reflected in animal performance? It has been found in practice ⁽¹⁵⁸⁾ and in controlled experiments ^(159,160) that cocksfoot pastures do not sustain milk production by cows at as high a level as that concurrently obtained from ryegrass; a corresponding difference in lamb growth-rates has also been reported.⁽¹⁶¹⁾ These effects, however, are probably not due simply to the lower digestibility or intake of cocksfoot; it is likely that they also reflect differences between the grasses in the metabolites they yield on digestion. When growing lambs were given equal amounts of digestible dry matter as either cocksfoot or ryegrass it was found ⁽¹⁶²⁾ that significantly more of the digestible energy of the ryegrass was retained as a significantly higher carcass gain, and that this grass gave a lower proportion of acetic acid in the ruminal VFA.

Do the molar proportions of VFA or their concentrations in the rumen provide a good index of nutritional value? As shown above and on page 21, relationships between the proportions and animal performance may be found in experiments where feed intake is controlled but the significance of, say, a high proportion of propionic acid cannot, as such, be readily assessed. If a "good" acetic:propionic:butyric ratio of 60 : 25 : 15 respectively referred to a total energy supply from these metabolites of 1 Mcal/day it could not be expected that an animal would fatten more quickly than on a feed yielding 2 Mcal/day of a "poor" 75 : 15 : 10 mix, although this mix might be used less efficiently for lipogenesis.⁽²¹⁾

There are still some further problems. The proportions of the acids may vary with time between animals and between sites in the rumen. Their concentrations at any particular point in time represent (134) the balance between production, absorption, passage along the intestinal tract and conversion to other compounds (134) in a rumen that can vary considerably in volume. (163) Recent work (133, 143, 262, 263) suggests that concentration does indicate the rate of production but account must also be taken of the contributions to the total energy and nutrient supply made by other metabolites. For example, when two dried grasses were given to lambs the resulting VFA patterns showed significant differences but energy retention by the animals were similar; it appears that other differences between the feeds, especially their nitrogen content, played a part in determining the result. (164)

If nitrogen retention by the animal is measured it can be used to assess the protein sufficiency of a feed only when the energy retention is zero or positive. When in negative energy balance the animal catabolizes body tissues with a consequent increase in urinary nitrogen excretion and its losses of nitrogen, which tend to steady at a certain maximum value before death ensues, are more related to a dietary deficiency of energy than of protein. (110)

Chemical Methods.

The marked changes in the chemical composition of herbage that occur as the plants mature provide obvious indexes of the accompanying changes in feeding value. Innumerable relationships have been reported and here they will be discussed only in the general terms of their validity and usefulness.

For the prediction of the available energy of herbage, expressed in such terms as dry matter digestibility, SE, TDN, etc., and as net energy values ⁽¹⁶⁷⁾, indexes used have included nitrogen, crude fibre, lignin, methoxyl (part of the lignin molecule), and normal-acid fibre (similar to the crude fibre determination but omitting the alkaline extraction).^(95,165,166) The most commonly used index of the digestible crude protein in a feed is its crude protein (N x 6.25) content.

In predicting energy values some relationships and indexes are relatively more successful than others. Raymond ⁽¹⁶⁸⁾ has demonstrated the inadequacy of nitrogen : OM digestibility equations; from the results of 260 digestibility trials with grassland herbage he showed that a content of 2.5 per cent N indicated only that the digestibility lay somewhere between 53 and 83 per cent - "one could easily have guessed better than this." To a greater extent than with structural carbohydrate and lignin the relationship of nitrogen with digestibility is associative rather than causative. Precision is increased if the range of feeds included in the regression equation is restricted, but the residual standard deviation is still no smaller than \pm 3 to 4 digestibility units which is the level of precision of most equations whatever chemical index is used. These values mean that little confidence can be placed in calculated differences between feeds if the differences are less than 7 to 9 digestibility units.

Prediction equations are usually based on data from a restricted range of feeds but far too often the equations are applied quite out of context. As an example the equation of Watson and Horton ⁽¹⁶⁹⁾ that related SE to crude protein content is often quoted although these authors warned that it should be applied only to "grassland herbage containing a fair proportion of clover." Even if this advice is

heeded and the application is appropriate, the precision with which SE will be predicted will not be high as they themselves pointed out; the equation had a residual standard deviation of ± 3.6 .

The failure of chemical methods to classify feeds according to their energy value with the precision that is often required reflects the inadequacy of the usual analytical techniques. Thus the determination of the gross amount of lignin in a plant does not indicate how it is distributed within the plant and its location relative to other components may be of importance.^(105,106,170) In addition, it is difficult to see how even quite extensive analyses could readily explain biological phenomena such as differences in feed acceptability. It is possible that a case could be made for simply measuring the proportion of a feed that was soluble in water⁽¹⁷¹⁾ for this would at least determine the most reactive substances entering the rumen, namely soluble carbohydrates and nitrogenous compounds. Nevertheless there is every reason to suppose that analytical techniques that have been current for 100 years or more, the crude fibre and similar methods, can be improved upon, leading to a much better identification of feed quality (see Chapter 1).

The digestibility of the crude protein in herbage or the amount of digestible crude protein (DCP) it contains can be predicted satisfactorily from the chemically determined N content. The true digestibility appears to show little variation around a value of 90 to 92 per cent but the apparent digestibility (Y) falls exponentially with decreasing concentration (X) because of the increasing amounts of MFN (p.16) excreted relative to the amounts of undigested feed N. This is illustrated by Mitchell's⁽¹⁷²⁾ equation $Y = 42.64 (X - 5)^{0.215}$ which he derived from a large body of data. Glover, Duthie and French⁽¹⁰⁹⁾ suggested that their equation $Y = 70 (\log_{10} X) - 15$, which was also derived from a large amount of published information, was more satisfactory at the lower values of X. Other rather similar

equations to describe relatively restricted ranges of temperate (114,173) and sub-tropical⁽¹¹⁰⁾ forages have been reported. The small differences between values of Y predicted from the various equations for a given value of X probably reflect differences between genera of animals (sheep vs. cattle) and between species (Bos indicus vs. B. taurus)⁽¹⁷⁴⁾ as well as between feeds. Whereas Glover et al found that Y became zero at a crude protein content of 1.8 per cent, Milford and Haydock⁽¹¹⁰⁾ observed a value of 3.9 per cent and also found that zero N retention in the animal was attained at a digestibility of 49.3 (95 per cent confidence limits approximately ± 2.5).

The amount of DCP (Y^1) in the feed may be of more interest than the digestibility of the crude protein when animals are hand-fed. Rectilinear regression equations of Y^1 on the amount of crude protein in the feed have been reported^(173,175) that had low residual standard deviations in the range ± 0.46 to 0.85 per cent.

Other Methods.

In-vitro digestibility. - A quasi-biological method, the in-vitro digestibility technique, is now being used increasingly. In one two-stage technique^(176,177) that is widely employed, small (0.5 g) samples of dried, ground, forage are incubated anaerobically at 38°C in glass tubes containing buffered ruminal liquor. After 48 h the tubes are centrifuged, or their contents are filtered, and the solid matter is incubated with pepsin solution for a further 48 h. From the weights of dry matter or organic matter remaining, which are adjusted by applying the results of determinations on blank and on standard samples, the in-vitro digestibility is calculated. In another technique⁽¹⁷⁸⁾ the proportion of the cellulose in a feed that has disappeared after incubation for 12 h with buffered ruminal liquor is related to the Nutritive Value Index. A further method⁽¹⁷⁹⁾ is to insert into the rumen of an animal by way of a fistula, a nylon mesh bag containing a

sample of feed and to measure the rate of loss from the bag.

Criticism of these techniques on the grounds that they do not - and cannot - exactly match in vivo digestion is misplaced. Their purpose is to obtain a useful and repeatable measurements, and the use of ruminal liquor as a source of a wide range of cellulolytic and other enzymes is primarily a matter of convenience rather than of imitation. It may become possible to replace the liquor by standardized enzyme preparations.⁽¹⁸⁹⁾ Unfortunately, the relationships of the results to digestibility values obtained for the same feeds from animals are often reported as correlation coefficients (r). The information required is not simply that the coefficient of determination ($r^2 \times 100$) is, say, 85 per cent, which may in any case be unduly affected by a few of the results obtained, but it is the precision with which a value can be predicted.

Tilley and Terry⁽¹⁷⁶⁾ applied their two-stage technique to measure the in vitro digestibility (X) of 148 different samples of grasses and legumes of known in vivo digestibility (Y). The residual standard deviation of the rectilinear regression equation of Y on X was ± 2.31 units of digestibility. This value, which is of the same order as those found from other, similar experiments,⁽¹⁷⁷⁾ still means that estimated values of Y that differ by less than 6 digestibility units will not be significantly different. Nevertheless this is a greater degree of precision than can be achieved with any other general relationship for the prediction of digestibility, such as those based on chemical composition. The technique can be applied to problems which purely chemical methods of analysis have been unable to solve, and which could not readily be studied in vivo. For example, the separate digestibilities of the leaf and stem fractions of growing herbage can be studied and the information obtained sheds light on the spring "plateau" of digestibility (Fig.2).^(176,180) It is also of great value in plant breeding work

where very large numbers of individual plants, each yielding rather small amounts of herbage, have to be examined; plants showing significant differences can be chosen for further study. For this work the index for the initial selection can be in vitro digestibility as such. If care is taken to maintain anaerobic conditions during the fermentation stage, and well defined standard samples of high and low digestibility are included in each run for comparison, the standard error of the mean of duplicate measurements is usually less than one digestibility unit; between runs it is a little over one unit.^(176,177) If the intention is to predict in vivo digestibility or metabolizable and net energy values,⁽²⁷⁰⁾ then a regression equation must be obtained by the individual worker for his own situation.

Date of Cutting. - Reid⁽¹⁸¹⁾ reported that the dry matter digestibility (Y) of first growths of herbage species grown in the N.E. regions of the U.S.A. was related to time of cutting in days elapsing after April 30 (X) by the equation $Y = 85.0 - 0.48 X$; the residual standard deviation was ± 1.65 per cent. This is a general description of digestibility: time relationships appropriate to the latitude where the data were obtained; other starting dates would apply in other latitudes.⁽⁹⁵⁾ The rate of decline in digestibility, 0.48 units daily, approximately corresponds to the rates illustrated in Fig. 2 but would not take account of the early "plateau" in digestibility of ryegrass and cocksfoot found in the U.K. Cocksfoot varieties grown in Europe have not been found to be as digestible as 85 per cent, the theoretical maximum from the equation which does not distinguish between this and other species or between early and late growing varieties. Minson et al.⁽⁹⁹⁾ pointed out that on one day the digestibilities of first growths of cocksfoot (var.S37), ryegrass (S24) and ryegrass (S23) were 59, 65 and 75 respectively.

This type of equation is not readily derived for second and

later growths of herbage but is of value in practice when the time to harvest a first cut for conservation has to be decided.

Plant Morphology. - Although a leafy herbage can be expected to be more digestible than one containing a high proportion of stem the relationship between digestibility and the per cent of dry matter yield as leaf lamina is by no means precise. When monthly regrowths of ryegrass and cocksfoot were examined⁽⁹⁹⁾ it was found that the second growth was more digestible than the first although it had the lowest leaf percentage in the series and contained some flowering stems. In subsequent regrowths the leaf percentages increased but so also did the contents of hemicellulose and lignin⁽¹¹⁵⁾ and the digestibility of the whole plants fell. Data on the in vitro digestibility of leaf, leaf sheath and stem fractions and on the in vivo digestibility of feeds made up to contain these fractions in different proportions show that stem, particularly if of recent growth, can be at least as digestible as leaf.⁽³³⁾

Entries in tables of feed composition are frequently in such terms as, "meadow hay, good average".⁽¹⁸²⁾ Morphological characters are also the basis of the official hay grading system in the U.S.A.⁽¹⁸³⁾ When forages so identified are given to animals the results are frequently a salutary reminder of human fallibility.

Miscellaneous. - Attempts to substitute small laboratory animals for the larger ruminants to determine digestibility have not been very successful.⁽¹⁸⁴⁾ Other methods of evaluation proposed have included measurements of the weight gains of cricket nymphs given ground herbage,⁽¹⁸⁵⁾ microscopic examination,⁽¹⁸⁶⁾ the rate of breakdown during mechanical maceration,⁽¹⁸⁷⁾ leaf strength⁽¹⁸⁸⁾ and various enzymic and chemical procedures^(171,189) (see Chapter 1).

General.

The nearest approach to a single, comprehensive measure of nutritional value is probably the voluntary intake by animals of digestible dry matter but if low values are found they may be due to any of a number of causes that will not be directly measured. The criteria of nutritional value chosen will depend on the facilities available, the precision required and any special circumstances. Biological methods are to be preferred to chemical if the number of feeds to be examined is not too large but it may be wise to determine mineral content(s) when deficiencies are liable to occur. In temperate areas energy value is of prime importance; in sub-tropical areas Milford⁽⁴¹⁾ suggests that voluntary intake, the digestibility of dry matter and crude protein, and nitrogen balance should be measured. If prediction equations are used their validity should be checked and notice should be taken of their precision as indicated by the residual standard deviations rather than by correlation coefficients. Digestibility determinations in vitro are generally more precise, and with proper care are more accurate than values calculated from the chemical composition of the feed.

MINERALS. FERTILIZERS.

An extensive review of world literature on deficiencies and excesses of minerals in pasture herbage was published in 1956.⁽¹⁹⁰⁾ Since that time it has been recognized that selenium, already known to be present in excess amounts in the vegetation of considerable areas of the N. American continent where chronic selenium poisoning occurs, is an essential nutrient and that deficiency states in grazing animals are of widespread occurrence.^(191,192,193,265) The major clinical manifestation is a muscular dystrophy in lambs and calves often referred to, descriptively, as white muscle disease; infertility in

ewes has also been observed. Growth is retarded when available selenium levels in herbage are below about 0.1 p.p.m.; there have been many reports of increased rates of liveweight gain after the sub-cutaneous injection or oral administration of 1 to 5 mg (lambs) or 10 mg (calves) of the element, usually as selenate or selenite. The very narrow margin between sufficiency and toxicity makes the direct application of seleniferous fertilizer to pasture too hazardous a means for correcting Se deficiency.

A second major advance made in recent years has been the development of the cobalt "bullet", now very widely and successfully used for the prevention and correction of Co deficiency in grazing animals.⁽¹⁹⁴⁾ The bullet, about 2 cm³ in volume, contains cobalt oxide and in order to reduce chance regurgitation⁽²⁶⁴⁾ is so made that it has a high specific gravity. It remains in the reticulo-rumen after oral administration and yields a steady supply of Co to the ruminal liquor. A steel grub-screw of similar size is also usually administered so that the surface of the bullet will be abraded continually, preventing the deposition of an impermeable coat of calcium phosphates.⁽¹⁹⁵⁾

The concentrations of minerals in plants reflect the inter-relations between (1) genus, species or strain of plant; (2) the nature of the soil; (3) climate and season; and (4) the stage of maturity of the plant.⁽¹⁹³⁾ It has to be remembered however, that a change in the amount of a mineral in plant matter does not necessarily represent a change in the amount available to the animal⁽¹⁹⁶⁾ and that a dietary level adequate in one situation may be insufficient in another (as, for example, in the case of the copper-molybdenum-sulphur synergism Chapter 10).

Apart from large genetic differences between plants, as between legumes and grasses where legumes almost invariably contain

higher concentrations of calcium and phosphorus and of many but not all trace elements, variation in mineral content has also been observed where the differences are relatively small. For example, ten-fold differences in iodine content⁽¹⁹⁷⁾ were found among strains of ryegrass growing together and differences between species and varieties of grasses in the uptakes of major minerals (i.e., those measured as per cent rather than p.p.m. of dry matter) have been reported.^(198,199,200) Changes in the mineral contents of plants as they mature do not conform to a single pattern and are generally of less importance in temperate than in tropical areas where, for example, the progressive fall in phosphorus and sodium levels will aggravate any incipient deficiencies of these nutrients.⁽¹¹⁹⁾

The mineral composition of plants reflects to some degree the nature of the soil and responds to the alterations brought about by applications of fertilizers and trace elements or other treatments, e.g., changes in pH due to liming.^(201,202) Thus an increase in the relative concentration in the soil of any one cation will increase its concentration in the plant and reduce that of the others but fertilizers have additional effects of wider significance, namely the promotion of increased plant growth and of changes in the botanical composition of grasslands. Discussion of the effects of fertilizers will be confined to those that supply the major plant nutrients nitrogen, phosphorus and potassium; it will be assumed that there are no gross deficiencies of these or other minerals essential for plant growth.

Plants normally need more nitrogen than any other nutrient and a shortage of nitrogen commonly limits herbage production.⁽²⁰³⁾ Unless applications in fertilizer so enhance the growth of grasses that the uptake of nitrogen does not keep pace with the large increases in dry matter yield that can be obtained,⁽⁵⁾ the nitrogen content of the grasses will be raised. When light intensity and photosynthetic activity are

low but there is abundant soil moisture and a high temperature this increase may, rather uncommonly, be due in part to the accumulation of nitrate with consequent risk to animal health.^(111,205) Nitrogenous fertilizers applied to temperate grasslands have often been shown to reduce the clover population.⁽²⁰⁶⁾ Unless the amount applied is large enough, say 40 kgN/ha/year or more, to compensate for the reduced contribution of N from the rhizobia associated with the clovers, the crude protein content of the whole herbage and even its dry matter yield may be reduced. Nitrogen does not appear to have any large direct effects on the digestibility of herbage plants⁽²⁴⁵⁾ but their energy value may be changed because of the marked reduction in fructosan content that it causes.^(100,207,208) The ruminal liquor of sheep grazing pasture heavily fertilized with N was found⁽²⁰⁹⁾ to contain higher concentrations of soluble non-protein N, ammonia and nitrate, a lower total VFA concentration and proportion of butyric acid, and a higher proportion of acetic acid than that of sheep grazing lightly fertilized pasture. Nitrogenous fertilizers increase the carotene content of grasses⁽¹⁰⁰⁾ but only minor changes have been found in trace element concentrations even with applications as large as 390 kgN/ha/year for several years.^(206,210)

It is most improbable that the needs of animals for potassium would not be met from grassland herbage, even that grown where the amounts available for the plants were grossly insufficient. Potassic fertilizers applied for the maintenance of a high level of herbage production, which is particularly necessary if the growth is cut and removed for conservation, will raise the K content of the feed. It has been suggested, notably by Dutch workers,⁽²¹¹⁾ that excessive applications will, by altering mineral composition, promote the development of hypomagnesaemic tetany in lactating dairy cows and sheep. Experimental evidence generally does not give very much support to this view. Hypomagnesaemia, if found, may be of little significance unless it is also found that there is an increase in the incidence of clinical tetany; the number of animals

used in experiments has frequently been too small, and the frequency of tetany too low, to yield unequivocal results⁽²¹²⁾ (see Chapter 29).

Phosphatic fertilizers increase the P content of herbage but by far their most important use is to raise the phosphorus status of the soils of the pastoral areas of the world, thence to promote the growth of legumes and set in train events that lead to enormous increases in pasture productivity. As an example the native pastures of the northern tablelands of New South Wales, Australia, can with difficulty support two wether sheep per hectare. The application of a few hundred kg of superphosphate and oversowing with clover rapidly allows a safe stocking rate of 10 breeding ewes per hectare to be achieved. Whether from a higher requirement for P or an inability to compete successfully with grasses for this nutrient,⁽²¹³⁾ many legumes do not persist when the soil P status is low. One noteworthy exception is Townsville lucerne (Stylosanthes humilis) which is becoming an increasingly important pasture plant in northern Queensland.⁽²¹⁴⁾

There are some reports on the effects of the major mineral fertilizers on the acceptability of the herbage to animals. Reid and Jung⁽²¹⁵⁾ found that sheep offered the free choice of a number of herbage types tended to prefer those containing the higher levels of phosphorus and to eat less of those from plots heavily fertilized with nitrogen. There was, however, a large variation between individual animals in their preferences and when the feeds were given singly, without choice, there were no differences in the intakes. Milford⁽⁴⁷⁾ reported that the intake of three sub-tropical feeds was reduced by nitrogenous fertilizer but no such effect was found⁽⁷⁹⁾ in an experiment with temperate pasture species.

VITAMINS

Vitamin B12 - cobalt, and vitamin E - selenium relationships in ruminant animals are discussed in Chapter 10.

Fresh herbage, silage made from fresh rather than wilted herbage⁽¹⁰⁰⁾ and dried grass normally contain abundant β carotene, the principal precursor of vitamin A, for the immediate needs of cattle and sheep and provide a surplus for storage in the liver. Carotene levels are low in mature dry herbage, such as that available during drought or persisting in cold winters, and decrease in hay and dried grass during storage due to oxidation.⁽²¹⁶⁾ The liver stores of animals normally maintain a supply of vitamin A for several months to animals given such feeds⁽²¹⁷⁾ but reproductive efficiency and the viability of offspring may ultimately deteriorate. If young are born they may show signs of vitamin A deficiency, particularly night blindness, in the first few months of life because lambs and calves as a rule have only small stores of this vitamin in the liver at birth.⁽²¹⁸⁾

The vitamin D content of fresh green herbage is not as low as was once thought⁽²¹⁹⁾ and deficiency states in grazing animals are rare. They have been reported in lambs when a rachitogenic factor in the feed, possibly carotene, was implicated.^(220), 223, 339) Ultra-violet irradiation converts ergosterol in the skin of animals to ergocalciferol (vitamin D₂) and a similar change occurs in cut grass during haying. If the herbage is cut for ensiling there may be only a short period of exposure to the sun and the gain in vitamin D activity may be small. The gain will also vary between different latitudes because of variation in the period of time that the elevation of the sun exceeds 35° and thence in the amount of incident ultra-violet radiation. The variation that has been reported in the anti-rachitic activity of American and European herbages,^(219, 221, 222, 223) both fresh and preserved in various ways, has

not been shown to have practical importance in animal feeding though effects on the vitamin D content of milk could be of significance in human nutrition.

CONSERVATION

Drying and ensiling are the two main methods employed in practice for the preservation of cut herbage so that losses in store due to fungal and microbial spoilage and to enzyme activity are minimised. There are innumerable variations in technique.⁽²²⁴⁾ Drying may be done entirely in the field, as in haymaking, or partly or wholly indoors where air, either at ambient temperature or heated, is blown through the material; the final moisture content should be 15 per cent or less. In the ensiling process the pH of the herbage is reduced to a level where bacterial and enzymic activity is inhibited either as a result of natural fermentation, sometimes aided by the addition of fermentable material such as molasses, or by the addition of inorganic or organic acids or other chemicals; some of the latter substances may act primarily as sterilants.

The digestibility of well conserved fodder dried or ensiled is similar to, and reflects, the stage of growth of the herbage when cut. Modern techniques and notably the introduction of the flail type of harvester allow much freedom of choice in the time of cutting and the decision that is made can be determined by the requirements of the animals that will be given the product. If they are simply to be maintained for a period of time then harvesting may be delayed until the weight of crop approaches the maximum. If the feeds are to be used for the production of meat or milk then earlier harvesting is necessary so that the digestibility is higher (Fig.2). The yields of dry matter will then be reduced, though there will be some compensatory production

from aftermath; the yields per unit area of metabolizable energy and production net energy may also be lower. On the other hand the actual output of animal products can be two to four times greater because voluntary intakes by the animals, and thence the quantities of energy available for production after maintenance needs are met, will be much higher than with late-cut fodders. (64,82,98)

The method of conservation employed may be determined by economic and technical considerations such as the implements and storage facilities that are available, the greater dependence of haymaking than ensiling upon weather conditions, and the difficulty of handling short growths of herbage dried in the field. Some nutritional consequences of various methods of conservation and the nature and extent of the losses of nutrients incurred are discussed below.

Hay.

Herbage continues to respire after it has been cut until its moisture content is reduced to below about 35 per cent. (225) The major changes involved are the oxidation of readily available carbohydrates and the hydrolysis of protein. There will be further losses due to leaching and perhaps to mould growth if rain falls on cut grass in the field, and even with careful handling there will be mechanical losses which will be greater from the leaf than from the stem fraction. The final yield of dry matter is often found to be less than 80 per cent of that in the original material (82) but the reduction in feeding value will usually be greater because soluble components and leaf have suffered proportionately greater losses than structural materials and stem. In an experiment where small quantities of hay were made carefully, it was found (226) that the digestibility of the organic matter was 2 percentage units lower than for the fresh material; the difference was due entirely to a decrease in the digestibility of protein. The net availabilities of the metabolizable energy of the fresh and dried

feeds, measured in a calorimeter, were identical although an increase in methane production when the hay was given indicated that there was some change in the pattern of rumen fermentation.

Unless the moisture content of the hay in the stack remains so high that it ignites spontaneously the quantitative losses in store will be much smaller than those usually incurred during the making. It was found in the Netherlands⁽²²⁷⁾ that when hays were stacked at initial moisture contents of 15, 20 and 25 per cent the losses of dry matter were 1.7, 3.3 and 5.0 per cent respectively. The moisture content usually falls in store but if it does not the losses of dry matter increase sharply above about 15 per cent moisture.⁽²²⁸⁾ Sugars and fructosans are broken down, and moulds that are likely to grow reduce the feeding value because animals will reject hay that is affected.

Qualitative losses due to the heating that will occur increasingly with rising moisture content may be more serious.^(227,229) The digestibility of the crude protein is affected first and may be reduced to zero if heating is severe. The digestibility of the organic matter also falls markedly due to the production of polymeric materials from xylan and other substances.^(101,105) Dutch workers⁽²³⁾ have devised a colorimetric method for estimating the degree to which hay has been heated and the extent of the fall in nutritional value.

Dried Grass.

In a well organized grass-drying enterprise the fresh herbage is placed in the dryer soon after it is cut and respiration losses will be small. The air blown through the material is in some machines heated to over 200°C but provided that the drying time is measured in minutes rather than in hours and the outlet temperature is low the changes in nutritional value will be small. Heat damage is insignificant below about 50°C, but the apparent lignin content, of young grass

especially, may be increased three-fold by ordinary drying at 80 to 100°C.⁽¹⁰⁵⁾ Prolonged drying at these or higher temperatures, particularly in the presence of moisture which catalyses damage reactions, will cause a reduction in the digestibility of protein and organic matter. In one experiment⁽²³¹⁾ the ME content of grass dried in the laboratory at 100°C was reduced by 4 per cent compared with the fresh material but the efficiency of utilization for fattening was unaccountably increased by 9 per cent. Evidence that rumen fermentation patterns differ between fresh and dried grass has been reported.⁽²³²⁾

Silage.

In silage made from freshly cut herbage by fermentation processes the object is to reduce the pH of the material as quickly as possible to a value below 4.2; at this point the undesirable activity of Clostridium butyricum in particular is inhibited.^(233,234) Lactobacilli continue to ferment soluble carbohydrate when conditions are more acid and at pH 4.0 the silage dry matter contains about 6 per cent of lactic acid. Some hemicellulose is hydrolysed⁽²³⁵⁾ but rapid transfer of the cut grass to the silo and compaction to promote anaerobic conditions will minimize the loss by respiration of the more readily available carbohydrate substrates. If the sugar content of the herbage is low the addition of molasses, whey, or similar materials will be advantageous.

There is considerable breakdown of protein to a wide variety of substances of low molecular weight so that, in temperate herbages, a 1 : 4 ratio of water-soluble : insoluble nitrogen compounds may be reversed; nitrogen equilibrium is reached at about pH 4.3.^(237,238) Undesirable types of fermentation are characterized by the formation of large amounts of butyric acid and volatile bases including ammonia. The pH of silage is not a certain index of its quality. Satisfactory silage is frequently made from herbage wilted in the field to about 40 per cent dry matter even though high

concentrations of lactic acid are not obtained and the pH is about 5.0;⁽²³⁶⁾ it appears that the high osmotic pressure retards the development of undesirable types of bacteria.⁽²³⁴⁾ The activity of Cl. butyricum is also inhibited above a temperature of about 50°C but the nutritional value of the resulting feed is then reduced by heat-damage. Many workers advocate that during fermentation the temperature of the silage should not rise above 20 to 30°C;⁽²³⁴⁾ usually, little butyric acid is formed unless the herbage is ensiled when very wet.⁽²³⁹⁾

Losses of dry matter are incurred by plant respiration, bacterial fermentation, seepage from the silo and surface wastage and in practice they rarely total less than 20 per cent of the weight in the fresh herbage;^(224,236) surface wastage may be very large during storage unless air and rain are excluded.⁽²⁴⁰⁾ The losses may be overestimated if in the determination of dry matter content account is not taken of the volatile substances in silage that are lost during oven-drying.⁽²⁴¹⁾

Provided that the silage has not overheated, its digestibility generally differs little from that of the original herbage however it is made⁽²⁴²⁾ but its energy value may be lower because of the breakdown of sugars to lactic acid.⁽¹⁰⁰⁾ The breakdown of protein to a wide variety of less complex nitrogenous compounds may not be of great importance to ruminant animals but poor silage containing large amounts of volatile bases and butyric acid is not eaten in as large amounts as is hay made at the same time from the same raw materials.⁽⁸³⁾ This phenomenon, discussed earlier, is perhaps the major problem in the nutrition of animals given silage, but appears to be overcome if the herbage is wilted to about 50 per cent dry matter before ensiling.⁽²⁴³⁾ If inorganic acids are used to preserve herbage the acid-base balance of animals given the resulting silage may be disturbed; the addition

of a neutralizing mineral mixture to the feed is recommended.⁽²³⁴⁾

Cold Storage.

Cold storage is a laboratory technique that is useful if, for example, the feeding value of herbage at a particular date and stage of growth is to be studied.^(244,266) Quantities sufficient for a digestibility trial, which with the preliminary feeding period will normally extend over a 3-week period, can be frozen quickly and then stored satisfactorily at -18°C . The product is readily eaten by animals which soon become accustomed to it, and the process causes only minor changes in chemical and physical characteristics, in digestibility and in energy value.⁽²³¹⁾

PROCESSING.

Chopping, wafering, grinding, and the pelleting of ground feed facilitate the handling, storage and rationing of dried fodders but such treatments may have nutritional consequences.

Chopping, usually into lengths of 1 to 2 cm, and wafering, where chopped or long fodder is compressed into blocks 5 to 12 cm in diameter or square and 1 to 5 cm thick, have little effect upon nutritional value.^(246,247) The rate of eating (g/min) might be increased, and wastage may be reduced because it will be more difficult for the animals to eat selectively, and to reject any less acceptable (or noxious) components, than when the same feed is given in long form.

Grinding has a number of important consequences. Feed passes through the alimentary tract of ruminants more rapidly when it is given in ground rather than in long form and the amount eaten, the digestibility, the products of digestion, and production by the animal

can all be affected.^(246,247)

As described earlier, voluntary feed intake is related to the rate of emptying of the reticulo-rumen, and to leave this organ the ingesta must be in a finely divided state. Intake of a feed may not be altered by grinding if it is of very poor quality or is given as a dry meal, perhaps because animals dislike the dustiness, but it is generally increased if the meal is moistened⁽²⁴⁸⁾ or pelleted. The extent of the increase shows an inverse relationship with the quality of the feed as illustrated by data⁽²⁴⁹⁾ on the voluntary intake of dried lucerne, cocksfoot and timothy, each harvested at three stages of growth at dry matter digestibilities in the range 71 to 50 per cent. At the highest digestibilities, intakes were increased by some 40 per cent by pelleting and the actual intakes of pellets at the various growth stages were not significantly different; in contrast, the intakes of the long forages decreased markedly with advancing maturity and differences between the two physical forms became more pronounced so that at the lowest digestibilities only about half as much of the long as of the pelleted feeds were eaten.

The increase in the intake of digestible energy that occurs is smaller than the increase in gross energy intake because grinding reduces digestibility,^(249,250,251) and in particular that of the structural carbohydrate components. This effect is probably a consequence of the increased rate of passage;^(24,251,252) crude fibre is exposed to microbial attack for a shorter period of time and there is evidence that the rate of cellulose digestion decreases and that changes occur in the microbial population.^(54,253) These changes may stem from the alterations in eating behaviour that follow the substitution of long feed by pellets. Pellets are eaten more rapidly, rumination times fall, and it appears that the volume of saliva entering the rumen decreases which, because of reduced buffering,

would account for the lower ruminal pH observed.^(247,254,255) The changes in digestibility are reflected in the volatile fatty acids produced; the proportion of propionic acid tends to be higher and that of acetic acid to be lower.⁽²⁵⁹⁾ This effect can cause a reduction in the fat percentage in milk secreted by dairy cows.⁽¹³⁶⁾ Liveweight gains of fattening animals can be much increased when a feed is pelleted and given ad lib but have been found to be similar to those obtained from long roughage when dry matter intakes of the feed in its two physical forms are equalized.⁽²⁴⁶⁾ This is a surprising result because digestible dry matter intakes will differ but it has been confirmed in a calorimetric study.⁽²⁵⁰⁾ It was found that an increase in the faecal loss of energy (from 19.4 to 26.9 per cent of gross energy intakes) due to pelleting a dried grass was compensated for by a reduction in methane production and an increase in the efficiency of utilization of the ME by the fattening sheep that were used. The latter effect could have been due to a higher proportion of propionic acid in the ruminal VFA. Similar results were obtained in an experiment where energy gains by sheep were estimated from carcass analyses.⁽²⁵⁶⁾ There could be a lower expenditure of energy in the prehension, mastication and rumination of pellets; energy costs of the order of 0.5 kcal/hr/kg liveweight for eating and 0.2 kcal/hr/kg for rumination have been reported⁽²⁵⁷⁾ and a diminution in these activities, which is a typical result of pelleting,⁽²⁵⁴⁾ could appreciably reduce the energy costs per g of feed.⁽²⁵⁸⁾

GRAZING

Information on the nutritional value of cut herbage is not directly applicable to grazing conditions, and if combined with information gained from separate studies on the effects of cutting on the growth of ungrazed swards, will not necessarily lead to improved

systems of grazing management. Very many experiments on grass plots, notably those of Woodman and his colleagues at Cambridge some 30 to 40 years ago, have shown that the desirable characteristics of leafiness and digestibility are positively related to the frequency and severity of defoliation while the annual yield of herbage dry matter is negatively related. It came to be accepted, but usually without reference to the grazing animal, that a satisfactory compromise between quantity and quality in the herbage grown and thence maximum animal production from a pasture could be achieved only by intermittent grazing. The length of the grazing and intermittent rest periods, and the area of pasture allotted per animal, would vary with the current rate of herbage growth. When actually put to the test, these expectations have not been realized.

It has been found that intermittent grazing can assist management for the needs of particular classes of livestock. e.g., lactating vs. non-lactating cattle, and for the conservation of herbage surplus to immediate requirements but the anticipated major benefit, a large increase in animal production, has generally not been obtained. (271,272,273,274) Provided that comparisons are made using similar numbers of animals on similar areas of pasture, animal productivity under intermittent grazing is usually very little different from that obtained under a system that was thought to be harmful to both pasture and animal outputs, namely the continuous grazing of a pasture with a more or less fixed number of animals. A detailed discussion of this topic is outside the scope of this Chapter but when it is stated that animal production from pasture is determined by:

- (1) the amount, the quality and the seasonal pattern of the herbage growth,
 - (2) the proportion of the growth that is harvested by the animals,
- and
- (3) the efficiency with which the animals utilize the herbage they consume

- it has to be remembered that all these factors are interdependent. Grazed pastures yield an ever-varying supply of feed to the animal from a heterogeneous plant population in which substantial and progressive changes, botanical, morphological and chemical, are continually occurring. All the changes reflect the mutual interactions of climate, soil moisture and fertility, plant species, the species, type, number and activities of the grazing animals, and the dynamic populations of parasites and other organisms. (268,269,275) Pastoral enterprises are in fact very complicated exercises in applied ecology.

Significant progress has been made only during the past two decades in the development of techniques that are essential if the understanding of the nutrition of grazing animals is to be increased; even now, the measurement of the quantity and quality of herbage grazed by livestock is beset with difficulties. Without this information, claims such as that the higher liveweight gains by lambs grazing on one type of pasture rather than another are due to differences between the herbages in their carbohydrate contents (146,147) are doubtful. Nor, lacking data on herbage intakes, is it sufficient to state that there were no apparent differences in the amounts of feed available to the animals. (277) What herbage is left on a pasture at any one time is a function not only of the amounts removed by grazing but also of the rates of growth by and the decay of the plants. (285) Visual appraisals of quality can also be misleading; the apparent predominance of one species in a mixed pasture may be the result of rejection by the animals which in fact are hard-grazing some other species that is, in consequence, not readily seen to be present.

Estimation of Feed Intake.

Estimates of intakes gained from measurements of the amounts of herbage on a pasture before and after periods of grazing are subject

to many errors⁽²⁷⁸⁾ and are too imprecise to be of any real value in nutritional studies. There has been intensive work on another method^(278,279,280,281) that depends on measurements of faecal output (F), which is the apparently indigestible fraction of the herbage grazed, and of the apparent digestibility (D) of that herbage. Intakes (I) can then be calculated from the expression $I = A \times F$, where $A = (100/100 - D)$ (feed/faeces) and is termed the Intake Factor. The intake of digested feed is given by the term $(F \times (A - 1))$.

Faecal outputs can be measured directly by collection in bags attached to harness worn by the animals but is more often estimated from the concentration in the faeces of a totally inert material that is administered regularly in standard amounts. The substance that is most frequently used for this purpose is chromium sesquioxide (Cr_2O_3). In a typical application, sheep are dosed by mouth twice daily with a capsule or impregnated paper⁽²⁸²⁾ containing 1 g Cr_2O_3 . The mean daily excretion in the faeces is similar to the amount (2 g) given and, provided that an adequate sampling procedure is adopted,⁽²⁸³⁾ a concentration of 4 mg Cr_2O_3 /g faecal organic matter indicates that the daily organic matter output is 500 g. The same concentration in the faeces of cattle given two 10 g Cr_2O_3 doses daily would indicate an output of 5 kg organic matter/day. This method is usually more practical than harnessing when a large number of animals is to be studied, and it generally causes less disturbance to them.

Herbage plants or parts of plants at many different stages of growth, varying widely and continually changing in digestibility, are normally present in a pasture. The mowing machine removes this material unselectively down to a certain height and does not simulate the selective harvesting by the animal. In consequence, digestibility values obtained directly from cut herbage cannot validly be applied to the herbage that is grazed. The values can be related to the

concentrations of various index substances in the faeces. From such relationships, established in digestibility trials with stalled animals,⁽²⁸⁴⁾ the digestibility of herbage eaten by animals at pasture can be estimated from the concentrations of the indexes in their faeces. The nitrogen concentration is most widely employed. Faecal nitrogen comprises undigested feed nitrogen, which is 10 per cent or less of that in the fresh herbage eaten (see p.30) and large amounts of metabolic faecal nitrogen (M.F.N., see p.16). Since the M.F.N. excretion is positively related to feed dry matter intake, the greater the digestibility of the dry matter the higher is the total nitrogen concentration in the faeces. Among other indexes that are used, chromogen is derived from the chlorophylls and related pigments of the plants.⁽²⁷⁸⁾ The chromogen concentration in an acetone extract of faeces is positively related to digestibility because herbage of high digestibility generally has a high concentration of the pigments.

In recent years techniques for the permanent fistulation of ruminants at the oesophagus have been developed⁽²⁸⁶⁾ so that animals can now be quite simply prepared and maintained, and they are widely used. Herbage can thus be collected as it is ingested; measurements can be made of botanical⁽⁹³⁾ and chemical composition, and of digestibility by in vitro procedures (see p. 31).

All these techniques demand great care in their application lest the results obtained should include serious bias. Chromium sesquioxide is not excreted in a uniform manner, and because the calculation of intake requires the indigestibility value, an estimated digestibility that is in error by 5 units will give a bias of 20 per cent or more in the estimated intake. Such an error can readily occur if, for example, a faecal index : digestibility relationship derived from herbage cut from one pasture is applied to another, or even to the same pasture at a different time of year.^(280,284,318)

Measurements cannot be made on herbage samples collected from oesophageally fistulated animals without difficulties. The material is contaminated with saliva,⁽²⁸⁹⁾ is damaged to some extent during prehension and mastication,⁽⁵³⁾ and may deteriorate due to fermentation or during drying while being prepared for analysis. In addition sampling errors arise from variability between animals, and between times of day for individual animals.^(287,288,289)

With care and in favourable circumstances feed intakes by individual animals on temperate pastures might be estimated with a standard error as low as ± 6 per cent,^(37,278) but one may have to be content with ± 20 per cent.⁽²⁹⁰⁾ There have been rather few reports of measurements of intakes on tropical and sub-tropical pastures;^(344,345,346) significant faecal index : digestibility relationships have not always been obtained.⁽⁸⁵⁾

Selective Grazing.

Measurements of intakes by the techniques referred to above have yielded information on the extent of the selectivity exercised in grazing by animals, a feature that has long been recognized. Selectivity^(70,319) is partly mechanical - the consumption of herbage nearest the muzzle. Since this will often lead to the consumption of more leaf than stem the digestibility of the feed eaten and its content of nitrogen and sugars will tend to be higher, and of fibre lower, than for the pasture herbage as a whole. These effects will be enhanced by the deliberate selection of leaf, and of green rather than dry or dead material; choices by the animal among the usually large number of species present in a pasture further distinguish grazing from mechanical cutting. There do not seem to have been any reports that grazed feed was less digestible than the material from which it was selected. It may be only slightly more digestible when the pasture includes a large proportion of new growth⁽²⁹¹⁾ but where the range and opportunity for

for selection is large the difference can be 15 units or more.⁽²⁹²⁾

Selection by the animals of the higher quality fractions of the feed offsets the decline that occurs in the digestibility of pasture herbage as it grows and matures so that a fall in the digestibility of the grazed herbage will tend to occur more slowly. Perhaps for this reason, and because of the difficulties in measurement, there is uncertainty about the importance under grazing conditions of relationships between digestibility and intake (Fig.1) though these have been observed.^(37,45,294)

Probably the greatest opportunity for selection occurs when plant growth is most rapid, that is in spring or at the start of the wet season; in temperate areas the rate of increase in herbage dry matter can approach a maximum of about 200 kg/ha/day, but in winter or in drought it will be virtually nil. If no attempt is made to restrict the area available for grazing the animals may at times consume much less than 10 per cent of the current herbage production⁽²⁹⁵⁾ though the discrepancy can be reduced by management, as in seasonal dairying, so that the patterns of animal demand and herbage growth roughly correspond.⁽²⁹⁶⁾ Selective grazing can be turned to advantage if lactating dairy cows or, by suitable fencing, suckling lambs but not their mothers are allowed the first pick at a growth of pasture and the residual herbage is subsequently grazed by animals in a less productive state.^(269,297,319)

Availability of Herbage.

The term "availability" refers not only to the actual amount present on the area of pasture allotted to an animal but also to the manner of its distribution. Sheep would have considerable difficulty in gathering sufficient feed from a pasture yielding a uniform 50 g dry matter/m² (i.e., 500 kg/ha) but not if the same amount of material were

disposed in a few large clumps. There are undoubtedly critical limits in height/density patterns of growth below which intakes by animals, and thence their productivity, will be reduced. Comprehensive measurements of the yield and structure of pasture are difficult to make^(269,293,298,299,300,317) and must take account of the fact that animals, especially sheep, can graze herbage only just above ground level and below the height at which it can be cut by many types of machine. Sheep will in fact dig in very bare pastures to gain underground parts of plants. It has been reported⁽³⁰¹⁾ that the liveweight gains of grazing lambs increased with an increasing supply of green herbage up to a level of 1570 kg DM/ha but gains did not continue to rise at higher yields. Because of the immense range of pasture types, of differences in grazing behaviour and in the acquisition of herbage, as between sheep and cattle,^(302,303,304,319) and the difficulty of making appropriate measurements, any such relationships, if found,⁽³⁰⁵⁾ are likely to be of rather local applicability.

Grazing Behaviour.

The total time spent in grazing by cattle and sheep, often about 8 h/day,⁽¹⁹⁾ varies with the availability of feed and may have a positive but imprecise relationship with feed intake.^(70,306) When the herbage is very sparse, grazing times increase⁽³⁰⁷⁾ but it does not seem that animals will work at feed collection for more than half of the 24 h even under the most difficult conditions. The remainder of their time is spent in resting, and in ruminating which generally occupies some 6-8 h/day; the longer rumination periods occur when the herbage is of rather poor quality.⁽³⁰⁷⁾ Adaptation of grazing habits to new conditions occurs very rapidly; thus the total grazing time is made up of a number of periods of activity which are most intensive in the hour or two after sunrise and again towards sunset,⁽²⁶⁹⁾ but if the day is very hot the main grazing activity may be deferred until the cooler night hours.^(308,309)

The effects of a 'little and often' regime of feeding have been studied with housed animals.⁽³¹⁰⁾ It has been found on a number of occasions that liveweight gains were increased by giving a ration as a number of small feeds at intervals throughout the day rather than as one or two larger feeds. This result could be due to greater uniformity in the supply of metabolites to the tissues of the animal.⁽³¹¹⁾ A frequent-feeding regime also tends to increase ad libitum intakes, and a herbage is generally consumed in greater amounts when grazed than when given freshly cut to confined animals, as in the 'zero-grazing' system of management.⁽³¹²⁾

Advocates of this system point to the wastage of herbage by trampling⁽³¹³⁾ and fouling with excreta that occurs during grazing, and the increased expenditure of energy by animals at pasture compared with those that are penned (see p.58), but when it is applied to dairy cows the milk production per unit area of grassland is generally similar to that obtained by grazing.⁽³¹²⁾ In the latter case the animals have greater opportunities for dietary selection and may benefit from more frequent feeding. Zero-grazing might give the higher yields of animal products per unit area if instead of utilizing swards that were developed primarily for grazing, herbage plants were bred specifically for cutting. A growth habit that intercepted the maximum amounts of solar energy could then be selected.⁽³¹⁴⁾ It can also be noted here that although large quantities of plant nutrients are returned to pastures in animal excreta they are often distributed very unevenly.⁽³¹⁵⁾ With animals that are gregarious during rest a large proportion of a pasture may even be depleted of nutrients due to their transfer in excreta on to the small habitual resting areas.⁽³¹⁶⁾

Large amounts of nitrogenous substances are returned by animals, especially when they graze intensively managed pastures yielding herbage of high crude protein content. Concentrates or other feeds

might be given in these circumstances, the intention being to increase the supply of non-protein energy and perhaps to improve the utilization of dietary nitrogen, or in other circumstances to add to the energy supplied by herbage of rather low digestibility. In practice such supplements have neither large nor economically favourable effects on the production of animals provided that there is sufficient herbage readily available to meet their needs.^(273,309,320,321) Unless the herbage is scanty, supplementary feeds are more correctly described as substitutes because, when they are consumed, herbage intakes fall. This effect is illustrated by the results of a number of experiments with dairy cows which yielded⁽³²²⁾ the expression $I = 6.2 - 0.075 D$, where I is the increase in total feed intake in kg per kg concentrate consumed, and D is the digestibility of the herbage organic matter. It will be seen that the increase in the total amount of feed eaten is likely to be small; unless the concentrate is of much higher nutritional value than the herbage it replaces, the net effect on nutrient intake will also be small.

Stocking Rate.

The stocking rate (the number of animals per unit area) is the major factor determining the output of animal products from any given pasture and certainly has very much larger effects than changes in grazing management as such.^(272,323,324) Doubling the number of animals on an understocked pasture might almost double the production. An increase in stocking rate from a very low level may initially increase the output per head although there is little change in the amount of high quality feed available for selection.⁽²⁹⁴⁾ With sheep this effect was thought to be due to a low intake per bite from understocked erect open growths of herbage compared with a shorter and more dense growth.⁽⁷⁰⁾ With further increases output per head falls, at first slowly but then with increasing rapidity. The increasing number of animals generally gives increasing output per unit area beyond the

point where the productivity of individual animals starts to fall quite sharply. (323,324) Ultimately the production on either basis must fail entirely.

The continual problem facing the grazier is the attainment of optimum outputs per head and/or per pasture; in milk or meat production there might be greater emphasis on output per head than, for example, in wool production. In addition the stocking rate has to be adjusted with an eye on the maintenance of a productive sward. Continued hard grazing and severe defoliation will reduce leaf area and so reduce the amount of solar energy that is intercepted and used in photosynthetic activity and regrowth. (2,275,325)

Energy Costs.

Although increasing the stocking rate reduces the amount of herbage offered per animal, feed intakes per head may well be increasing as individual productivity declines. (294,326) This indicates a progressively inefficient utilization of feed by the grazing animal. (327) Quite a large number of estimates of efficiency have now been made from measurements of feed intakes (I), usually as digestible organic matter, and of the liveweights (W) and production of the animals as milk (M), gain in weight (G) etc. Values for the constants in equations of the type $I = aW^k + bG + cM$, or $I = aW^k \cdot e^{bG}$, are obtained by least-square procedures.

When sheep or cattle have been confined to small areas of pasture yielding abundant high quality herbage it has been found that the value for the constant "a", which is taken to be the amount of energy required by the animal for maintenance, is about 20 per cent greater than that obtained from similar animals given cut herbage in stalls. (328,329) As the area available for grazing and perhaps the activity of the animal and the opportunity for the consumption of feed in excess of

immediate requirements increase, so the maintenance costs appear to rise.⁽³²²⁾ The greatest increases, however, have been observed where there was a deficit rather than an excess of pasture herbage. An increase to three times or more the indoor maintenance requirement was found⁽³²⁶⁾ on a very sparse pasture where sheep had the utmost difficulty in obtaining feed, and they were able to maintain themselves only at a liveweight very much lower than the normal for these animals. It does appear that the less herbage stock have on offer, the more they need.

These input/output studies are subject to several criticisms. Firstly, of all the variables only milk yield can readily be measured with accuracy and precision. Liveweights often show large short-term changes that reflect only changes in the weight of gut contents.^(330,331) In addition the estimated intakes could include large biases. Secondly, the mathematical model used may be biologically inappropriate; for example, it is usually assumed that G and M are directly related in a rectilinear manner to feed intake and no allowance is made for diminishing returns effects. Thirdly, the statistical method used ~~might~~ be inappropriate in a situation where the variables are often correlated and where the data may be heterogeneous. Regression analysis may be convenient where the object is to predict intakes from a number of independent variables (W, G, M etc.) even though these are not measured without error, but a functional type of analysis that examines the underlying relationships between all variables will probably give rather different, and perhaps more valid results.⁽³²⁹⁾ Despite these criticisms it is unlikely that they can explain away such large increases in maintenance requirements as have been found on a number of occasions^(332,333,334,335,336,337) in addition to those already mentioned.

The increases have been shown^(21,338) to have some plausibility by calculations based on separate measurements of the energy costs of locomotion,⁽⁸⁸⁾ standing, grazing, rumination etc., and the effects of climatic factors such as wind on the rate of heat loss by the animal.^(340,341) These calculations are simply summative in type whereas the mathematical model truly representing the biological situation is likely to be very much more complicated. Direct measurements of energy expenditures, by measurements of oxygen consumption^(342,343) or other means, are required, first to confirm the findings and then to assist definition of the many factors that will affect the nutritional efficiency of grazing animals.

The application to grazing animals of these and other techniques⁽²⁶³⁾ that have so far been used almost exclusively under necessarily stereotyped laboratory conditions is long overdue. They must be applied if there is to be real understanding of the relationships between animals and pastures in all their fascinating complexity.

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TABLE 1. Relationships between the digestibility and the voluntary intake of feed by sheep. Intakes (I) expressed as g dry matter per (kg liveweight)^{0.73}

Plant Species	No. of Observations	Range in Digestibility % (D)	Range in I	Change in I per unit change in D	Intakes at	
					D = 70	D = 55
Temperate						
1. <u>Lolium multiflorum</u> var.S22	10	60.0 - 84.6	62.5 - 90.9	1.12		74.2
2. <u>L. multiflorum</u> x <u>L.perenne</u> var.H1	10	67.3 - 82.9	54.0 - 93.8	1.66		67.0
3. <u>Festuca arundinacea</u> var.S170 (year 1)	6	65.7 - 79.5	51.8 - 81.4	1.33 (N.S.) ^a		68.9
4. <u>Phleum pratense</u> var.S48 (year 1)	7	66.8 - 75.4	56.4 - 68.8	- 0.55 (N.S.)		64.8
5. <u>Festuca pratensis</u> var.S215	8	60.9 - 81.2	52.1 - 91.8	1.55		71.8
6. <u>Dactylis glomerata</u> var. Germinal	11	58.0 - 77.9	39.4 - 90.2	1.64		71.2
Species 1 - 6, combined data	52	58.0 - 84.6	39.4 - 93.8	1.36		69.6
<u>F. arundinacea</u> & <u>P. pratense</u> (year 2), combined data	11	62.5 - 83.3	39.9 - 64.8	0.77		51.9
Tropical						
1. <u>Setaria sphacelata</u> var. Nandi	11	46.7 - 63.0	28.3 - 70.0	1.26 (N.S.)		36.8
2. <u>Digitaria decumbens</u>	15	40.7 - 68.9	25.7 - 65.5	0.72 (N.S.)		37.7
3. <u>Chloris gayana</u> (CPI16144)	7	54.0 - 60.0	34.3 - 46.1	0.57 (N.S.)		39.7
4. <u>C. gayana</u> var. Callide	9	48.7 - 62.5	51.3 - 64.3	0.53 (N.S.)		58.1
5. <u>Sorghum alnum</u>	33	35.6 - 67.8	37.8 - 86.0	0.74		57.7
6. <u>Pennisetum clandestinum</u>	16	52.9 - 68.7	21.4 - 75.1	1.18 (N.S.)		51.5
7. <u>Cenchrus ciliaris</u> var. Molopo	22	34.1 - 60.6	21.6 - 78.9	1.20		63.2
8. <u>Phaseolus atropurpureus</u> var. Siratro (Legume)	12	40.3 - 56.8	50.5 - 82.2	1.05		69.2
9. <u>Glycine javanica</u> var. Cooper (Legume)	5	46.1 - 60.7	68.7 - 91.5	1.38		82.0
10. Various	90	28.0 - 76.0	9.9 - 82.3	1.22		49.5
11. Various (fresh herbage and dried fodders)	21	46.3 - 68.4	30.0 - 69.3	0.42 (N.S.)		43.2
12. Various	20	55.0 - 71.3	42.6 - 103.3	2.05		54.3

a. - Regression not significant

Sources: Temperate species ref.33; Tropical species nos. 1-9 ref.47; no. 10 ref.41; no. 11 ref.35; no. 12 ref.350.

Values of I for nos. 10, 11 and 12 recalculated from the published data.

TABLE 2. Composition and nutritional value of a grass, *Lolium perenne* var. S23, at four stages of growth.

(Sources : refs. nos. 97, 98, 99).

	<u>CUT 1</u>	<u>CUT 2</u>	<u>CUT 3</u>	<u>CUT 4.</u>
Date Cut	11 May	25 May	1 June	29 June
Stage of growth ^(a)	Young Leafy	Late Leafy	Head Emergence	Seed Setting
% Leaf lamina	73	58	48	25
Yield of dry matter (DM), kg/ha	2490	3814	4071	6089
<u>Chemical composition (% in DM)</u>				
1. Ether solubles	9.1	7.6	6.5	4.7
2. Water-soluble carbohydrates ^(b)	13.8	11.8	11.3	10.6
3. Organic acids	4.2	4.9	4.6	2.9
4. Protein nitrogen x 6.25	14.6	11.6	10.6	6.4
5. Non-protein nitrogen x 6.25	3.9	3.6	3.2	3.2
6. Cellulose	21.3	22.1	23.9	26.7
7. Hemicelluloses ^(c)	15.8	18.9	19.4	25.7
8. Pectin	2.4	2.1	2.2	2.2
9. Lignin	2.7	3.6	4.3	7.3
10. Ash	8.1	8.5	7.8	5.7
Total 1 - 10	95.9	94.7	93.8	95.4
Crude protein (4 + 5)	18.5	15.2	13.8	9.6
Crude fibre	21.2	21.8	25.6	31.6

TABLE 3. Concentrations, rates of production (entry rates), interconversions and effective production rates of acetic, propionic and butyric acids in the rumen of grazing sheep.

Sheep no.*	Weight of sheep (kg)	Total VFA concentration (m-moles/l)	Molar percentage of total VFA as :				Entry rates (m-moles/min)			Acetic acid produced from butyric acid %	Butyric acid produced from acetic acid %	Conversion rates m-mole/min		Effective production rates (m-moles/min)	
			Acetic acid	Propionic acid	Butyric acid	Branched-chain and higher acids	Acetic acid	Propionic acid	Butyric acid			Acetic to butyric acid	Butyric to acetic acid †	Acetic acid	Butyric acid
2	42.5	60	69	17	12	2	1.70	0.50	0.40	-	33.8	0.27	0.09	1.43	0.31
4	44.5	50	73	17	5	5	0.79	0.18	0.15	-	-	-	-	-	-
5	38.5	102	68	20	9	3	2.60	0.77	0.62	-	40.4	0.51	0.14	2.09	0.48
6	45.0	103	68	17	11	4	-	-	0.71	13.6	-	-	-	-	-
7	38.0	128	66	18	11	5	3.63	0.98	0.77	-	43.5	0.67	0.20	2.96	0.57
8	39.5	100	66	15	11	2	1.60	0.43	0.37	-	41.9	0.31	0.09	1.29	0.28
9	43.0	146	63	19	13	5	-	-	0.48	11.6	-	-	-	-	-
10	35.0	68	66	17	11	6	1.11	0.31	0.18	-	30.6	0.11	0.06	1.00	0.12
11	41.0	65	66	18	11	5	-	-	0.17	9.1	-	-	-	-	-

* Sheep nos. 6, 9 and 11 were infused intra-uminally with a mixture of [2-3-T] and [1-2-¹⁴C] butyrate. The remainder were infused with a mixture of [U-¹⁴C]acetate, [U-¹⁴C]propionate and [2-3-T]butyrate.

† Calculated on the assumption that, on average, 11% of acetic acid entry rate arises from conversion of butyric acid (see text).

Title and Legend for Fig. 1.

Title: Fig. 1. DIAGRAMMATIC REPRESENTATION OF RELATIONSHIPS BETWEEN FEED DIGESTIBILITY AND THE INTAKE AND EXCRETION OF DRY MATTER (D.M.) PER UNIT OF LIVEWEIGHT ($W^{0.73}$).

Legend: For the purposes of this diagram the dry matter intake, A, was taken to be $40 \text{ g/kgW}^{0.73}$ at a digestibility of 45 per cent; the intake was assumed to increase by $1.5 \text{ g/kgW}^{0.73}$ per unit change in digestibility over the range < 45 to about 65 per cent (see text and Table 1).

FEED D.M. INTAKE PER UNIT $W^{0.73}$

2.0A
1.8A
1.6A
1.4A
1.2A
1.0A

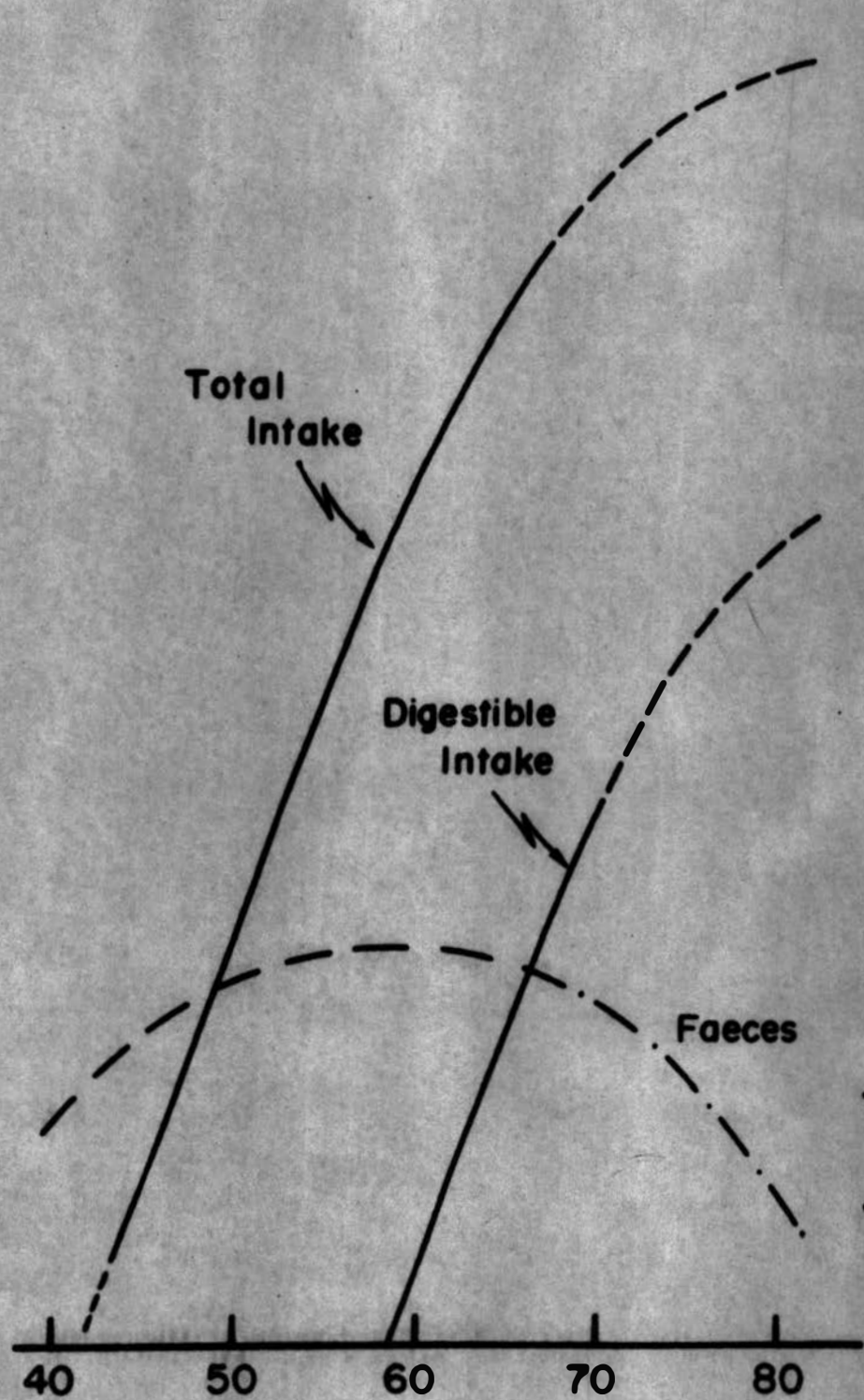
PER CENT DIGESTIBILITY OF FEED D.M.

Total Intake

Digestible Intake

Faeces

0.6A
0.5A
0.4A
FAECAL OUTPUT



Title and Legend for Fig. 2.

Title: Fig. 2. CHANGES IN THE DIGESTIBILITY OF TEMPERATE
AND TROPICAL GRASSES AND LEGUMES WITH
INCREASING AGE AND MATURITY OF THE HERBAGE.

Legend: Temperate species. Spring growths; dates of first
measurements varied between species and between localities
(U.K., refs. 33, 96, 99; Netherlands, ref. 260;
Sweden, ref. 95).

- L.P. : Lolium perenne var.S23 (ryegrass)
- P.P. : Phleum pratense var.S48 (timothy)
- F.A. : Festuca arundinacea var.S170 (tall fescue)
- D.G. : Dactylis glomerata var.S37 (cocksfoot or orchard grass)
- T.R. : Trifolium repens var.S100 (white clover)
- T.P. : Trifolium pratense var. Ultuna (red clover)
- M.S. : Medicago sativa var. Dupuits (lucerne or alfalfa)

Tropical species. (ref. 47)

- S.A. : Sorghum alnum
- C.C. : Cenchrus ciliaris var. Molopo (Buffel grass)
- C.G. : Chloris gayana var. Callide (Rhodes grass)
- P.C. : Pennisetum clandestinum (Kikuyu grass)
- D.D. : Digitaria decumbens (Pangola grass)
- P.A. : Phaseolus atropurpureus var. Siratro
- G.J. : Glycine javanica var. Cooper

