CONTRACT REVIEW

THE PLANT-ANIMAL INTERFACE REVISITED

H. DOVE

CSIRO Division of Plant Industry, GPO Box 1600, Canberra, A.C.T. 2601

In 1991-92, the gross value of the output from grazing animals in Australia was $9.2 billion, and projections for the 1992-93 financial year indicate an even higher value (ABARE 1993). It is a sobering thought that every dollar of this huge sum has its origins in the interactions between animals and the pastures which they graze. The scientific study of the "plant-animal interface" can therefore readily be justified in financial terms.

To date, the study of grazing processes has been what Demment and Laca (1993) describe as "phenomenological", that is, it has described what has happened or been observed, rather than elucidated the basic mechanisms by which the process of grazing proceeds. In this Contract Review, we aim to present new concepts and techniques which should allow the mechanistic study of the plant-animal interface in a manner and at a level of detail not possible before. We will not discuss, in any detail, the interplay between sward structure, bite size and biting rate, since these have been reviewed recently by others (Hodgson 1985; Demment and Laca 1993) and are discussed by Demment (1994). Rather, we will discuss new techniques for monitoring grazing behaviour and for estimating diet selection and total intake in the grazing animal, and will also discuss the way in which the type of the animal and the physical and chemical characteristics of the herbage influence these processes.

PLANT CUTICULAR WAX ALKANES - A NEW TECHNIQUE FOR ESTIMATING DIET SELECTION AND INTAKE IN THE GRAZING ANIMAL

H. DOVE

CSIRO Division of Plant Industry, GPO Box 1600, Canberra, A.C.T. 2601

The study of the plant-animal interface requires accurate information about the nature of the sward or plant biomass on offer, the nature of the diet consumed by the grazing animal and the total intake of plant material by the animal. There seems little doubt that, at present, our understanding of the process of grazing is hindered by deficiencies in the quality of all of these sources of information, reflecting in turn deficiencies in methodology, especially for estimates of apparent diet selection and intake.

Herbage intake in the grazing animal has been calculated most frequently from estimates of total faecal output and the digestibility of the consumed diet. Usually, these estimates are based, respectively, on the faecal dilution of an external marker (commonly Cr_2O_3) and an *in vitro* determination of digestibility on herbage samples collected by oesophageally-fistulated (OF) sheep. The problems attendant to this approach have been discussed elsewhere (eg. Dove and Mayes 1991), with the main cause for concern being the digestibility estimate. The Cr_2O_3/*in vitro* approach requires the assumption that the OF sheep consume, in a single short grazing, a diet similar in composition and thus digestibility to that consumed by the test animals over a longer period. A second disadvantage is that the single *in vitro* estimate of digestibility is applied to all the test animals, even though the extent to which they digest herbage would be expected to differ, because of differences in their level of intake, or because of the effects of supplement consumption or parasite burden. The use of alkanes from plant cuticular wax to estimate intake can overcome the second disadvantage and, as discussed below, may also obviate the need for OF sheep.

The cuticular wax of pasture plants contains saturated hydrocarbons (alkanes) of carbon-chain length C_{25} to C_{35}. Those with odd-numbered carbon chains predominate, with C_{27}, C_{29}, C_{31} and C_{33} alkanes being present in the greatest amount. Mayes *et al.* (1986) demonstrated that by dosing the test animals with synthetic, even-chain alkanes (eg., D_j mg/day of C_{32}), and measuring the herbage and faecal concentrations of the natural alkane (H_i, F_i respectively) and the dosed alkane (H_j, F_j respectively), herbage intake can be calculated from the equation:

$$\text{Intake} = \frac{F_i}{F_j} D_j \Big/ \left[H_i - \frac{F_i}{F_j} H_j \right]$$

Although the faecal recovery of alkanes is incomplete, the data presented by Mayes *et al.* (1986) and reviewed by Dove and Mayes (1991) indicate that the recoveries of the dosed and natural alkane pair are so similar that any errors arising from incomplete recovery cancel out in the ratio F_i/F_j. As a result, the largest reported discrepancy between known herbage intake and that calculated using alkanes is 1.7% (see Dove and Mayes 1991).

A device for the controlled, intra-ruminal delivery of even-chain alkanes is now available (see Dove and Mayes 1991) and we are using this approach routinely to estimate herbage intake, since it confers several major advantages over the Cr_2O_3/*in vitro* approach. First, the alkane method automatically allows for the differences in herbage digestibility occuring between individual animals. Second, the estimate is an individual one, and is likely to be more useful in genetic studies of food conversion efficiency. Third, the estimate of intake requires only 1 form of chemical analysis (gas chromatography) compared with *2* for the Cr_2O_3/*in vitro* procedure. Finally, the estimate of herbage intake can be extended to the estimation of diet selection.

Previous studies of diet selection in grazing animals have been based usually on some combination of 3 basic approaches (see Arnold 1981; Hodgson 1985; Dove and Mayes 1991). The first approach involves the hand-harvesting of the plant material on offer, either to ground level or within operator-defined "grazing horizons". While this is a useful first approximation of the diet, it does not mimic the process of selective grazing and is thus frequently replaced by, or combined with, the use of OF sheep to obtain samples of "the selected diet". The use of OF animals provides a better estimate of selection, however it can only be regarded as apparent selection, since the OF animals may select a diet different from that of the test animals, either because they are surgically prepared or because they have grazed only for a short period. Attempts to use indirect, plant-based markers of selection, as a means of avoiding the use of OF animals, generally have not been successful and in any event do not provide an estimate of selection to the plant species level.

Table 1. Typical concentrations (mg/kg DM) of cuticular alkanes in temperate pasture species

Species	Alkane of carbon chain length				
	C_{25}	C_{27}	C_{29}	C_{31}	C_{33}
Perennial ryegrass	6.3	20.0	109.0	215.2	141.4
Annual ryegrass	29.7	82.9	195.7	298.1	47.1
Subterranean clover	3.6	15.5	250.4	74.3	9.6
Lucerne	13.0	54.8	206.9	103.5	7.6

One of the most exciting features of plant alkanes is that individual plant species have their own alkane "fingerprint" (Table 1). These fingerprints can be used to estimate the species composition of herbage mixtures, based on the alkane levels in the mixtures and the component species (Dove 1992). Similarly, with due correction for the incomplete recovery of alkanes (Dove and Mayes 1991), diet composition can be estimated from the alkane concentrations in faeces (Dove and Mayes 1991; Dove *et al.* 1993). In Table 2, the botanical composition of a pasture dominant in subterannean clover is presented, together with the species composition of the diet of OF sheep, estimated using alkane concentrations either in their OF samples or their faecal samples. It is of interest that in this case, the diet selected by the animals over several days (faecal sample) was similar to that selected at a single grazing (OF sample), but both estimates of diet selection differed markedly from the botanical composition of the pasture. Although plant species is the major determinant of alkane concentrations, there are also differences between plant parts (Dove and Mayes 1991; Baker and Klein 1994). While these have the potential to complicate the estimate of species selection, they can also be used to estimate the intake of different plant parts (Simpson *et al.* 1993).

Table 2. Species composition (%) of the herbage on offer (by hand-sorting) and of oesophageal fistula (OF) samples and the diet consumed over a 6-day period (both from alkanes)

Sample	Sub. clover	Sorrel	Yorkshire fog grass	Perennial ryegrass	Other grasses[A]	Dead material
Herbage	58.9	19.0	0.8	2.4	3.2	15.7
OF sample	84.5	8.7	3.5	0	3.5	0
Diet (6 days)	88.0	3.0	0	0	1.8	7.3

[A]Chiefly *Vulpia* sp. and annual ryegrass

Plant wax alkanes thus allow the estimation of the species composition of the diet of grazing animals. If, in addition, herbage intake has been estimated, then the total intake can be partitioned into the intake of individual plant species. A major advantage of this approach is that the estimate of diet selection does not require the use of OF animals. However, as in all grazing studies, it does require that the nature of the pasture on offer be described as accurately as possible. In particular, the samples of each pasture species harvested for alkane analysis have to be as representative as possible.

We are currently investigating whether it is possible to use alkanes to estimate the intake of different plant parts from different plant species in the sward. Such data, combined with the measurement of chewing and rumination in free-grazing animals (Klein *et al.* 1994), would greatly enhance the study of the mechanisms of grazing.

PHYSICAL CHARACTERS OF FORAGES AS CONSTRAINTS TO VOLUNTARY INTAKE

S.K. BAKER[ABC], L. KLEIN[AC] and D.B. PURSER[A]

[A]CSIRO Division of Animal Production, Private Bag, PO Wembley, W.A. 6014
*Faculty of Agriculture, The University of Western Australia, Nedlands, W.A. 6009
[C]Centre for Legumes in Mediterranean Agriculture, The University of Western Australia, Nedlands, W.A. 6009

Feeding value of herbage and pasture has been defined as a function of voluntary intake, digestibility and the efficiency of utilization of digested nutrients for maintenance and production (Ulyatt 1973; Purser 1980). Of these, variation in voluntary intake accounts for at least half of the variation in feeding value among different herbage materials (Ulyatt 1973).

Weston has introduced the concept that in ruminants fed forages, voluntary intake is regulated in an interplay of the rate of clearance of dry matter from the rumen, and the amount of useful energy that is available to the animal from the forage relative to the animal's capacity to use energy (eg. Weston 1982). In a study of 14 forage diets fed to Merino sheep (Weston and Davis 1991), Weston calculated the extent to which voluntary intake of forage was constrained (FCC) as the difference between the quantity of forage that a sheep should attempt to consume to satisfy its capacity to use energy (a theoretical maximum intake) and the voluntary intake that was achieved. The data were from experiments in which it was unlikely that poor palatability of forages, the presence of deleterious secondary compounds or an inadequate balance of essential nutrients would be constraints to voluntary intake. The content in the forage of neutral detergent fibre, indigestible fibre and lignin, and the comminution energy of the forage each were more strongly related to FCC than to voluntary intake. Comminution energy showed the strongest correlation with FCC; comminution energy and digestibility of forage organic matter together accounted for nearly 95% of the variation in voluntary intake.

Differences between forages in their resistance to comminution during mastication and rumination, and the rate of removal of particles from the rumen, are reflected in differences in comminution (or shear or grinding) energy of the forages (Laredo and Minson 1973; McLeod *et al.* 1990). For the forages in the studies used by Weston and Davis (1991) intake of digestible organic matter decreased as the length of time the sheep spent eating ($R = -0.76$; regression standard deviation (RSD) $= 1.16$; $P < 0.001$) or ruminating ($R = -0.52$; $RSD = 0.81$; $P = 0.02$) increased.

We have developed techniques to measure the energy required to shear or to compress plant material

(Baker *et al.* 1993) to simulate the processes of comminution during mastication and rumination. We have found that when penned sheep were offered dry, mature subterranean clover of different genotypes, voluntary intake decreased as the energy required to shear the material increased (Table 3). Spencers Brook and Collie A which were most difficult to shear, contained the most stem and petiole (ca. 95% by weight; Taylor *et al.* 1989) but FCC of these genotypes differed. In dry, mature subterranean clovers stem is more difficult to comminute or shear than is leaf (S.K. Baker, L. Klein and D.B. Purser, unpublished data), but in this study the energy required to shear the unfractionated clover material was not solely a function of the content of leaf and stem; Mt Barker was significantly easier to shear than the remaining 2 genotypes, 69S30 and Mt Helena A (Table 3), yet they all contained similar proportions of leaf, stem and petiole. In addition there were differences among these 3 genotypes in FCC which are not explained solely by the physical characters of the material. Mt Barker was highly digestible yet FCC was higher than would be expected from its digestibility, and as high as the FCC of Mt Helena A.

Table 3. Feeding value for sheep of genotypes of dry, mature subterranean clover

Genotype	Voluntary intake^{A} (g DM/day)	Digestibility of dry matter^{A} (%)	Constraint to intake^{B} (FCC) (g OM/day.kg $BW^{0.75}$)	Energy required to shear^{C} (KJ/m^2)
Spencers Brook	381^{a}	48.6^{a}	96^{a}	23.8^{a}
Collie A	499^{ab}	49.9^{ab}	88^{b}	22.8^{a}
Mt Helena A	605^{bc}	52.3^{ab}	77^{c}	14.5^{b}
69S30.5.4.1	600^{bc}	55.6^{ab}	70^{d}	15.9^{b}
Mt Barker	732^{c}	58.0^{c}	61^{e}	12.3^{c}

Within columns, values with different superscripts are significantly different ($P < 0.05$).
[A] From Taylor *et al.* (1989).
[B] Calculated according to Weston and Davis (1991).
[C] From Baker *et al.* (1993).

Table 4. Liveweight gain of grazing sheep in relation to some physical characters of genotypes of dry mature subterranean clover*

Genotype	Proportion of stem and petiole to leaf (%)	Energy required to shear^{B} (Kg/m^2)	Energy required to compress^{B} (KJ/kg DM)	Liveweight gain (g/day) Days 14 to 43	Liveweight gain (g/day) Days 43 to 90
Trikkala	10	16.2^{a}	4.25^{a}	90^{a}	-6^{a}
Dinninup	10	16.6^{a}	5.03^{b}	100^{a}	-21^{a}
Dalkeith	35	21.9^{b}	4.99^{b}	76^{b}	-17^{a}
Daliak	25	17.8a	4.84^{b}	93^{a}	-49^{b}

Within columns, values with different superscripts are significantly different ($P < 0.05$).
[A] From D.B. Purser, S.K. Baker and L.Klein, unpublished data.
[B] Measured at the start of the grazing period as described by Baker *et al.* (1993); it is unlikely that these changed during the grazing period since the clovers were mature and dry.

Recently we have extended the concept of constraint to intake to studies of grazing sheep. Sheep grazing nearly-pure swards of each of 4 genotypes of dry, mature subterranean clover initially gained liveweight, but then began to lose liveweight (Table 4) even though voluntary intake in this study was not constrained by the availability of pasture. The high resistance of Dalkeith to shear reflects the larger proportion of stem and petiole in the pasture on offer compared with the other genotypes. In another study using material harvested from these swards penned sheep found the stem fraction ("stem-enriched") more difficult to chew than the leaf fraction ("leaf-enriched") (Figure 1) during 3-minute eating-rate tests. The energy required to shear or compress the "leaf-enriched" fraction was lower than it was for the "stem-enriched" fraction in each of the genotypes except Dalkeith where the "leaf-enriched" fraction was as difficult to compress as the "stem-enriched" fraction (data not shown). These differences were reflected in the rates of intake of these fractions.

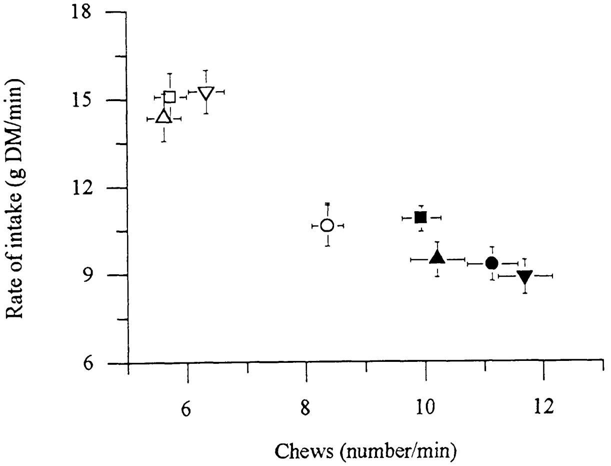

Figure 1. Rate of intake of dry matter and ease of chewing (mean and standard error) of fractions of genotypes of dry, mature subterranean clover; Daliak (triangles), Dalkeith (circles), Dinninup (inverted triangles) and Trikkala (squares). "Leaf-enriched" fractions are represented by open symbols, and "stem-enriched" fractions by closed symbols. From X.R. Wang, S.K. Baker and D.B. Purser (unpublished data)

These observations explain only part of the increased constraint to voluntary intake as the sheep continued to graze the pastures. Two newly-developed techniques are being used in this study to identify constraints to voluntary intake for grazing sheep. Telemetry, with small microphones glued to the sheeps' heads (Klein *et al.* 1994), can be used to monitor daily grazing behaviour, mastication and rumination by each sheep. Measurement of long-chain plant alkanes relative to dosed alkanes (Dove and Mayes 1991) permits determination of voluntary intake and the composition of the diet that each sheep consumes in terms of plant species, and possibly plant parts (Baker and Klein 1994).

The energies required to shear or compress dry, mature subterranean clovers appear to reflect different physical characters of the plant material and together can be used to discriminate among the genotypes (Baker *et al.* 1993; Table 4). A programme of selection of annual ryegrass for low shear strength of individual leaves resulted in plants with leaves that were thinner, narrower and lighter than the leaves of plants with a high shear strength (Easton 1989). Subsequent work with ecotypes of annual ryegrass from sites across southern Australia (Henry *et al.* 1993) has shown that there are differences among ecotypes in the inherent strength of individual leaves. These studies indicate that there may be potential in pasture breeding programmes for selection of pasture species on the basis of physical and compositional properties of the plants.

PLANT NON-STRUCTURAL CARBOHYDRATES, DIET SELECTION AND INTAKE

R. J. SIMPSON and H. DOVE

CSIRO Division of Plant Industry, GPO Box 1600, Canberra, A.C.T. 2601

As pasture plants mature, the concentration of structural carbohydrates (cell wall constituents) in their tissues increases, with a concomitant decrease in digestibility and feeding value (eg. Purser 1980). To an extent, the grazing animal can compensate for this by selection of more digestible components from the pasture, but eventually, the reduction in the feeding value of the pasture will be such that animal performance will decline. We have discussed elsewhere how alkane (Dove, this contract) and telemetry (Klein *et al.* 1994) techniques may be used to quantify this selection process more accurately than was previously possible.

Since digestibility is an important component of nutritive value (Ulyatt 1973; Purser 1980), there has been an understandable and justifiable concern of animal nutritionists with the cell wall components of herbage. However, we suggest that the concern about structural carbohydrates has resulted in insufficient attention being paid to the contribution of cell contents to the nutritive value of the herbage. For example, in maturing grass and in mature clover stems, 60-80% of the variance in digestibility is associated with the differences in the proportion of cell contents (Taylor *et al.* 1987; Ballard *et al.* 1990). Future studies should re-evaluate the effects of cell contents in general, and the non-structural carbohydrates in particular, on the processes of diet selection and herbage intake.

Arnold (1980) cited a wide range of chemical constituents of herbage which have been shown to influence its acceptability by livestock, so that it is likely that the grazing animal is integrating a complex set of chemical signals when making a dietary choice. He also suggested that, since the effect of a plant constituent will be mediated via the effect of definable chemical entities on receptor systems, care is needed in interpreting responses to more gross components such as "soluble" or "storage" or "non-structural" carbohydrates. Nevertheless, there is evidence both in his review and other publications (eg. Michell 1973; Jones and Roberts 1991; Simpson *et al.* 1993) that diet selection and intake by ruminants are influenced by the level of non-structural carbohydrates in herbage.

We have recently shown that herbicide treatment can be used to manipulate the concentrations of non-structural carbohydrates in senescing annual ryegrass, with profound effects on both diet selection and intake by grazing sheep (Simpson *et al.* 1993). When applied to annual grass pastures at anthesis, at the rate of 180 g/ha, the herbicide glyphosate ("Roundup CT") stops plant growth but allows photosynthesis to continue for a period of 3-4 weeks, albeit at a declining rate. This results in the maintenance of a relatively high soluble carbohydrate concentration in herbicide-treated plants, especially in the stem. As a result of this accumulation, for a period of up to 5 weeks after spraying the digestibility of the treated herbage remains high relative to unsprayed, senescing herbage. In annual ryegrass pastures grazed by Merino wethers, glyphosate-treated herbage had a markedly higher soluble carbohydrate content and digestibility, which resulted in greater voluntary intakes of herbage (Table 5) and significantly heavier liveweights ($P < 0.05$) compared with animals grazing unsprayed plots.

Table 5. Influence of glyphosate treatment of annual ryegrass pasture on its soluble carbohydrate content (g/kg DM) and *in vivo* organic matter (OM) digestibility (%), and on the voluntary intake (g OM/day) of herbage by grazing Merino wethers (measurements made in mid-November, 32 days after spraying)^A

	Untreated	Glyphosate-treated	LSD ($P < 0.05$)
Soluble carbohydrate	~~82.8~~ 158.3	~~127.8~~ 234.7	-
Digestibility	49.3	65.5	3.41
Herbage intake	774	1070	126.9

^{A}Unpublished data of K.L. Gatford, C. Siever-Kelly, T. Ciavarella, H. Dove, B.J. Leury and R.J. Simpson. Herbage intake calculated using C_{31} and C_{32} alkanes, faecal output and thus digestibility calculated using C_{36} alkane (Simpson *et al.* 1993).

Analysis of the alkane concentrations in the different plant parts (viz., leaf plus sheath, stem and flower spike) allowed us to partition the total intake into the intakes of these plant parts. In unsprayed herbage, the intake of the different plant parts reflected their in *vitro* digestibility, but in sprayed herbage it seemed more closely related to the soluble carbohydrate content (Table 6). Grazing animals rejected the stem component of unsprayed herbage, but in sprayed plots, stem was the preferred component. The preferences exhibited by the grazing animals were confirmed in preference tests conducted in penned animals (C. Siever-Kelly, B.J. Leury, K.L. Gatford, R.J. Simpson and H. Dove, unpublished data). Hence, the manipulation of the level and distribution of non-structural carbohydrates in the plant increased overall herbage digestibility and was associated with increased organic matter (OM) intake and a marked shift in the preference shown by the animals for different parts of the plant.

The results presented by Dove and Milne (1994) indicate that higher soluble carbohydrate concentrations in herbage can also result in improvements in the efficiency of microbial protein synthesis. These authors measured intake, abomasal digesta flow and the efficiency of microbial protein synthesis in a group of ewes grazing the same perennial ryegrass pasture either in spring/summer or in autumn. Despite the fact that the herbage digestibility was very similar at these 2 times, the efficiency of microbial protein synthesis in animals consuming autumn herbage was less than half of that observed in animals grazing spring/summer herbage (117 v. 255 g microbial crude protein/kg OM apparently fermented in the rumen, respectively). Efficiencies of microbial protein synthesis were closely related to the rumen concentrations of propionate, which were much lower in animals consuming autumn herbage. Reduced propionate concentrations in the rumen are a frequent outcome of the consumption of herbage with low soluble carbohydrate concentrations (Dove and Milne 1994).

Table 6. Influence of glyphosate treatment of annual ryegrass pasture on the soluble carbohydrate content (g/kg DM) and *in vitro* DM digestibility (%) of plant components, and on the voluntary intake of plant components (g organic matter/day) by grazing Merino wethers (measurements made in mid-November, 32 days after spraying)[A]

	Untreated				Glyphosate-treated			
	Leaf	Sheath	Stem	Flower	Leaf	Sheath	Stem	Flower
Soluble carbohydrate	72.6	78.1	196.3	178.1	134.1	133.9	371.6	160.4
In vitro digestibility	69.9	52.3	36.1	60.7	73.6	60.9	57.0	71.8
Intake[B]	490		0	284	9		844	221

[A]Unpublished data of Gatford *et al.* (see Table 5).

[B]Treatment differences in the intake of (leaf + sheath) and of stem are highly significant ($P < 0.001$).

These results reinforce our view that the manipulation of the cell content of forages, particularly the content of soluble carbohydrates, could significantly improve their acceptability, intake and utilisation by grazing animals. Cultivar development in perennial ryegrass has already resulted in lines with higher soluble carbohydrate concentrations and increased in *vitro* digestibility (Radojevic *et al. 1994).* We suggest that the telemetry (Klein *et al.* 1994) and alkane (Dove, this contract) techniques will provide a means of establishing whether these cultivars are preferred by the grazing animal, and whether this significantly improves animal performance and the profitability of the grazing enterprise.

DIET SELECTION AND INTAKE BY GRAZING ANIMALS - THE ANIMAL CONNECTION

R.A. DYNES[AC] and R.H. WESTON[B]

[A]CSIRO Division of Animal Production, Private Bag, PO Wembley, W.A. 6014
[B]45 Park St, Glenbrook, N.S.W. 2773
[C]Centre for Legumes in Mediterranean Agriculture, The University of Western Australia, Nedlands, W.A. 6009

Diet selection and voluntary feed intake (VFI) are integrated responses to a complex matrix of plant factors, discussed above, and animal factors including species, breed, age and physiological state of the animal. The effects of species, breed and physiological state on diet selection have been examined, or at least described and reviewed, by several authors (Arnold 1980; Hodgson 1985).

Species differences in diet selection have been observed between sheep and cattle on the one hand and goats alone on the other, probably reflecting the amount of browsing done by the goats (Arnold 1980). Observed selection differences between sheep and cattle are inconsistent. Arnold (1980) suggests mechanical differences in harvesting between sheep and cattle will be most influenced by the characteristics of the pasture on offer, thus difficulties may arise in comparing between experiments. Reliable estimates of species differences in intake are limited by the lack of an appropriate reference weight, and the potential effect of breed or strain differences makes comparisons difficult (Weston 1982). However, per unit difference in body size, there appears little difference between sheep, goats, cattle and buffalo. A significant VFI advantage has been reported in *Bos taurus* over *Bos indicus* cattle but findings in sheep breeds remain equivocal (Weston 1982).

Age differences appear to have little effect on the diet selected within species for sheep and cattle (Hodgson 1985). Voluntary food intake expressed per unit metabolic body weight ($BW^{0.75}$) increases progressively from weaning to 35% of mature weight, with a steady decline in intake per unit weight after this point. The VFI at maturity is about 50% of the maximum VFI attained for both sheep and cattle (Weston 1982).

Variations in physiological state can have a significant impact on ingestive behaviour. The ruminant achieves its highest VFI during lactation, with more time being spent in both eating and ruminating and the rate of intake increases (Weston 1982). During early pregnancy, VFI increases in sheep and cattle to match enhanced demand. However in late pregnancy, intake fails to increase despite the extra nutrient needs for the pregnancy products (Weston 1982). Increased body fatness may lead to a decline in intake (Weston 1982) and in rate of intake (Arnold 1980) but the quantitative relationship between VFI and body composition remains to be clearly defined.

Much work on ingestive behaviour to date has been descriptive in nature. Our studies have sought to elucidate the mechanisms underlying selection and VFI and to quantify the effects of these mechanisms. Effective plant breeding and grazing management strategies will evolve from the understanding of the mechanisms driving selection and intake in grazing animals.

Weston (1982) has explored the concept that intake is an interplay between tissue energy transactions and the clearance of organic matter from the rumen. Our data indicate that in grazing animals, energy intake is below the potential demand of body tissues and rumen digesta load less than the physiological upper limit. Hence appreciable increases in VFI appear possible for existing sheep genotypes. For example, intake and gut load of weaners fed a spring-harvested, dried annual pasture were significantly lower than for animals fed an optimum diet or an energy limiting diet despite being of similar digestible organic matter content (Table 7).

Table 7. Mean (± SE) voluntary feed intake (VFI; g DM/kg $BW^{0.75}$.day) , digestible organic matter intake (DOMI; g/kg $BW^{0.75}$.day) and rumen DM load (g/kg BW) for weaners fed dried subterranean clover, an optimal diet or an energy limiting forage (n = 12)

	Clover diet	Optimal diet	Energy limited diet
VFI	44 (3.1)^a	95 (1.8)^b	70 (2.3)^c
DOMI	30 (2.2)^a	67 (1.3)^b	41 (1.4)^c
Rumen DM load	25 (0.5)^a	16 (0.7)^b	34 (2.7)^c

Within rows, means with different superscripts are significantly different ($P < 0.05$).

Table 8. Mean (± SE) feed intake (g/kg $BW^{0.75}$) for adults and weaners offered a basal ration (80% of maintenance) plus lucerne or long or short chopped straw *ad libitum*

	Adults	Weaners
Basal ration	23	24
Lucerne intake	73 (2.1)	76 (1.8)
Short straw	26 (0.7)^a	8 (0.5)^b
Long straw	25 (3.3)^a	4 (0.9)^b

Within rows, means with different superscripts are significantly different ($P < 0.05$).

The role of a number of plant factors in intake has already been discussed. Comminution or grinding energy of a forage, which is probably an indicator of forage toughness or resistance to breakdown, is highly correlated with voluntary feed intake of the forages by animals (Weston and Davis 1991). We have found an interaction between age of the animal and responses to changing comminution energy. The rate of intake by weaners declined more rapidly than did the rate of intake of adults as forage toughness increased. The observed fall in intake was not only due to changes in toughness of the forage because there was an interaction with the particle length of the forage, independent of toughness. Observations suggest bulk density of the forage may be an important component of these changes in rate of intake with changes in forage length, in addition to components of comminution or shear energy outlined above. Furthermore weaners were much less willing to meet a dietary energy deficit by eating "tough" forages than were adults (Table 8), despite a calculated 30% higher energy demand per kilogram liveweight for growth. These findings indicate that forages of high comminution or shear energy are more detrimental to weaner performance than to adult performance and suggest the potential for cost-effective responses by manipulating intake, particularly of weaners.

Feed intake can readily respond to a change in energy demand. For example, oestradiol impairs fat synthesis and enhances fat mobilisation and accordingly its administration should reduce the capacity to store energy and result in lower food intake. We have observed this type of effect in adult sheep with plasma free fatty acids increasing and feed intake declining in a dose related manner following oestradiol administration. Further, fat sheep showed more food intake decline than thin sheep, possibly due to a greater release of fatty acids and glycerol from adipose tissue. Increasing body fatness in some situations may reduce the ability of the animal to increase VFI to meet changes in the energy supply although a clear quantitative relationship has not been demonstrated in grazing animals (Weston 1982).

Our understanding of mechanisms controlling selection in grazing ruminants remains limited. Aside from those factors discussed earlier there is likely to be considerable progress in the next decade in understanding endogenous signals in ruminants that not only drive intake but also determine selection. A number of recent studies suggest neurochemical control of nutrient selection occurs in non-ruminants. For example, in the rat the stimulation of eating by noradrenaline, neuropeptide Y and serotonin appears to favour the selection of carbohydrate rather than fat while the reverse applies for galanin (Levine *et al. 1986)* The extent to which neurochemical control of nutrient selection is operating in ruminants is not known.

CONCLUSIONS

D.B. PURSER

CSIRO Division of Animal Production, Private Bag, PO Wembley, W.A. 6014

The grazing industries of Australia are under increasing economic and social pressures due to declining terms of trade and demands that agriculture be more ecologically sustainable. An understanding of the interaction of the grazing animal with its pasture is thus of pivotal importance in relation to the achievement of both the economic and ecological objectives of farming.

Weston's concept of the regulation of the voluntary intake of forages (Weston 1982; Weston and Davis 1991) emphasises that most of the variation in voluntary intake by an animal can be explained by a combination of the physical characters of the herbage, its digestibility and the animal's capacity to use energy. This was a model of regulation of voluntary intake where poor palatability, the adverse effects of secondary compounds or an imbalance of essential nutrients did not constrain intake, but now we have used the model to identify those forages in which these latter factors are likely to be constraints to intake (Baker *et al.,* this contract). Weston's model has been a major advance, but was based on data obtained in penned animals; the challenge has been to apply it to the grazing animal.

One of the major advantages of the telemetry and alkane techniques discussed above is that they will allow us to apply this model of the regulation of voluntary intake to the grazing animal, and will permit the identification of secondary compounds or imbalances of essential nutrients as constraints to intake in the field. The model will accommodate the physiological state of the grazing animal and selective grazing behaviour, to explain differences in animal performance.

We suggest that these developments place us in a better position than ever before to make useful measurements of grazing behaviour, diet selection and intake by the grazing animal. However, to really understand the mechanisms driving the grazing process, it will be necessary to have much better measurements, in Australian pastures, of the physical nature of the herbage material, its chemical composition and particularly the way in which the herbage is presented to the animal in the sward. This remains a challenge for the future.

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