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Estimating the voluntary intake by sheep of tropical grasses from digestibility, regrowth-age and leaf content: a meta-analysis

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Abstract

Context. The voluntary intake (VI) of forages by ruminants is usually estimated from diet DM digestibility (DMD), but may be related also to the age of regrowth and the leaf blade content (Leaf) of the forage.

Aim. To examine the reliability of the prediction of the VI of tropical grasses by sheep from the DMD, Leaf and Regrowth-age characteristics of the forage.

Methods. Data from eight experiments with mature sheep fed tropical grass hay diets ($n = 229$) were used to explore prediction of VI of DM (VI_{DM}), digestible DM (DDM) (VI_{DDM}) and estimated metabolisable energy from the DMD, Leaf and Regrowth-age of the forage.

Key results. The variables were generally correlated. In data pooled across experiments the VI (g/kg $W^{0.75}$.day) of DM was poorly correlated with DMD, Leaf or Regrowth-age ($r = 0.30–0.52$). The regressions between VI and each of the variables differed among experiments in elevation ($P < 0.001$) but generally not in slope. When 'experiment' was included as a factor the VI_{DM} (g/kg $W^{0.75}$.day) = K + 0.0912 × DMD (R^2 0.80; r.s.d. 6.8; K range –26.0 to +7.8; $P < 0.001$). Also VI_{DM} = K + 0.069 × DMD + 0.020 × Leaf (R^2 0.88; r.s.d. 5.4; DMD and Leaf, $P < 0.001$); thus inclusion of Leaf reduced the r.s.d. while K ranged widely (–20.5 to +12.0). The voluntary intake of digestible DM (VI_{DDM}) = K + 0.081 × DMD + 0.011 × Leaf (R^2 0.89; r.s.d. 3.2; DMD and Leaf $P < 0.001$; K range –35.0 to –16.3). Regrowth-age was correlated with both Leaf and DMD, and VI_{DM} was predicted by Regrowth-age or Leaf with comparable error. Because numerous factors alter the composition of grasses at a specific Regrowth-age the DMD should be a more generally suitable variable to predict intakes of forage DM and DDM.

Conclusions. The estimation of the VI of ruminants ingesting tropical grass forages can be improved if the diet Leaf is included with diet DMD as a predictor. However, the general prediction of VI of sheep may involve large errors.

Implications. Knowledge of the leaf content as well as the digestibility should improve estimation of VI of tropical grasses by ruminants.

Additional keywords: forages, digestibility, leaf, prediction of intake, regrowth, ruminants.

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Introduction

The nutritive characteristics of forage diets for grazing sheep and cattle are usually described in terms of the amounts and composition of the fibrous components, N and minerals, and the digestibility of dry matter (DMD) or organic matter. Differences among botanical classes (e.g. grasses vs legumes) and morphological components (e.g. leaf blade vs stem) in nutritive characteristics, and the major role of selection of pasture components during grazing, on voluntary intake (VI) of DM (VI_{DM}) and nutrients are well known. In particular, the digestibility, the concentrations of essential nutrients such as N and minerals, and VI are usually higher for the leaf blade than in the stem components, despite the variation with maturity and plant environment, especially in mature tropical grasses (Norton 1982; Minson 1982, 1990). Regardless, the VI_{DM} generally has a much more important effect than has DMD on the intakes of digestible DM (VI_{DDM}) or metabolisable energy (ME, VI_{ME}) of grazing ruminants, since the variation in VI is generally much greater than that of DMD (Coleman and Moore 2003). Even though the differences among plant fractions, including between leaf and stem, are well known and their effects are often confounded, the VI_{DM}, of VI_{DDM} and of VI_{ME} of forages, including of tropical grasses, are generally estimated from the

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DMD and concentrations of essential nutrients in the whole plant, with consideration of the physiological status, liveweight and age of the animal (ARC 1980; NRC 1996; CSIRO 2007). The DMD of forage diets selected by grazing ruminants can be rapidly and economically measured with faecal near-infrared reflectance spectroscopy (F.NIRS) where appropriate calibrations are available (Dixon and Coates 2009, 2015). The CSIRO (2007) approach to predicting VI_{DM} includes consideration of the legume content of the diet, which can be estimated from evaluation of the pasture, and in tropical grass-legume pastures from the $^{13}\delta C$ in faeces (Jones *et al*. 1979) or F.NIRS (Coates and Dixon 2008). Leaf content has been rarely included in predictions of VI, presumably because its composition and characteristics vary with plant genotype and phenotype and it is usually correlated with DMD, but also, importantly, because routine evaluation of leaf content is difficult; measurement has usually depended on laborious and often inaccurate hand-sorting of forage samples. Since the electrical energy required to mechanically grind forage leaf is much lower than that required to grind stem, the 'grinding energy' of forages under standardised conditions has been examined as a proxy for leaf content and resistance to physical breakdown (Foot and Reed 1981; Minson 1990). However, 'grinding energy' measurements have not been adopted for routine forage evaluation. It has been established that near-infrared reflectance spectroscopy measurements of forages can be developed to measure the leaf blade content of forages and this technology may allow routine measurements. The importance of the leaf content of tropical grass forages, independently of its correlations with digestibility and nutrient concentration, has not been clearly delineated. Another approach has been to use measurements including the time for regrowth of the pasture since the previous harvest (regrowth age), the type of forage and agronomic conditions as has been investigated primarily by research groups working with pastures in the humid tropics (Chenost *et al*. 1975; Aumont *et al*. 1995; Archimede *et al*. 2000; Assoumaya *et al*. 2007; Boval *et al*. 2007).

In the present meta-analysis study, the importance of DMD, leaf content and regrowth-age in influencing VI of tropical grasses by ruminants were examined in a meta-analysis using data from a series of experiments published by a ruminant nutrition research group in subtropical Australia. The DMD, leaf blade content (Leaf) of offered forages and stage of regrowth (Regrowth-age) of forages were reported in the experiments under consideration and were often correlated. The diet DMD and Regrowth-age were considered as the primary variables, and the Leaf and Regrowth-age were considered as additional variables, in multiple regression models to predict VI. These models examined the prediction of the VI_{DM}, VI_{DDM} and VI_{ME} of tropical grass hay forages offered *ad libitum* to mature sheep in pens. A second objective was to examine the errors in prediction of VI from DMD in sheep fed tropical grasses.

Materials and methods

Source of the data considered in the multiple-regression models

Data were used from eight experiments where 224 diets (Table 1) were fed to sheep and which were published from 1967 to 1985. The following describes the conduct of these experiments, but, unfortunately, detailed descriptions of the animals and the procedures are sometimes lacking. Tropical grasses were grown on fertile alluvial soils with application of fertiliser, and, in most studies with irrigation, near Lawes, south-eastern Queensland, Australia, and were from one research group. Following establishment, the forages were harvested during the summer and autumn months at 2–11 intervals of regrowth, ranging from 0.93 to 6.22 months (28–188 days). Hay was prepared by field-wilting followed by artificial drying (inlet temperature 80–100°C), or, for two experiments (A and B), artificially dried without wilting. The hays were chopped into ~25–50-mm-length material. The forages were fed in this form in five experiments (A–D and H). In three other experiments, a gravity separator was used to separate the chopped forages into leaf-rich and stem-rich fractions, which then constituted the diets fed (Experiments E–G; Table 1). The forage diets were fed to Merino wether sheep ($n = 8$–10 per diet) that were mature or approaching maturity; liveweight was usually in the range of 30–50 kg, and a standard reference weight was assumed (CSIRO 2007). The sheep were housed indoors in individual metabolism pens or crates. Following a 7-day adaptation interval, the VI and total excretion of faeces were measured during a 10-day interval for determination of *in vivo* DM digestibility. Forage was offered at 1.10–1.15 of previous consumption to achieve '*ad libitum*' intake. In Experiments E–G, additional casein and mineral supplements were fed to avoid the possibility of deficiencies in these nutrients.

Leaf contents of the mixed, leaf-rich and stem-rich hays fed to sheep were determined by manual separation, although the classification as the 'leaf' fraction apparently differed slightly among experiments. In Experiments D and H, it was stated that the leaf was measured as the proportion of the leaf lamina, and, although not stated explicitly, apparently in Experiments A–C. For Experiments E–G with diets comprising leaf-rich or stem-rich forage fractions, it was stated that 'the leaf fraction contained: leaf lamina, seed head and leaf sheath that had separated from the stem and the lighter fractions of the stem; stem fraction contained: leaf sheath, true stem and some leaf lamina'. Hence, this 'leaf' classification for these experiments differed slightly from that used for Experiments A–D and H. No measurements of the Leaf of the forage refusals were reported. Total N concentration of individual diets was reported in Experiments A, B, E, F and G. VI was reported per unit metabolic liveweight (g/kg $W^{0.75}$) in all experiments except one and, hence, this unit of VI was used for the meta-analysis. The exception was Experiment G, where the VI was reported per unit $W^{0.9}$; these VI data were recalculated to g/kg $W^{0.75}$ units based on the mean sheep liveweight. In Experiment H, where there was a factorial design of cultivars and regrowth intervals for only one grass species, the results were reported only as main effect means and these were considered as diet treatments.

Calculations and statistical analyses

The estimated ME concentration of the forages (M/D, MJ ME/kg DM) was calculated from the DM digestibility (DMD) as: $M/D = (0.172 \times DMD\%) - 1.707$ (CSIRO 2007). VI_{ME} was calculated from the DM intake and the M/D. Data were analysed in multiple regression step-up using GENSTAT (version 16, VSN International, Hemel Hempstead, UK).

Table 1. Summary of the experiments used in the meta-analysis where tropical grass forages were fed as hays to mature sheep

Measurements were made of the leaf-blade content (Leaf), *in vivo* DM digestibility (DMD) and total N concentration of the forages, and the voluntary intake (VI) of DM and of metabolisable energy (ME) by sheep. The values given are means (s.d.) measured in 8–10 sheep. Experiments were as follows: A, Minson and Milford (1967); B, Milford and Minson (1968); C, Minson (1971); D, Minson (1972); E, Laredo and Minson (1973); F, Laredo and Minson (1975*a*); G, Poppi *et al*. 1981; H, Minson and Bray 1985. Supplements of casein and minerals were also given in Experiments E–G, so as to avoid possible diet deficiencies of rumen-degradable N and mineral nutrients

Experiment	Grasses	Maturity and preparation	Number of diets	Number of sheep per diet	Leaf (g/kg)	DMD (g/kg)	Total N (g/kg)	VI (g DM/kgW$^{0.75}$.day)	ME intake (kJ ME/kgW$^{0.75}$.day)
A	*Chloris gayana*	2 varieties cut at 4 stages of maturity (50–188 days regrowth)	8	8	305 (109)	484 (68)	12 (5.6)	41 (12.6)	279 (124)
B	*C. gayana*	6 varieties cut at 8 stages of maturity (28–140 days regrowth)	43^{A}	10	401 (148)	597 (53)	21(5.8)	48 (5.4)	411 (82)
C	*Panicum maximum* and *P. coloratum*	3 varieties of each species, 11 stages of regrowth (28–98 days)	63^{A}	8	411 (147)	563 (56)	n.a.	59 (10.1)	479 (125)
D	*Setaria splendida*, *Paspalum dilatatum*, *Chloris gayana*, *Panicum maximum*, *Pennisetum clandestinum* and *Digitaria decumbens*	1 variety of each species, 11 stages of regrowth (28–105 days)	61^{A}	8	362 (154)	577 (61)	n.a.	27 (5.5)	223 (67)
E	*Chloris gayana*, *Digitaria decumbens*, *Panicum maximum*, *Pennisetum clandestinum* and *Setaria splendida*	1 variety of each species, 3 stages of regrowth (52–87 days). Separated into ‘leaf’ and ‘stem’ fractions which constituted separate diets	30	8	416 (376)	542 (56)	13 (3.9)	49 (13.3)	374 (128)
F	*Digitaria decumbens*, *Chloris gayana* and *Setaria splendida*	1 variety of each species, 3 stages of regrowth (56, 127 and 150 days). Separated into ‘leaf’ and ‘stem’ fractions, which constituted separate diets	6	8	450 (420)	464 (66)	10 (2.9)	35 (6.7)	225 (79)
G	*Digitaria decumbens* and *Chloris gayana*	1 variety of each species, 2 stages of regrowth (42 and 84 days). Separated into ‘leaf’ and ‘stem’ fractions, which constituted separate diets	8^{B}	4	488 (487)	506 (56)	11 (2.4)	46 (6.6)	320 (74)
H	*Cenchrus ciliarus*	5 varieties, mean values for 5 stages of regrowth (28 to 98 days).	5^{C}	10	370 (47)	582 (17)	17 (0.8)	53 (2.8)	436 (37)

[A] Some varieties × stage of regrowth were not represented.

[B] Results for voluntary intake reported as W$^{0.9}$ were recalculated as W$^{0.75}$.

[C] Only main effect means of the data were reported.

Results

The grass species, cultivars and regrowth-age and other attributes at harvest for each experiment are given in Table 1. The Leaf of the mixed hays (Experiments A–D, H) ranged from ~100 to 700 g/kg (Fig. 1), with the means for experiments ranging from 305 (s.d. 109) in Experiment A to 411 (s.d. 147) in Experiment C (Table 1). The Leaf of the leaf-rich and stem-rich diets (Experiments E–G) averaged 816 g/kg (s.d. 98, range 578–960) and 51 g/kg (s.d. 40, range 10–155) respectively. The DMD of the diets ranged from ~400 to 700 g/kg (Fig. 1), with means for individual experiments ranging from 464 (s.d. 66) in Experiment E to 597 (s.d. 53) in Experiment B. Within each experiment, the correlations among the measured attributes of diet DMD, leaf content, regrowth-age, total N concentration and VI (Table 2) were often significant ($P < 0.05$ or $P < 0.01$) for Experiments A–D and H, but less often for the separated diets in Experiments E–G. When the data was pooled across experiments, and with 'Experiment' being included as a factor, these correlations were all significant ($P < 0.01$; the exception being for DMD and Leaf), with the correlation coefficient ranging up to 0.91. However, when 'Experiment' was not included as a factor in the model, the correlation coefficients were generally much lower and were not suitable for prediction of VI (Table 2). Regrowth-age was negatively correlated with DMD, Leaf and VI, while DMD and Leaf were positively correlated with VI.

The linear regression models to predict $\mathrm{VI_{DM}}$ and $\mathrm{VI_{DDM}}$ from diet DMD (g/kg) in g DM/kg $\mathrm{W^{0.75}}$ units for the pooled data across all experiments were as follows:

$$\mathrm{VI_{DM}} = 7.49 + 0.0664 \times \mathrm{DMD} (n = 229,\ R^2 = 0.08,\ P<0.01)$$

$$\mathrm{VI_{DDM}} = -18.87 + 0.0789 \times \mathrm{DMD} (n = 229,\ R^2 = 0.27,\ P<0.01).$$

The model to predict estimated ME intake (kJ ME/kgW$^{0.75}$.day) from the estimated ME content of the diet (M/D, MJ ME/kg DM) was

$$\mathrm{VI_{ME}} = -214 + 72.3 \times \mathrm{M/D}; (n = 229,\ R^2 = 0.32,\ P < 0.01).$$

The multiple-regression model to predict $\mathrm{VI_{DM}}$ from both DMD and Leaf was

$$\mathrm{VI_{DM}} = 9.57 + 0.0434 \times \mathrm{DMD} + 0.0272 \times \mathrm{Leaf}\ (n = 224;$$

$$R^2 = 0.22;\ \mathrm{r.s.d.} = 13.4;\ P < 0.001)$$

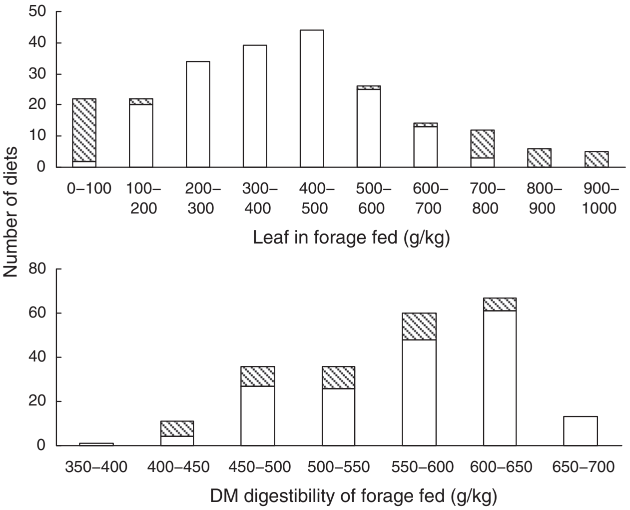

Fig. 1. The distribution of leaf-blade content (Leaf, g/kg) and of *in vivo* DM digestibility (DMD, g/kg) among the 224 tropical grass forage hay diets fed to sheep in eight experiments. Hays containing the proportions of Leaf as harvested are represented by open bars, while hays comprising separated leaf-rich or stem-rich fractions are represented by shaded bars.

Table 2. Correlation coefficients (*r*) among the concentrations (g/kg DM) of leaf blade (Leaf), total N, DM digestibility (DMD), days of regrowth of grasses at harvest and voluntary intake (VI-DM) of DM (g/kg W$^{0.75}$.day) within each experiment

In addition, the correlation coefficient for data pooled across all experiments when parallel response lines were fitted are given. In Experiments E, F and G, the diets consisted of separated leaf or stem fractions. *n*, number of diet treatments fed in each experiment; diet N concentration was not reported for Experiments C and D and the value in parenthesis is the number of diet treatments for the correlations with diet N concentration. Each diet was fed to 8–10 sheep. n.a., data not available; n.s., not significant, *, $P < 0.05$, **. $P < 0.01$

Experiment	*n*	Regrowth				Leaf			N		DMD	Regrowth	Leaf	DMD
		Leaf	DMD	N	$\mathrm{VI_{DM}}$	DMD	N	$\mathrm{VI_{DM}}$	DMD	$\mathrm{VI_{DM}}$	$\mathrm{VI_{DM}}$	$\mathrm{VI_{DDM}}$	$\mathrm{VI_{DDM}}$	$\mathrm{VI_{DDM}}$
A	8	–0.85*	–0.93**	0.64n.s.	–0.68n.s.	0.92**	0.52ns	0.55ns	0.70ns	0.90**	0.80*	0.81*	0.74*	0.92**
B	43	–0.67**	–0.88**	–0.81**	–0.66**	0.60**	0.70**	0.79**	0.77**	0.71**	0.73**	0.80**	0.76**	0.90**
C	63 (0)	–0.55**	–0.88**	n.a.	–0.67**	0.66**	n.a.	0.87**	n.a.	n.a.	0.76**	0.79**	0.84**	0.90**
D	61 (0)	–0.58**	–0.83**	n.a.	–0.78**	0.58**	n.a.	0.45**	n.a.	n.a.	0.79**	0.83**	0.51**	0.89**
E	30	–0.10n.s.	–0.81**	–0.76**	–0.51**	–0.20n.s.	0.56**	0.74**	0.50**	0.72**	0.30n.s.	0.71**	0.56**.	0.58**
F	6	0.10n.s.	–0.83*	–0.82*	–0.44n.s.	0.13n.s.	0.44n.s.	0.80n.s.	0.89*	0.85*	0.68n.s.	0.67n.s.	0.54n.s.	0.90*
G	8	0.07n.s.	–0.95**	–0.55n.s.	–0.34n.s.	0.02n.s.	0.76*	0.74*	0.59n.s.	0.77*	0.40n.s.	0.74*	0.49n.s.	0.80*
H	5[A]	n.a.	–0.99**	n.a.	–0.97**	0.93*	0.18n.s.	0.77n.s.	0.09n.s.	–0.18n.s.	0.93**	0.99**	0.38n.s.	0.13n.s.
Experiment not included as a factor in the model														
All experiments	224 (100)	–0.30**	–0.83**	–0.71**	–0.30**	–0.09n.s.	0.32**	0.43**	0.78**	0.55**	0.28**	–0.49**	0.44**	0.52**
Experiment included as a factor in the model														
All experiments	224 (100)	–0.86**	–0.86**	–0.87**	–0.88**	0.55**	0.76**	0.90**	0.81**	0.70**	0.89**	–0.87**	0.83**	0.91**

[A] Only five observations for leaf-blade content and total N concentration.

The individual regression relationships between VI_{DM} and DMD for Experiments A–D and H differed significantly ($P < 0.001$) in elevation, but only slightly in slope (Fig. 2). When 'Experiment' was considered as a factor in the regression models. The VI of DM, DDM and ME could be estimated from the diet DMD, Leaf and Regrowth-age (Tables 3–5). the following general relationship was observed between VI_{DM} and diet DMD (Table 3):

$$VI_{DM} = K + 0.0912 \times DMD (n = 224;\ R^2 = 0.80;\ r.s.d. = 6.8).$$

The 'Experiment' constant (K) ranged from –26.0 to +7.8 (Table 5). The K for Experiment D (–26.0) was lower ($P < 0.01$) than that for the other experiments, while the K for Experiment C was higher ($P < 0.05$) than for Experiments B, F and D. These relationships between VI_{DM} and DMD indicated that the increase in VI was 0.91 g DM/kgW$^{0.75}$ per day for each 10 g/kg increase in DM digestibility of the diet. At DMD = 550 g/kg, the VI_{DM} ranged from 24 to 58 g DM/kg kgW$^{0.75}$.day among experiments, which is a 2.4-fold difference. Similar linear regressions with a range in values of K were also observed for prediction of the VI_{DDM} and VI_{ME} from DMD, Leaf and Regrowth-age as the independent variables (Tables 3–5).

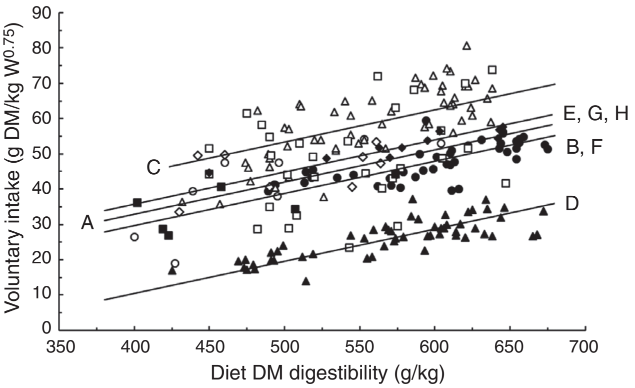

Fig. 2. The relationship between the voluntary intake of DM and the DM digestibility of the diet in the eight experiments: A (○), B (●), C (△), D (▲), E (□), F (■), G (◇) and H (◆). The intercepts of these regression lines are given in Table 5. Merino wether sheep were fed chopped tropical grass hay diets *ad libitum* and DM digestibility was measured by total collection of faeces. The slopes of the regression lines indicated that voluntary intake (VI) increased 0.912 g DM/kgW $^{0.75}$.day for each 10 g/kg increase in diet DM digestibility.

The multiple-regression model to predict VI_{DM} (g DM/kg W$^{0.75}$.day) as a function of both DMD (g/kg) and Leaf (g/kg) was as follows (Table 3):

$$VI_{DM} = K + 0.0689 \times DMD + 0.0205 \times Leaf (n = 224;$$
$$R^2 = 0.88; r.s.d. = 5.4).$$

The DMD and Leaf variables were significant ($P < 0.001$), but the DMD × Leaf interaction was not ($P = 0.55$). Similar multiple-regression models were observed for prediction of DDM or estimated ME. The multiple-regression model to predict VI from DMD and Regrowth-age had a lower R^2 (0.80) and a higher r.s.d. (6.8), and the variable Regrowth-age and the DMD × Regrowth interaction did not contribute significantly to the model ($P > 0.05$). The variability explained by the latter multiple regression was similar to that explained by the simple regression (Table 2).

The multiple regression model to predict VI_{DDM} (g/kg W$^{0.75}$) was

$$VI_{DDM} = K + 0.0808 \times DMD + 0.0111 \times Leaf (n = 224;$$
$$R^2 = 0.89; r.s.d. = 3.2),$$

where the DMD and Leaf variables were both significant ($P < 0.01$) and there was a range of K values (Tables 3 and 5). A comparable multiple-regression model to predict the VI_{ME} (kJ ME/kg W$^{0.75}$.day) is also given in Tables 3 and 5 with the difference that the DMD and DMD × Leaf interaction terms were significant ($P < 0.001$ and $P < 0.05$ respectively); Leaf was not significant ($P = 0.20$), but as a main effect, it was retained in the model. The multiple-regression models to predict VI_{DM}, VI_{DDM} and VI_{ME} from Regrowth-age or Regrowth-age and Leaf are given in Tables 4 and 5. The errors associated with these predictions, as indicated by the R^2 and the r.s.d., were higher than those when DMD and Leaf variables were used to predict these various units of VI.

Table 3. Regression models to predict the voluntary intakes of DM, digestible DM (DDM) and estimated metabolisable energy (ME) per unit metabolic liveweight (W) from the independent variables diet DM digestibility (DMD, g/kg) and leaf-blade content (Leaf, g/kg) of the diet

The factor 'Experiment' was included in the model and was always significant ($P < 0.001$). The coefficients and s.e. of the predictor variables applicable to all experiments are given in this table. The coefficients for the individual experiments are given in Table 5 below. n.s., not significant; *, $P < 0.05$; **, $P < 0.01$

Voluntary intake (VI)	DMD		Leaf		DMD × Leaf		R^2	r.s.d.
	Coefficient	s.e.	Coefficient	s.e.	Coefficient	s.e.		
DM (g/W$^{0.75}$.day)	0.0912**	0.0079	–	–	–	–	0.80	6.8
	–	–	0.0258**	0.0020	–	–	0.81	6.5
	0.0689**	0.0067	0.0205**	0.0017	–	–	0.88	5.4
DDM (g/W$^{0.75}$.day)	0.0932**	0.0046	–	–	–	–	0.84	3.9
	–	–	0.0174**	0.0017	–	–	0.69	5.5
	0.0808**	0.0040	0.0111**	0.0011	–	–	0.89	3.2
ME (kJME/W$^{0.75}$.day)	1.447**	0.066	–	–	–	–	0.84	56.4
	–	–	0.255**	0.0259	–	–	0.66	83.5
	1.272**	0.058	0.156**	0.0152	–	–	0.89	46.7
	1.030**	0.112	–0.158n.s.	0.126	0.00059*	0.00023	0.90	46.2

Table 4. Regression models to predict voluntary intakes of DM, digestible DM (DDM) and estimated metabolisable energy (ME) per unit metabolic liveweight (W) from the independent variables of regrowth-age (months) of the grasses at harvest for hay and leaf-blade content (Leaf, g/kg) of the diet are given

The factor 'Experiment' was included in the model and was always significant ($P < 0.001$). The coefficients (s.e. in parenthesis) of the predictor variables applicable to all experiments are given in this table. The coefficients for the individual experiments are given in Table 5 below. *, $P < 0.05$; **, $P < 0.01$

Voluntary intake (VI)	Regrowth-age		Leaf		Regrowth-age × Leaf		R^2	r.s.d.
	Coefficient	s.e.	Coefficient	s.e.	Coefficient	s.e.		
DM ($g/W^{0.75}.day$)	–4.75**	0.48	–	–	–	–	0.78	7.2
	–3.21**	0.42	0.0207**	0.0019	–	–	0.85	5.8
DDM ($g/W^{0.75}.day$)	–4.64**	3.15	–	–	–	–	0.76	4.8
	–2.43**	0.56	0.0195**	0.0032	–0.0036**	0.0013	0.83	4.1
ME ($kJME/W^{0.75}.day$)	–71.7**	4.66	–	–	–	–	0.76	70.3
	–37.5**	8.38	0.2918**	0.0481	–0.0589**	0.0197	0.82	61.1

Table 5. The individual 'constant' terms (K) for the regression models (Tables 3, 4) calculated for each of the experiments to predict the voluntary intakes (VI) of DM (g/day), digestible DM (DDM; g/day) and estimated metabolisable energy (ME) each per unit metabolic liveweight (W; kJ ME/kg $W^{0.75}$.day) from the independent variables diet DM digestibility (DMD) (g/kg) and leaf-blade content (Leaf, g/kg) of the diet, and to predict the same measurements of voluntary intake from regrowth-age (months) and Leaf of the diet

These values for the 'constant' K indicate how much the prediction of VI will vary with forages fed in each of the eight experiments

Voluntary intake	Prediction variable	Experiment							
		A	B	C	D	E	F	G	H
DM	DMD	–3.5	–6.8	7.8	–26.0	–0.7	–7.1	–0.6	–0.6
	Leaf	32.8	37.3	48.5	17.3	38.0	23.6	32.9	43.0
	DMD, Leaf	1.0	–1.7	12.0	–20.5	2.8	–6.0	0.7	4.8
DDM	DMD	–24.9	–27.0	–18.7	–38.1	–23.9	–26.7	–24.0	–23.5
	Leaf	15.0	21.7	26.6	9.3	19.4	8.8	14.7	24.2
	DMD, Leaf	–22.2	–24.0	–16.3	–35.0	–21.8	–25.9	–23.1	–20.5
ME	DMD	–422	–453	–336	–612	–410	–447	–412	–403
	Leaf	202	309	374	131	269	110	196	342
	DMD, Leaf	–384	–410	–301	–567	–380	–435	–399	–361
	DMD, Leaf, DMD × Leaf	–261	–283	–174	–439	–248	–306	–268	–231
DM	Regrowth	59.6	56.3	66.9	34.5	59.9	52.6	55.4	60.3
	Regrowth, Leaf	47.1	41.2	55.9	24.4	47.7	37.6	42.1	–
DDM	Regrowth	38.7	37.0	41.3	23.3	37.6	33.6	32.8	38.6
	Regrowth, Leaf, Regrowth × Leaf	27.8	27.4	31.9	14.4	27.7	22.9	22.4	–
ME	Regrowth	565	541	596	341	544	488	470	561
	Regrowth, Leaf, Regrowth × Leaf	402	397	456	209	399	332	316	–

Discussion

Effects of inclusion of diet leaf content as a variable to improve prediction of VI

The eight experiments published by one research group used for the present meta-analysis reported the VI for 229 tropical grass hay diets (means for 8–10 sheep per diet) provided an unusually large and comprehensive dataset measured using similar experimental procedures to examine the effects of DMD, Leaf and Regrowth-age on VI by sheep fed chopped hay in pens. Although in this dataset, the VI could be described with similar reliability as a linear function of either DMD or Leaf (Table 3 and 5) it was considered most appropriate to follow the approach in many feeding standards and to continue to use DMD as the primary variable to predict VI. The inclusion of the Leaf of the hay forage as an additional independent variable with DMD in a multiple regression model significantly ($P < 0.01$) and substantially improved the prediction of VI, with an increase in the R^2 from 0.80 to 0.88, and decrease in the r.s.d. from 6.8 to 5.4 (i.e. a 21% reduction). This showed unequivocally that the leaf content, as measured in these experiments, contributed to prediction of the VI of tropical grass hays fed to sheep in pens despite the correlation between DMD and leaf content (R^2 = –0.30; Table 2). An additional consideration in interpretation of the relative effects of DMD and leaf content on VI is the expected range of these variables in diets of ruminants grazing tropical grass pastures. Leaf content is likely to range widely (e.g. 100–900 g/kg), whereas the DMD is likely to range from ~450 to 700 g/kg (Norton 1982). Hence the leaf content of the diet may often be as important as the DMD in influencing VI, despite the lower coefficient for Leaf in the multiple regression models. A further consideration is the extent to which the measurements of sheep fed in pens on chopped hay and with little opportunity for selection of the hay components can be extrapolated to the animal grazing fresh pasture where numerous additional and important factors will determine the diet ingested. Clearly, numerous spatial and temporal factors affect the selection of pasture and the voluntary intake by grazing ruminants (Minson 1990; Baumont *et al*. 2004; Boval *et al*. 2014), and VI of fresh tropical grass forage may be higher than that for hay of the same composition (Archimede *et al*. 1999). Nevertheless, the sward components considered in the present meta-analysis are likely often to be important.

It is well established that the nutritional value and VI by ruminants of forages decreases with an increasing plant maturity and stage of regrowth (Chenost *et al*. 1975; Minson 1990; Aumont *et al*. 1995; Archimede *et al*. 2000; Coleman and Moore 2003; Boval *et al*. 2010, 2014). Stage of growth, or regrowth-age, has often been correlated with the concentrations of essential nutrients such as total N, the concentrations of fibre components and lignin, DM digestibility and VI of DM. Changes in these attributes with an increasing maturity of the grass is especially marked in tropical grasses. In the present meta-analysis dataset where sheep were fed in pens, the regrowth-age of the hays was also correlated with VI, Leaf and VI (Table 2), but the regrowth-age did not contribute significantly ($P > 0.05$) in multiple-regression models that included DMD as an independent variable. Although regrowth-age may well be useful in some circumstances, we consider it to be generally less suitable than are DMD and Leaf as a predictor of VI. First, as described above, the use of DMD, or constituents of forage associated with DMD such as fibre-fraction concentrations, have been adopted in many mainstream feeding-system standards (ARC 1980; NRC 1996; CSIRO 2007). Second, in the present dataset, 'regrowth-age' contributed less as an independent variable than did Leaf in a multiple-regression model already including DMD as a variable. Third, regrowth-age does not encompass the variation among grass genotypes or phenotypes in their composition of Leaf. Fourth, except where pastures are harvested or grazed intensively for brief intervals with closely controlled management, the regrowth-age of specific grass plants in a pasture sward will vary widely depending on the time since their most recent defoliation. Thus, in many grazing circumstances, any estimated 'regrowth age' is likely to be associated with a wide variation within the sward in the time since the most recent defoliation. Furthermore, because plant growth will be influenced by numerous environmental factors, the regrowth-age is likely to be more specific for seasonal and regional circumstances and, thus, will be generally less suitable than DMD as a variable to predict voluntary intake. Nevertheless, the regrowth-age may be a more useful as a practical predictor for pasture management than is diet DMD in some circumstances such as when the DMD cannot be measured using F.NIRS. In addition, in humid tropical environments, regrowth-age has been closely correlated with DMD and N concentration of the pasture on offer (Aumont *et al*. 1995) and of the diet selected by cattle grazing sown pastures (Dixon *et al*. 2020).

An explanation for the association between leaf-blade content and VI is that grass leaf blade is more easily fragmented and reduced in particle size than is grass stem during chewing and rumination, thus allowing more rapid passage of undigested forage leaf residues from the rumen and through the gastrointestinal tract. This is in accord with the understanding that forage-particle breakdown and passage is the principal constraint to VI of lower-quality, more fibrous and lower-DMD forages (Allen 1996; Weston 1996; Wilson and Kennedy 1996). The forces required to fracture and break stems are much greater than for leaf, and are also generally higher in tropical grasses than in temperate grasses (Hughes *et al*. 2000; Zhang *et al*. 2004; Benvenutti *et al*. 2009; Jacobs *et al*. 2011). These studies also indicated that the resistance to physical breakdown during ingestion and rumination of tropical grasses will vary widely, depending on the species and cultivar, and possibly also the growing conditions of the forage. Tropical grasses are generally more resistant to physical breakdown than are temperate grasses; Laredo and Minson (1975*b*) reported that the effect of leaf content on VI was much higher in tropical grasses than in the temperate perennial grass *Lolium perenne*. Where the effects of leaf content on VI are associated with resistance to physical breakdown, the importance of the leaf content can be expected to vary depending on both the absolute and the relative resistance of the leaf and stem components to physical breakdown. Furthermore, the forces required to fracture and break stems varies substantially among tropical grasses (Benvenutti *et al*. 2009; Jacobs *et al*. 2011). These observations may partly explain the differences among experiments in the present meta-analysis in the elevation of the regressions of the VI with DMD, Leaf and Regrowth-age; the lower intake of some grasses at the same digestibility may have been associated with differences in resistance to physical breakdown. Improved prediction of VI of forages may well need to include measures of differences among grasses in resistance to particle breakdown.

The forages examined in all the experiments used in the meta-analysis and for validation (see below) were tropical grass hays. An important question is whether the same relationships to predict VI would also apply to both hays and fresh forages, as selected by a grazing ruminant. If the effects of Leaf on VI are primarily a consequence of the differences between the leaf blade and stem in the rate of fragmentation during rumination and on passage of digesta residues from the rumen, then similar outcomes can be expected for forage in the forms of either hay and fresh pasture. The information available does not allow a definitive conclusion.

The effects of high diet leaf content to increase VI are in agreement with experiments with sheep, goats and cattle fed a range of tropical grass hays, where allowing a greater selection and ingestion of leaf by increasing the amount of forage offered has often substantially increased VI (Zemmelink *et al*. 1972; Bitende and Ledin 1996; Mbwile and Uden 1997; Zemmelink and Mannteje 2002). Similarly, allowing greater selection of leaf has increased VI of stover from C_4 millet, sorghum and maize cereals (Savadogo *et al*. 2000;

Methu *et al*. 2001), C_3 barley straws (Wahed *et al*. 1990; Rafiq *et al*. 2002) and cowpea or peanut legume crop residues (Rao *et al*. 1994; Savadogo *et al*. 2000). However, interpretation of the effects of higher content to increase VI must also consider that a higher VI may often be associated with a higher digestibility and a higher nutrient concentration of the leaf than stem as well as the physical attributes of these components.

The generally higher nutrient concentrations in leaf are not likely to have been important in the present meta-analysis, since the hays used were grown on fertile soils and were generally high in N (>10 g N/kg DM). However, this may have been important in other experiments where low N concentration was likely to be a constraint to VI. Experiments where an intake response has been observed to increased leaf content will be useful for validation of the models in the present meta-analysis only when there is evidence that a response was not due to the Leaf component providing nutrients (e.g. such as N) that were deficient. Two experiments do provide appropriate data for validation of the prediction of VI from DMD and Leaf. In one study where sheep were fed leaf-rich or stem-rich fractions of barley straw supplemented with additional N and S microbial substrates, there was a close agreement between the increase in VI_{DM} estimated by the multiple-regression model from the present meta-analysis and the VI_{DM} measured in the experiment when a leaf-rich straw diet replaced a stem-rich straw diet (36% and 39% increases respectively; Rafiq *et al*. 2002). Also, in a second experiment (Mero and Uden 1998) where sheep were fed four tropical grass species at two stages of maturity, offered in amounts ranging up to about three times the VI to allow selection of leaf, the VI of forage DM predicted from the DMD and Leaf as described in Table 3 was within 3% of the measured increase.

The hypothesis that evaluation of the VI and nutritional value of some classes of forages, including tropical grasses, could be improved by measurements of diet leaf content was supported by the present meta-analysis. However, because leaf content of the grass hays examined was correlated with DM digestibility, the improvement in prediction was not large. Thus, the leaf content and regrowth-age may be useful in some circumstances to improve prediction of VI of tropical grass forages, providing consideration is given to the potential environmental effects on regrowth. Diet DMD can be measured with F.NIRS. The scarcity of studies reporting the morphological components during nutritional evaluation of forages is presumably because such measurements by manual sorting are laborious and often inaccurate, rather than lack of recognition of the importance of the leaf content. Near-infrared spectroscopy may facilitate measurements of Leaf, since calibrations for the leaf blade and botanical contents can be developed for temperate grasses (Leconte *et al*. 2000), tropical grasses (Smart *et al*. 1998, 2004; Dixon and Zhu 2007; Dixon *et al*. 2007) and *Medicago sativa* (Hill *et al*. 1988; Andueza and Munoz 2004).

Accuracy of prediction of VI from diet DMD

In the present meta-analyses, the linear relationships between DMD and VI of forages within experiments (Tables 3 and 5) are in accord with the results of numerous past studies, and this is a fundamental relationship used in many feeding standards to estimate of VI of forages (ARC 1980; CSIRO 2007). Consequently, the large differences among experiments in VI_{DM} at a given DMD in the present dataset, and the poor relationship between DMD and VI_{DM} or VI_{DDM} if the data were pooled across experiments (Fig. 2), are disconcerting and demonstrated that a large error can occur in the prediction of VI from diet DMD. This is especially so given that the experiments for the present dataset were all undertaken by one research group, with a specific class of ruminants (i.e. mature Merino wether sheep) and using similar experimental procedures. This variation leads to concerns about the magnitude of the error associated with the general prediction of VI by feeding standards, particularly with tropical grass forages. Because, in the meta-analysis, the grass species examined were confounded with the groups of animals in each of the eight experiments, the relative contributions of plant and animal factors to the variation in VI could not be determined. However, the observation that VI was particularly low in Experiment D and high in Experiment C (as indicated by the K values in Table 5), each of which measured six grass species or cultivars, and that the same grass species were also measured in other experiments in the series, suggests that in the present meta-analysis data, the differences were due to animal factors rather than plant factors. These Experiments C and D also comprised 54% of the total dataset and were, therefore, not aberrant small experiments. Furthermore, inclusion of the Leaf of the diet as a variable did not resolve this difficulty associated with the sometimes poor relationships between VI and DMD across populations of sheep fed tropical grass forages.

A further consideration is that the predicted VI_{DM} for mature wether sheep, as used in the present dataset and calculated following CSIRO (2007) equations, was usually substantially higher than was the VI_{DM} observed in the experiments examined in the meta-analysis data (Fig. 2). This predicted VI_{DM} at DMD = 550 g/kg was ~70 g DM/kg $W^{0.75}$.day, by using best estimates for the standard reference weight and liveweight (50 and 45 kg respectively). Error of this origin may be one important reason for the substantial differences that have been observed by some authors (McLennan and Poppi 2005; Dove *et al*. 2010; McLennan 2014) between measured forage intakes and productivity of cattle consuming tropical forage diets and the intake and productivity predicted by nutritional models.

In conclusion, a meta-analysis of the data from experiments reported by one major research group has shown that the VI of tropical grass forages by sheep was predicted more satisfactorily by multiple-regression models that included the leaf content as well as the DMD of the diet. Measurements of the morphological components of forage diets are likely to improve the prediction of VI of forages, particularly tropical grasses, for evaluation of their feeding value.

Conflicts of interest

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