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Energy requirements of cattle for standing and for ingestion, estimated by a ruminal emptying technique¹

A. Susenbeth^{*2}, T. Dickel^{*}, K.-H. Südekum^{*}, W. Drochner[†], and H. Steingäß[†]

^{*}Institute of Animal Nutrition, Physiology and Metabolism, Christian-Albrechts-University, 24098 Kiel, Germany and [†]Institute of Animal Nutrition, Hohenheim University, 70593 Stuttgart, Germany

ABSTRACT: Energy requirements for ingestion and standing were determined in open-circuit respiration chambers with four ruminally cannulated German Red Pied steers weighing 617 ± 53 kg of BW (mean \pm SD). The requirement for standing over lying was derived by regressing heat production on time spent standing within 2-h periods when no feed was offered to avoid any interference with eating activity, and amounted to 14 kJ/(d·kg of BW). The energy requirement for ingestion was determined by calculating the difference between heat production during a 2-h period without feed and during a consecutive 2-h period in which straw of different particle sizes, fresh and conserved grass, or rolled barley were offered for ad libitum intake. Before measurements, the rumens of the steers were emptied, washed, and filled with a buffer solution to avoid heat production by metabolism of absorbed nutrients from the feed ingested during the experimental periods. The

mean value for all feeds tested was 20 J/(min of ingestion · kg BW). Relating heat production to the amount of DM or fiber ingested did not decrease variation among feeds. This confirms the observations of earlier studies, that energy requirement for ingestion is mainly determined by time spent eating. Results of additional measurements, in which the same amounts of the respective feeds ingested in preceding periods were put into the emptied rumens via the cannulas, showed that the presence of the feed in the rumen did not increase heat production, indicating that the increment of heat production during eating is mainly caused by ingesting and chewing the feed. Further measurements in the same animals with an ingesta-filled rumen showed that ingestion of straw led to an increase in heat production per minute of chewing similar to those with emptied rumens, which confirms the validity of the experimental procedure using ruminally emptied animals to determine the energy requirement for ingestion.

Key Words: Cattle, Energy Cost of Activities, Energy Requirements, Ingestion, Rumen

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Introduction

Energy requirement for eating and chewing represents a considerable proportion of the total energy metabolism in ruminants and other herbivores. In a previous study, we determined the energy requirement for eating activity in steers by measuring the increased heat production during a 2-h period (in which straw was offered for ad libitum intake), and compared this to the directly preceding 2-h period without any feed intake (Susenbeth et al., 1998). The limit of this experimental procedure is that energy requirement for ingestion

can be determined only for feedstuffs with very low degradation rates, of which it can be assumed that heat production associated with absorption and metabolism of their nutrients during the experimental period is negligible. Experiments with cattle reported in the literature provide evidence that the energy requirement for ingestion is determined by the time spent eating rather than by DMI rate for different feeds (Dahm, 1910; Adam et al., 1984). These measurements were made on a limited number of feedstuffs by using a ventilated hood or trachea-fistulated animals.

The aim of this study was to determine the energy requirement for chewing in cattle for feedstuffs differing in ruminal degradability, particle size, and type of conservation by using the aforementioned procedure (Susenbeth et al., 1998). To enable measurements for a longer period, and to avoid fermentation and absorption of nutrients from the feed ingested during the experimental period, the rumens were emptied manually through a large ruminal cannula, washed, and filled with a buffer solution. Therefore, it was necessary to

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²Correspondence—phone: +49-431-880-2013; fax: +49-431-880-1528; e-mail: susenbeth@aninut.uni-kiel.de.

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carry out additional measurements within this study to confirm that ruminally emptied animals gave results similar to those with ingesta-filled rumens. Furthermore, we investigated to what extent other physical activities, such as standing and gastrointestinal tract motility, might be enhanced during ingestion and how that may account for the increased heat production during ingestion.

Materials and Methods

Feedstuffs and Analytical Methods

Four differently treated barley straws from the same batch were used: chopped (long straw), ground using a 14-mm sieve (medium straw), ground using a 4-mm sieve (short straw), and chopped straw that was treated with 30 g/kg of NH_3 in air-tight barrels during a 5-wk period (NH_3 -treated long straw). A first-cut mixed grass sward was harvested on May 17, 1999, of which one part was conserved in vacuum-packed plastic bags at 4°C 1 to 4 d before feeding (fresh grass), another part was ensiled as compressed bales wrapped in plastic stretch film over 7 wk (grass silage), and a third one was artificially dried at approximately 40°C air temperature for 3 d (grass hay).

Proximate analyses and determination of detergent fiber fractions of the feedstuffs were carried out according to Bassler (1993) and Van Soest et al. (1991), respectively. The detergent fiber analyses were performed without the use of decalin. Sodium sulfite was omitted and triethylene glycol was used instead of 2-ethoxyethanol in the NDF procedure. Digestibility of OM and the ME contents of feedstuffs were estimated based on 24-h in vitro gas production and chemical composition according to the procedure of Menke and Steingass (1988) using the following equations:

Roughages:

$$\text{OM digestibility, \%} = 15.38 + 0.8453 \cdot \text{GP} + 0.0595 \cdot \text{CP} + 0.0675 \cdot \text{ash}$$

$$\text{ME, MJ/kg of DM} = 2.20 + 0.1357 \cdot \text{GP} + 0.0057 \cdot \text{CP} + 0.0002859 \cdot \text{EE}^2$$

Barley:

$$\text{OM digestibility, \%} = 9.00 + 0.9991 \cdot \text{GP} + 0.0595 \cdot \text{CP} + 0.0181 \cdot \text{ash}$$

$$\text{ME, MJ/kg of DM} = 1.06 + 0.1570 \cdot \text{GP} + 0.0084 \cdot \text{CP} + 0.0220 \cdot \text{EE} - 0.081 \cdot \text{ash}$$

where GP is gas production after 24 h (mL/200 mg of DM) and EE is ether extract (crude fat); CP, ash, and EE are given as g/kg of DM.

Weight distribution of feedstuff particles was determined by dry sieving, using sieves (20 cm i.d.) with

square apertures of 8.0, 4.0, 2.0, 1.0, and 0.5 mm on a side, with an electromagnetic sieve shaker (Vibrotonic type VE-1, Retsch, Haan, Germany) for 12 min. The sieve shaker was operating with an amplitude of 2 mm and the vibrations were interrupted every 20 s for approximately 2 s. Triplicate samples of 20 to 30 g of roughages and 100 g of the rolled barley were sieved and the material retained was weighed. The mean particle size was estimated by fitting the percentage of cumulative material oversize from each sieve to an exponential model (Fisher et al., 1988) using the NLIN procedure of SAS (SAS Inst., Inc., Cary, NC). For longish particles (roughages), aperture values of the squares were multiplied by $2 \times 2^{0.5}$ to receive the mean particle size (Vaage et al., 1984). Grinding energy requirements of the feedstuffs were measured according to the methods outlined by Paul et al. (1981) and Paul and Schild (1982). The chemical composition, OM digestibility, ME contents, particle size, and grinding energy requirements of the feedstuffs are summarized in Table 1.

Animals and Housing

The experiments were carried out from April to July 1999 at the Institute of Animal Nutrition, Hohenheim University, Stuttgart, Germany. Four ruminally cannulated German Red Pied steers weighing 617 ± 53 kg of BW (mean \pm SD) and ranging in age from 27 to 31 mo were used. Two additional steers served as donors of ruminal liquid. Animal care and experimental procedures were conducted according to the German Guidelines and Regulations on Animal Care ("Deutsches Tierschutzgesetz, 1998: Durchführung von Tierversuchen") and were approved by the University of Kiel Committee on Animal Care.

Animals were kept in straw-bedded pens with free access to water. They were given 1.4 kg/d of a commercial concentrate consisting of (as-fed basis) 40% barley, 33% wheat, 22% soybean meal, 2% soybean oil, 3% mineral-vitamin premix, and the respective roughage for ad libitum intake during at least 4 to 5 d before the experimental periods. The experiments could be carried out without any problems; the animals were well adapted to handling and the respiration chambers. Two animals suffered once from ruminal acidosis during a short period, which was successfully treated with NaHCO_3 and ruminal fluid from the donor animals.

Main Experiment

On the day before the gas exchange measurements were performed, animals were transferred to a tie stall, where they received 0.7 kg of concentrate and about 1 kg of DM of one of the experimental feedstuffs at 1600. The next morning, between 0700 and 0800, the rumens were manually emptied, washed with warm water, and filled with 30 L of a buffer solution (300 mOsm/L), which contained 75 M NaCl, 45 M NaHCO_3 , 2 M Na_2HPO_4 , 5 M KCl, 20 M KHCO_3 , and 2 M CaCl_2 . Immediately

Table 1. Chemical composition and characteristics of the feedstuffs

Feedstuff	Composition of DM, g/kg								Characteristics ^a			
	DM, g/kg	Ash	CP	EE	CF	NDF	ADF	ADL	OMD, %	ME, MJ/kg of DM ^b	MPS, mm ^c	GER, J/g of DM
Long straw	901	82	45	12	435	832	548	66	49	6.2	11.3	326
Medium straw	901	82	45	12	435	832	548	66	49	6.2	5.8	325
Short straw	901	82	45	12	435	832	548	66	49	6.2	3.3	291
Long straw, NH ₃ -treated	899	80	81	10	423	784	581	65	60	7.9	13.3	342
Fresh grass	226	98	107	25	265	535	343	35	75	10.6	ND	104
Grass silage	310	97	102	25	306	566	354	26	72	10.2	ND	102
Grass hay	868	96	101	25	264	502	289	30	76	10.8	ND	105
Barley, rolled	881	30	134	32	44	164	64	10	88	13.6	1.7	50

^aOMD = estimated OM digestibility; MPS = mean particle size; GER = grinding energy requirements. For detailed definitions see Materials and Methods section.

^bEstimated ME as outlined in the Materials and Methods section.

^cND = not determined.

afterwards, the animals were put into the open-circuit respiration chambers. The first hour in the chamber served as an adaptation period. During h 2 and 3, gas exchanges were measured without any feed. After finishing measurements, ruminal levels of the buffer solution were controlled and, if necessary, restored to the initial levels. During h 4 and 5, animals were offered the respective feed for ad libitum intake, and gas exchange was recorded. The feeds were put into the chambers via airtight cylinders, which were attached to the chambers to enable feed application without any losses of gas or the necessity to enter the chambers. Animals were transferred to the pen after measurements, and the buffer and ingested feed were removed from the rumen. The normal ruminal contents, which had been kept at body temperature after emptying, were returned to the rumen and fresh ruminal liquid from the donor animals was added. Steers were used for further measurements in the respiration chambers after 2 d (at the earliest). Each feed was tested with each animal during two consecutive 2-h periods, resulting in a total of 64 respiration measurements.

Air temperature, air humidity, and air exchange rate in the chambers were 20°C, 60 to 70%, and 15 m³/h, respectively. Representative gas samples were taken and analyzed for O₂ (paramagnetic principle, Magnox 2T), and for CO₂ and CH₄ (infrared absorption principle, Uras 10E; both apparatuses from Hartmann und Braun, Frankfurt/Main, Germany). Additionally to the measurements of the volumes and the concentrations of gases in the inflowing and outflowing air, the amounts of O₂ and CO₂ present in the chambers (volume of the chamber multiplied by gas concentrations) were determined at the beginning and the end of the 2-h periods to enable corrections of the gas flows to receive values for gas production and consumption rates. Heat production was calculated from oxygen consumption using the oxienenergetic equivalent of 20.5 kJ/L of O₂ (McLean, 1972).

During the 2-h measurements of gas exchange, chewing activity was recorded. The animals wore a halter

to which was attached a small rubber balloon that was compressed by each jaw movement. The balloon was connected to a thin tube, from which airflow was detected. A computer recorded each jaw movement so that the time spent for eating as well as the number of chews could be determined. Less than two jaw movements within 4 s were not taken as eating activity, and a pause of chewing was defined as no jaw movement for eating within a 4-s period. This correction was necessary to remove signals by single jaw movements, which were not caused by eating; they accounted for 2.3% of the total signals.

Additional Measurements to Confirm the Suitability of the Experimental Procedure of the Main Experiment

Energy Requirement for Standing (Subtrial 1). In all experiments, time spent standing and lying and the number of changes in position were measured by a photoelectric barrier to enable correction of variations in heat production caused by differences in standing time, which might be correlated with eating activity. The requirement for standing could be estimated by regressing heat production data, received from the ruminally emptied animals of all respiration periods without feed, on time spent standing (72 observations). Animals were not forced to change their positions in order to observe spontaneous behavior in this environment, and variations in activity and heat production were not influenced by experimental treatment. All data on heat production and associated values were corrected to a situation where animals were continuously standing.

Circadian Variations in Heat Production (Subtrial 2). When using the procedure described above to estimate the increase in heat production associated with ingestion, it is necessary to suppose that the portion of heat production that is independent of physical activity is constant throughout the 4-h experimental periods. In an additional trial, the four steers were subjected to the same procedure as that used in the main experiment and their rumens were emptied; however, unlike the

first 2-h period, no feed was given to the animals. Differences in heat production between both periods would indicate circadian variations in heat production.

The Effect of the Presence of Feed in the Buffer-Filled Rumen on Heat Production (Subtrial 3). To evaluate possible effects of the presence of feed in rumens filled with buffer solution on oxygen consumption (i.e., ruminal motility, absorption, and metabolism of nutrients transferred to the lower digestive tract), the same amounts of the respective feeds that were individually ingested by the animals in preceding experimental periods were placed directly into the rumen via the cannula. Except for the way the feed reached the rumen, the same experimental procedure was used here as described above for the measurements with normally ingested feeds. Dry roughages were moistened before placing into the rumen. Therefore, an additional 64 respiration measurements were carried out. If the presence of feed in the rumen affects heat production, the effect would be quantified by these measurements and values could be used for a discrimination of heat production caused by ingestion against other factors.

Animals with Ingesta-Filled Rumen (Subtrial 4). To test whether the increase in heat production by ingestion in animals with empty rumens is similar to that in animals with normal, ingesta-filled (not inactivated) rumens, the four steers were adapted to long straw intake before the respiration measurements were taken in an additional trial when rumens were not emptied. The same experimental procedure used in the main experiment was used again, such that no feed was offered in the first 2-h respiration period, and long straw was offered for ad libitum intake in the second 2-h respiration period. Measurements were repeated for each animal ($n = 8$ observations) and compared to the results of the four straws treatments ($n = 16$) in the trials with emptied rumens.

Statistical Analysis

Energy requirements for standing were estimated by multiple linear regression analysis using the GLM procedure of SAS (SAS Inst., Inc., Cary, NC). As neither the absolute term (intercept) nor the independent variable "number of positional changes" showed significance ($P > 0.10$), when included in the equation, the following model was used:

$$H = b_1 \cdot T_l \cdot BW + b_2 \cdot T_s \cdot BW$$

where H is heat production (kJ), T_l is time spent lying (min), T_s is time spent standing (min), BW is expressed as kg or $\text{kg}^{0.75}$, and b_1 and b_2 are regression coefficients that represent heat production per kilogram of BW during lying and standing, respectively. To facilitate the comparison to other energy metabolism variables, data were converted into 24-h values. Data on energy requirement for ingestion, time spent eating, and feed intake were analyzed with the MIXED procedure of SAS (SAS Inst., Inc.) according to the model:

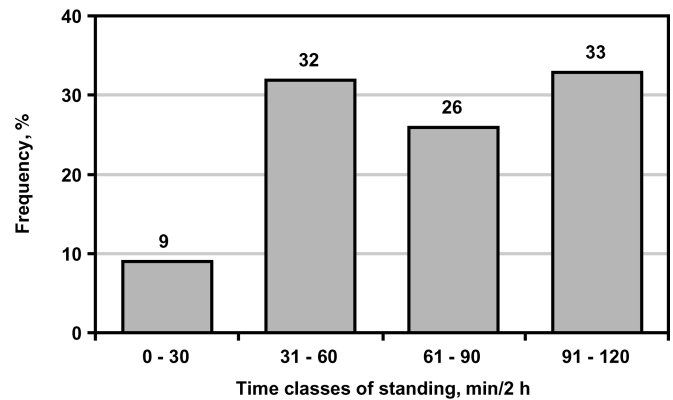


Figure 1. Relative frequency of the spontaneous standing time of the four steers within the 2-h periods of gas exchange measurements, when no feed was offered ($n = 72$; Subtrial 1).

$$y_{ij} = \mu + F_i + A_j + e_{ij}$$

where y is the observed value, μ is the mean, F is the effect of feed i , A is the effect of animal j , and e is the residual error. Significant ($P < 0.10$) treatment (feed) effects were further separated into the following pre-planned linear contrasts: feed type (**FT**, roughages vs. barley), roughage type (**RT**, straw vs. grass), grass treatment 1 (**GT1**, fresh vs. conserved), grass treatment 2 (**GT2**, silage vs. hay), straw treatment (**ST**, long straw vs. NH_3 -treated long straw), particle size 1 (**PS1**, long straw vs. medium and short straw) and particle size 2 (**PS2**, medium vs. short straw). Results are presented as least squares means.

Results

Measurements to Confirm the Suitability of the Experimental Procedure of the Main Experiment

Energy Requirement for Standing (Subtrial 1). Spontaneous standing time of the animals within the 2-h periods is shown in Figure 1. The relative frequency of less than 30 min standing was 9% of the total of 72 observations, whereas the proportion within the other three time classes was of similar magnitude between 26 and 33%.

Mean heat production during lying and standing is presented in Table 2. The differences between standing and lying of $14 \text{ kJ}/(\text{d} \cdot \text{kg} \text{ of } BW)$ and $54 \text{ kJ}/(\text{d} \cdot \text{kg}^{0.75} \text{ of } BW)$ can be taken as estimates for the energy requirement for standing, which corresponds to a relative increase of heat production of standing over lying by 19 and 14%, respectively. The correlation coefficient between heat production per kilogram of BW and standing time was 0.53 ($P < 0.001$). This estimate was used to correct variations in heat production caused by differences in standing time before using this data for further calculations.

Table 2. Heat production during lying and standing in cattle derived from the 2-h periods of gas exchange measurements when no feed was offered (n = 72; values are converted to a 24-h basis; Subtrial 1)

Heat production	Lying		Standing		Difference		Increase, % ^a
	Mean	SEM	Mean	SEM	Mean	SEM	
kJ/kg of BW	73.3	1.9	87.4	1.4	14.1	2.9	19.2
KJ/kg of BW ^{0.75}	376	10	430	7	54	14	14.4

^aPercent increase of standing over lying.

Circadian Variations in Heat Production (Subtrial 2). The mean heat production of the ruminally emptied animals was not different between the two consecutive 2-h periods when no feed was offered or put into the rumen in either period (4.18 MJ, SD = 0.32, n = 4 in the first period and 4.06 MJ, SD = 0.40, n = 4 in the second period). The mean difference of 0.12 MJ (SD = 0.17) corresponded to a relative change of less than 3%. Therefore, circadian variations in heat production within the 4-h experimental periods can be assumed to be very small and, with regard to the purpose of this study, negligible.

The Effect of the Presence of Feed in the Buffer-Filled Rumen on Heat Production (Subtrial 3). The mean heat production of 4.51 MJ (SD = 0.47, n = 32) during the first 2-h period without feed, and of 4.43 MJ (SD = 0.55, n = 32) during the second period without feed, when the respective feeds were placed into the rumen via the fistula, did not differ. The mean of the individual differences in heat production was 0.08 MJ (SD = 0.26, n = 32) and was of a magnitude similar to the above difference in heat production during the two periods without feed (0.12 MJ). There is no indication of special feed effects; even in rolled barley, the difference amounted to 0.07 MJ. Therefore, factors such as ruminal motility or nutrient absorption did not interfere with values for the increase of heat production caused by ingestion; as such, a correction of those values is not necessary.

Animals with Ingesta-Filled Rumen (Subtrial 4). As expected, the absolute values of heat production in both periods with and without feed intake were higher for animals with ingesta-filled rumens than for those with emptied rumens (data not shown). However, the mean increase in heat production in animals with ingesta-filled rumens caused by the ingestion of straw was 11.5 kJ/min of ingestion (SD = 6.7, n = 8) and did not differ from the mean value of 10.1 kJ/min (SD = 4.2, n = 16) for animals with emptied rumens.

Main Experiment

Least squares means for amounts of feed ingested, characteristics of ingestion, and the increase of heat production caused by ingestion are summarized in Table 3. Probability levels for linear contrasts between treatment (feedstuff) means for the same variables are

presented in Table 4. No ruminal activity was observed throughout all experimental periods. Because no effects were observed on the increment of heat production due to circadian variations, or the presence of feed in buffer-filled rumens, heat production values were corrected for differences in standing time only. The DMI of barley was highest (contrast FT; $P < 0.001$) and it was higher for grass than for straw (contrast RT; $P < 0.001$); intake increased ($P < 0.10$) in response to reduction of particle size and NH₃ treatment of straw. Ingestion time was not different between roughages and barley (comparison FT) or between straw and grass (comparison RT). In fresh grass and in long straw, the longest and shortest ingestion times, respectively, were observed. The number of chews were affected in a manner similar to ingestion time, resulting in a relatively small variability of chew frequencies; however, the number of chews and chew frequency were highest in fresh grass. Similar to DMI within the 2-h periods, DMI rate was highest (contrast FT; $P < 0.001$) in barley, higher ($P < 0.01$) in grass than in straw, higher ($P < 0.05$) in hay than in silage, and positively affected ($P < 0.01$) by the NH₃ treatment of straw. It has to be noted that these values should not be compared directly to values from animals with ingesta-filled rumens, although the effects of feeds on the ingestion rate are in accordance with those observed in intact animals.

The increase of heat production related to DMI was lowest for barley, higher ($P < 0.001$) for grass than for straw, and higher ($P < 0.001$) for fresh than for conserved grass. Straw treatment with NH₃ and particle size did not affect heat production. Heat production values related to fiber intake show that more energy per gram of CF or NDF was required for grass than for straw. It is worthy to note that fresh grass had the highest value and that heat production per gram of NDF in barley was of similar magnitude as that for the other feedstuffs. The proportion of heat production of the total ME supplied by the feed differed ($P < 0.001$) between barley and roughages and between fresh and conserved grass ($P < 0.05$). However, no difference occurred between straw and grass and no effects of straw treatment and particle size were observed.

Both heat production per chew and heat production per minute of ingestion time were affected similarly by the feedstuffs. Heat production related to ingestion time or chew was not different between barley and

Table 3. Least squares means for feed intake, characteristics of ingestion, and heat production caused by ingestion in steers within a 2-h period (n = 4; main experiment)

Item	Long straw	Medium straw	Short straw	Long straw, NH ₃ -treated	Fresh grass	Grass silage	Grass hay	Rolled barley	SEM
Feed intake, kg	2.25	4.27	2.81	3.98	19.09	11.08	4.07	10.84	0.75
DMI, kg	2.00	3.85	2.57	3.54	4.32	3.27	3.71	9.65	0.46
Ingestion time, min	66	102	81	90	114	86	82	81	7.9
Chews, No.	4,922	7,702	5,895	6,863	9,223	6,310	6,345	5,947	692
Chew frequency, 1/s	1.23	1.25	1.21	1.27	1.34	1.22	1.29	1.21	0.04
DMI rate, g/min of ingestion	29.3	37.2	31.7	39.4	37.8	38.7	45.5	118.5	3.1
Heat production (H), kJ	629	1,249	667	1,125	2,199	1,140	1,256	790	205
H/DMI, kJ/kg	278	320	235	314	527	355	342	80	51
H/crude fiber intake, kJ/kg	638	734	540	743	1,992	1,161	1,296	1,826	185
H/NDF intake, kJ/kg	334	384	283	400	985	628	682	488	85
H/ME intake, kJ/kJ	0.045	0.052	0.038	0.040	0.050	0.035	0.032	0.006	0.006
H/chew, kJ	0.11	0.16	0.10	0.16	0.24	0.18	0.19	0.13	0.02
H/ingestion time, kJ/min	8.7	12.0	7.5	12.2	19.2	13.1	14.9	9.5	1.7
H/(ingestion time per unit of BW), J/(min·kg)	13.9	19.0	11.9	20.2	31.3	21.5	24.4	15.6	2.7

roughages. However, these values were higher ($P < 0.001$) for grass than for the other roughages, which was mainly caused by the high value for fresh grass. No difference between silage and hay and no effects of straw treatment with NH₃ or of particle size occurred. Additionally, heat production data related to the time spent for ingestion and to kilograms of BW are given in Table 3 to facilitate the comparison to literature data.

Discussion

In the present study, the energy requirement for standing was estimated as 14 kJ/(d · kg of BW), which agrees well with the mean of literature data (Table 5). However, the variation between studies is considerably high, which might be partly due to differences between experimental techniques (respiration chamber, mask

technique, or trachea fistulation; different time spans of and between the respective respiration periods) and between animals. Using the above value, an animal with 600 kg of BW standing 14 h/d needs 4.9 MJ of ME for standing, which corresponds to a requirement for 1 kg of 4% fat-corrected milk. Therefore in this study, heat production values were corrected for heat production caused by standing (14.1 kJ/d · kg) for further calculations.

It could be demonstrated by this study that the chosen experimental procedure was adequate to determine the energy requirement for chewing activity during eating by comparing the heat production of two consecutive periods with and without feed in ruminally emptied cattle. The proofs are given by the observations that no change occurred in basal heat production during the 4-h experimental periods. Although emptying of the

Table 4. Probability level ($P <$) for linear contrasts between feedstuff means for feed intake, characteristics of ingestion, and heat production caused by ingestion in steers within a 2-h period (n = 4; main experiment)

Item	Contrast ^a						
	FT	RT	GT1	GT2	ST	PS1	PS2
Feed intake, kg	0.001	0.001	0.001	0.001	0.056	0.097	0.102
DMI, kg	0.001	0.007	0.058	0.370	0.004	0.008	0.014
Ingestion time, min	0.371	0.113	0.004	0.724	0.042	0.013	0.062
Chews, No.	0.212	0.046	0.001	0.967	0.029	0.016	0.040
Chew frequency, 1/s	0.136	0.040	0.013	0.125	0.344	0.995	0.260
DMI rate, g/min of ingestion	0.001	0.001	0.125	0.044	0.004	0.074	0.095
Heat production (H), kJ	0.089	0.001	0.001	0.693	0.102	0.203	0.058
H/DMI, kJ/kg	0.001	0.005	0.009	0.856	0.621	0.994	0.249
H/crude fiber intake, kJ/kg	0.001	0.001	0.003	0.612	0.694	0.996	0.466
H/NDF intake, kJ/kg	0.661	0.001	0.005	0.659	0.588	0.996	0.409
H/ME intake, kJ/kJ	0.001	0.349	0.046	0.724	0.586	0.993	0.143
H/chew, kJ	0.174	0.001	0.063	0.656	0.144	0.553	0.079
H/ingestion time, kJ/min	0.101	0.001	0.019	0.462	0.152	0.631	0.067
H (ingestion time per unit BW), J/(min·kg)	0.120	0.001	0.020	0.460	0.122	0.658	0.077

^aFT = feed type (roughage vs. barley); RT = roughage type (straw vs. grass); GT1 = grass treatment 1 (fresh vs. conserved); GT2 = grass treatment 2 (silage vs. hay); ST = straw treatment (long straw vs. long straw, NH₃-treated); PS1 = particle size 1 (long straw vs. medium and short straw); PS2 = particle size 2 (medium vs. short straw).

Table 5. Compilation of literature data on energy requirement for standing in cattle^a

Source	BW, kg	No. of animals	No. of observations	Energy requirement for standing, kJ/(d·kg of BW)	Increase, % ^b
Dahm (1910)	220	1	—	11.2	8
Von der Heide et al. (1913)	530	1	1	18.7	20.7
Fries and Kriss (1924)	400	1	1	6.6	9.8
Forbes et al. (1927)	468	1	1	15.2	24.9
Hall and Brody (1933)	144 to 875	32	1,938	9.0	9.0
K. L. Blaxter and F. W. Wainman, unpublished data ^c	—	—	—	5.9	—
J. McLean, unpublished data ^c	—	—	—	10.0	—
Colovos et al. (1970)	540	3	18	14.1 ^d	16.1
Schiemann et al. (1971)	620 to 954	10	54	25.1	—
Clark et al. (1972)	460	4	32	11.6	12.2
Vercoe (1973)	194 to 334	11	24	13.5	18.7
Ku-Vera et al. (1989)	300	—	—	6.6	—
Neumann et al. (1994)	567	3	30	24.6	24.3
Present study	550 to 640	4	72	14.1	19.2
Mean ^e				13.3	

^aNot included here are the data of Armsby and Fries (1913, 1915) because the increment of heat production includes eating activity, or those of Schrama et al. (1993) and of Roefs et al. (1996) because the animals were only 6 d old.

^bPercent increase of standing over lying.

^cCited according to ARC (1965).

^dValue after 10 min of change in position.

^eUnweighted mean.

rumen decreased heat production, this did not affect the extent of the increase of heat production caused by ingestion of straw. Further, the absence of an increment of heat production by feed application to the rumen via the cannula indicates that the activity of eating and chewing is the dominant factor causing increased heat production during ingestion, and that possible other ingestion-related activities, such as blood flow to the intestinal tract or saliva production, are of minor relevance, which confirms similar observations in goats (Lachica et al., 1997) and sheep (Osuji et al., 1975).

The increase of heat production per kilogram of DMI showed a large variation between feedstuffs (Table 3). Therefore, the amount of DM ingested per time unit cannot explain variations in the energy requirement for ingestion, which is in accordance with results of Dahm (1910) and Adam et al. (1984). The attempt to reduce variation of heat production between feedstuffs by relating heat production to CF or NDF intake has failed, which means that heat production does not strongly depend on fiber intake; on the contrary, heat production per gram of barley NDF was similar to the mean value for the roughages. When heat production was related to the number of chews or to the time spent for ingestion, the variation between feedstuffs was reduced despite of the remaining significant differences between straw and grass and between fresh and conserved grass. Although significant differences in DMI existed, no differences in heat production per minute of ingestion occurred between barley and roughages, between silage and hay, between treated and untreated straw, or between straws of different particle size. Therefore, the number of chews or time spent for ingestion seems to be the main determinant of the energy requirement for ingestion. Because of the low variation

in chew frequencies between feedstuffs (CV = 3.6%), ingestion time and number of chews as references of heat production lead to similar differences between the feeds. The mean value for energy requirement of ingestion in the present study was 20 J/(min·kg of BW); the observed range of 12 to 31 J/(min·kg of BW) includes the value of our previous study (27 J/[min·kg of BW]; Susenbeth et al., 1998) and the mean value of the literature data (30 J/[min·kg of BW]; summarized by Susenbeth et al., 1998). All of these values are considerably higher than the average value for energy requirement of ruminating of 9 J/(min·kg of BW), as summarized by Susenbeth et al. (1998).

Implications

The energy required for ingestion of feed as a proportion of the total metabolizable energy intake accounted for 3.2 to 5.2% in roughages, without having any relationship to feed properties, and for 0.6% in barley. Assuming 9 h of chewing during ingestion for an animal weighing 600 kg, the energy requirement for ingestion alone would account for 6.5 MJ of metabolizable energy, which would be equivalent to an energy requirement for 1.3 kg of 4% fat-corrected milk. Assuming that an animal spends 7 h/d ruminating at an energy cost for ruminating of 9 J/(min·kg of BW), standing and ingestion together require 13.7 MJ of metabolizable energy/d, equivalent to 1.25 kg of dry matter of a typical diet for dairy cows.

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