Intake Regulation and Grazing Behavior of Dairy Cows Under Continuous Stocking

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ABSTRACT

This experiment aimed at studying the behavioral strategies grazing dairy cows use to satisfy their nutritional needs as the day progresses and the possible role of rumen fill in controlling these behavioral strategies. The day was divided into 3 main periods (0600 to 1200 h, 1200 to 1800 h, and 1800 to 2400 h), where the 3 main grazing bouts (dawn, afternoon, and dusk) of dairy cows usually occur. Four late lactating rumen-cannulated dairy cows were used in a repeated measures design; grazing bout was the within-subjects factor. Cows had access to a 1-ha grass sward under a continuous stocking system. To estimate dry matter intake, bite rate, bite mass (BM), and intake rate at the 3 grazing bouts, cows were rumen-evacuated at 0600, 1200, 1800, and 2330 h, and the jaw recorders were fitted to the cows between these time points. Time spent eating by dairy cows at the dusk grazing bout was much longer than that at the other 2 grazing bouts and composed about 40% of the daily total eating time. Total grazing jaw movement (TGJM) rate was constant during the day at around 75/min. Bite rate, BM, and, hence, intake rate increased, but chewing rate decreased as the day progressed. The increase in BM was mainly due to the increase in dry matter content of the grass at dusk rather than increased bite dimensions. Therefore, it could be concluded that the main behavioral strategies dairy cows use to satisfy their nutritional needs under continuous stocking include manipulating their eating time, biting rate, and chewing rate, with little control over TGJM rate and BM. Dairy cows interrupted the first 2 grazing bouts (dawn and afternoon) long before reaching their maximal rumen capacity, indicating that rumen fill is less likely to play a significant role in signaling the termination of these 2 grazing bouts. However, rumen pool sizes were always maximal at the time when the dusk grazing bout ceased, indicating that rumen fill is more

likely to play a major role in signaling the termination of the dusk grazing bout.

(Key words: rumen fill, grazing behavior, intake rate, bite mass)

Abbreviation key: BM = bite mass, NSC = nonstructural carbohydrates, Q_{NDFr} = NDF rumen pool, TET = total eating time, TGJM = total grazing jaw movements, WSC = water-soluble carbohydrate.

INTRODUCTION

In grazing animals, accurately estimating herbage intake (kg/d of DM) is considered one of the most important tools in improving management and production. An accurate estimation of daily herbage intake can be achieved as the product of total eating time (TET) and intake rate (Gibb et al., 1998). The latter is known to be the product of bite rate (bites/min) and bite mass (BM) (mg DM per bite) (Allden and Whittaker, 1970). Factors of plant (sward), animal, and environmental origin have been shown to influence TET, bite rate, BM, and, hence, herbage intake (Pulido and Leaver, 1995). Sward surface height, herbage allowance, tiller density, tensile strength, and fiber content are among the most important factors of plant origin (Penning et al., 1991; Gibb et al., 1997). Physiological status, lactation stage, BW, nutritional demand, and productive capacity are among the most important factors of animal origin (Gibb et al., 1999). Ambient temperature, relative humidity, and rainfall are important factors of environmental origin (Champion et al., 1994). Despite the above-mentioned factors (plant, animal, and environmental) and the grazing system, dairy cows have shown to exercise 3 main grazing events (bouts) during the day (dawn, afternoon, and dusk) (Rook and Huckle, 1997). However, plant, animal, and environmental factors and the grazing system may influence the duration of these 3 main grazing bouts. During a hot day, cows appear to be reluctant to graze before 1800 h, reducing the duration of the second (afternoon) and increasing the duration of the third (dusk) main grazing bouts (Gibb et al., 1998). When offered the new pasture at 1200 h (mid-

Received February 24, 2004.

Accepted May 26, 2004.

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day) in a strip grazing system, dairy cows tend to increase the duration of the second (afternoon) and reduce the duration of the first (dawn) main grazing bouts (H. Z. Taweel, personal observation).

To satisfy its nutritional needs under the circumstances imposed by the sward, management, and the environment, the grazing dairy cow maneuvers by adjusting its eating behavior in terms of eating time, bite rate, chewing rate, BM, and intake rate. Therefore, not only the duration of eating at the 3 main grazing bouts during the day will be different, but also bite rate, chewing rate, BM, and intake rate may differ as well. Daily herbage intake is the sum of the amount eaten at the different grazing bouts, which, in turn, is determined by the duration of the bout and the intake rate during that bout. Hence, estimating bite rate, BM, and intake rate at the 3 main grazing bouts as influenced by plant, animal, and environmental factors, presents an opportunity to improve the modeling of herbage intake and, hence, its prediction in grazing ruminants. Gibb et al. (1998) observed a significant effect of time of day on bite rate, BM, and intake rate. However, in that experiment, intake rate was measured using the short-term weight gain method in which the animals were deprived from food and water for 1 h to measure insensible weight loss rate before the 1-h intake rate measurement period commenced. This feed deprivation period that preceded the short measurement period might have made the animals hungry and, therefore, influenced their eating behavior, especially during the first hour after release.

Many theories as to what initiates and terminates a grazing bout and to what controls the short-term daily herbage intake exist. Rumen fill and distension, rate of disappearance of feed from the rumen, concentrations of fermentation end products (total VFA, acetate, propionate, butyrate, and NH_3) in the rumen, and/or blood and rumen osmolality are among the most plausible ones. However, Mbanya et al. (1993), Van Soest (1994), Forbes (1995), and Chilubrosté (1999) are in favor of the multifactorial control theory, which states that the initiation and termination of a meal seems more likely to be controlled by a combination of signals rather than a single signal. Chilubrosté et al. (1997) studied the first grazing session (bout) extensively and concluded that cows interrupted it before their maximum rumen capacity was reached, indicating that rumen fill does not play a major role in controlling the termination of the first grazing bout. However, this cannot be extrapolated to the other 2 grazing bouts, especially the third grazing bout at dusk. Therefore, an experiment was conducted to estimate eating duration, bite rate, BM, and intake rate at the 3 main grazing bouts during the day. Moreover, rumen pool

sizes and fermentation end product concentrations at the start and the end of each grazing bout were measured to investigate their role in controlling the initiation and termination of a grazing bout.

MATERIALS AND METHODS

Animals and Pasture

Four rumen-cannulated (10 cm i.d.; Bar-Diamond Inc., Parma, ID) Holstein-Friesian dairy cows (600 ± 20 kg BW) in late lactation (310 ± 21 DIM) were used in the experiment. Two cows were in their third lactation, and the other 2 cows were in their fourth and ninth lactations. All cows were pregnant at the onset of the experiment and produced 18.0 ± 0.4 and 19.1 ± 1.5 kg/d of milk at the start and the end of the experiment, respectively.

The pasture (1 ha) was sown in autumn 1999 with 2 varieties of perennial ryegrass. In 2003, the pasture was cut on May 25 for silage making and was allowed undisturbed growth until June 15 when the experiment actually started. The pasture had approximately 1700 kg of DM on it at the start of the experiment. The cows were allowed access to the whole pasture under a continuous stocking system with ad libitum herbage allowance, and no compound feed from the start (June 15) until the end (July 4) of the experiment.

Experimental Design

The experiment lasted 20 d, of which the first 10 d were for adaptation. On d 11, the cows were fitted with jaw recorders (Rutter et al., 1997) for 24 h starting at 0630 h just after the morning milking and ending at 0600 h just before the morning milking the next day. This was done to adapt the cows to the equipment and to determine the time of commencement and end of the 3 main grazing bouts during the day. On d 12, hourly rumen liquid samples were collected from the 4 cows, starting at 0630 h just after the morning milking and ending at 2330 h. This was repeated on d 13, but this time the jaw recorders were also fitted to the cows during the collection period (0630 until 2330 h).

On the basis of the temporal patterns of grazing activities found in the 24-h recordings of d 11, which showed that the first, second, and third main grazing bouts occur between 0600 to 1200 h, 1200 to 1800 h, and 1800 to 2330 h, respectively, it was decided to rumen-evacuate the animals at these time points. Therefore, on d 17 and 19, the jaw recorders were fitted to the 4 cows, starting at 0530 h before the morning milking, and 2 cows on d 17 and the other 2 cows on d 19 were rumen-evacuated simultaneously at 0600, 1200, 1800, 2330, and 0800 h the next morning. After

each rumen evacuation, the cows were allowed to graze freely, except after the evacuation at 2330 h when the jaw recorders were removed, and the 2 cows were tethered (in a small fenced area on the side of the pasture) and deprived from feed and water until 0800 h the next morning. This was done to allow an estimation of the clearance rate, which was needed to calculate the intake during each grazing bout.

Moreover, on d 17 and 19, grass samples were collected from the pasture at 3 time points: 0800, 1400, and 2000 h. These time points were chosen as they closely represent the quality of the grass the animal consumed during the 3 main grazing bouts. These samples (approximately 500 g fresh herbage) were weighed immediately and stored in the freezer (-20°C). At the end of the experiment, these samples were freeze-dried, ground to pass 1-mm screen, and analyzed for DM, OM, CP ($\text{N} \times 6.25$), water-soluble carbohydrates (WSC), and NDF as described by Goelema et al. (1998). Nonstructural carbohydrates (NSC) content was calculated as $\text{OM} - \text{CP} - \text{NDF} - \text{fat}$, assuming that fat content in grass was constant at all time points at around 40 g/kg DM.

Rumen Liquid Sampling

To take the hourly rumen liquid samples on d 12 and 13, the cows were brought to a small fenced area on the side of the pasture, and samples were collected from the rumen ventral sac using a solid plastic tube (85 cm long; 2.5 cm in diameter). In these samples, the pH was measured immediately, using an electronic pH meter (pH electrode type 62, Testo 252; Testo GmbH & Co, Lenzkirch, Germany). Then, 2 subsamples were taken, acidified with either phosphoric acid or TCA, and stored in the freezer (-20°C) pending VFA and NH_3 analyses, respectively, as described by Chilibroste (1999).

Rumen Evacuations

The cows to be rumen evacuated (2 on d 17 and 2 on d 19) were brought to a small fenced area on the side of the pasture and were rumen evacuated simultaneously. All rumen contents that could be removed by hand (called mat) were emptied into a large rectangular insulated container. During removal of rumen contents, a 10% sample was taken by putting each 10th handful in another small plastic container (20 L). Material not removable by hand (bailable liquid) was bailed into another 20-L plastic container using a 1-L plastic bottle. Rumen contents in the large and small containers were weighed, and the bailable liquid was proportionally added to the large and the small con-

tainers. The contents of the small container were mixed thoroughly, and 2 samples of 400 g were taken and stored in the freezer (-20°C) pending analysis for DM, ash, N, and NDF. After the rumen content samples had been taken, all rumen contents were put back in the rumen, and the time when the evacuation ended was noted.

Calculations

The basic idea of this experiment was to determine the intake and grazing behavior (eating time, number of bites, and number of chews) at the 3 main grazing bouts during the day. This information would allow the calculation of bite rate, BM, and intake rate at these 3 main grazing bouts. The intake during each of these grazing bouts was estimated from the changes in rumen pools and clearance of material during the grazing bout obtained from the rumen evacuation data on d 17 and 19. First, rumen pool sizes of the different components (DM, OM, and NDF) at each evacuation were estimated from the weight of the total fresh rumen contents and the percentages of these components in the rumen contents at each evacuation. Second, the fractional clearance rate (Kcl) was calculated from the last 2 evacuations at 2330 h and 0800 h the next morning based on the assumption of a first-order kinetics using the logarithmic transformation of the exponential equation: $\text{RP}_{(0800)} = \text{RP}_{(2330)} \times \text{EXP}^{-\text{Kcl} \times t}$, where RP is rumen pool size (kg) and t is the time elapsed between the end of the evacuation at 2330 h and the start of the evacuation at 0800 h next morning. Third, herbage intake at each grazing bout was calculated as shown in equation 1:

$$\text{Herbage intake} = (\text{RP}(t_2) - (\text{RP}(t_1) \times \text{EXP}^{-\text{Kcl} \times t})) / (\text{EXP}^{-\text{Kcl} \times (0.5 \times t)}) \quad [1]$$

where

- RP = rumen pool size (kg);
- t_2 = ending time of a grazing bout, which was 1200, 1800, and 2330 h for the dawn, afternoon, and dusk, respectively;
- t_1 = starting time of a grazing bout, which was 0600, 1200, and 1800 h for dawn, afternoon, and dusk, respectively;
- Kcl = fractional rate of clearance of material from the rumen by degradation and passage; and
- t = time elapsed between the start and end of a grazing bout.

The denominator in the equation was used to correct for the clearance of the freshly ingested material as-

suming that, on average, one-half of it is subject to disappearance, which may not be necessarily the case. Clearance by degradation is restricted to the potentially degradable pool, and passage comprises the entire pool. Nevertheless, the clearance of freshly ingested material generally represents a small portion of herbage intake and is therefore considered not to be of a major quantitative importance (Chilibroste et al., 1997).

Jaw recordings made on d 11, 13, 17, and 19 were analyzed using peak recognition algorithm software with a noise threshold capable of identifying periods of grazing and ruminating activity and biting and nonbiting grazing jaw movements (Graze Version 0.8, Institute of Grassland and Environmental Research 1994 to 1999) (Rutter, 2000). Total eating time and number of biting and nonbiting jaw movements during eating were determined for each grazing bout. In calculating bite rate, total grazing jaw movement (TGJM) rate, and chewing rate at each grazing bout, the time base used was the TET during that grazing bout. The BM at each grazing bout was calculated as the herbage intake at the grazing bout divided by the number of bites the animal made during that grazing bout. Intake rate in g/min at each grazing bout was calculated as the product of bite rate (bites/min) and BM (g DM consumed per bite) during that grazing bout.

Statistical Analysis

Grazing behavior, intake rate, and BM data were analyzed as repeated measures using GLM of SPSS (SPSS for Windows, Rel. 10.1.0, 2000; SPSS Inc., Chicago, IL). The within-subjects factor was the grazing bout, which had 3 levels: dawn grazing bout (0600 to 1200 h), afternoon grazing bout (1200 to 1800 h), and dusk grazing bout (1800 to 2400 h). Grass chemical composition data were analyzed as repeated measures with time as the within-subjects factor with 3 levels (0800, 1400, and 2000 h). Rumen pools (fresh, DM, OM, N, and NDF) were analyzed as repeated measures with time as the within-subjects factor with 4 levels: 0600, 1200, 1800, and 2330 h. Rumen fermentation end product concentrations (acetate, propionate, butyrate, and NH_3) were statistically analyzed in 2 ways [1] as a repeated measures with time of the day as the within-subjects factor and 2) fermentation end products at the beginning and end of each grazing bout for each cow were noted and analyzed using a paired *t*-test procedure to compare whether fermentation end product concentrations differed between the start and end of each grazing bout]. This was done by studying closely the grazing behavior recordings on the day the rumen liquid samples were collected and considering

periods of continuous grazing for >40 min as grazing bouts.

RESULTS AND DISCUSSION

Table 1 shows the mean chemical composition of the grass in the 2 d at the 3 main grazing bouts. Although DM content of the grass numerically and seemingly linearly increased, as the day progressed from 190 to 250 g/kg fresh matter, this increase was not statistically significant ($P = 0.34$). The OM content did not change as the day progressed and stayed constant at around 915 g/kg DM. The NSC content of the grass was influenced ($P = 0.04$) by time of day and tended to increase linearly ($P = 0.09$) as the day progressed from 257 to 293 g/kg DM. Many researchers (Delagarde et al., 2000; Lee et al., 2002) reported an increased DM and NSC content at evening compared with morning grass. In those studies, the increase in DM and NSC in the evening was attributed, respectively, to the loss of surface water and to the accumulation of photosynthesis end products, especially simple sugars. The CP content was not influenced significantly ($P = 0.10$) by time of day and tended to decrease linearly ($P = 0.17$) as the day progressed from 170 to 155 g/kg DM. The NDF content was influenced ($P = 0.02$) by time of day and showed a quadratic relation ($P = 0.04$), being highest at midday and lowest in the evening. In contrast, Delagarde et al. (2000) reported a nonsignificant change in both CP and NDF content of perennial ryegrass between the morning and the evening.

Table 2 shows grazing behavior parameters, DMI, BM, and intake rate of dairy cows at the 3 main grazing bouts of the day: dawn (0600 to 1200 h), afternoon (1200 to 1800 h), and dusk (1800 to 2400 h). Total eating time was different ($P < 0.05$) between the 3 main grazing bouts, and it increased linearly ($P < 0.05$) as the day progressed. Dairy cows grazed longer at dusk (on average 71 min more eating time than during the dawn grazing bout and 28 min more than during the afternoon grazing bout). Moreover, time spent eating during the dusk grazing bout made up about 40% of the daily TET. Rook and Huckle (1997) also reported a longer eating time by grazing ruminants during the dusk meal. The number of TGJM, bites, and chews increased linearly as the day progressed, being low during dawn and high during dusk grazing bouts. However, when TGJM rate, bite rate, and chewing rate were calculated as the number of TGJM, bites, and chews, respectively, divided by eating time in minutes, it appeared that TGJM rate was almost constant during the day at around 75/min. Bite rate increased linearly ($P = 0.08$) from 54 to 61/min, and chewing rate

Table 1. Mean chemical composition (g/kg DM) of perennial ryegrass (*Lolium perenne* L.) at different times during the day.

Fraction	Time of day			SEM	Significance of effect of		
	0800 h	1400 h	2000 h		Time	Linear	Quadratic
DM, ¹ g/kg	191.6	225.0	250.6	13.9	0.40	0.34	0.91
OM	913.3	914.6	917.0	0.7	0.20	0.19	0.26
CP	170.3	153.4	155.3	3.8	0.10	0.17	0.26
NSC ²	256.8 ^a	271.8 ^{ab}	293.3 ^b	6.8	0.04	0.09	0.53
WSC ³	134.6	168.3	190.3	10.6	0.06	0.16	0.07
NDF	446.1 ^b	449.5 ^b	428.4 ^a	4.4	0.02	0.10	0.04

^{a,b}Means in the same row with different superscripts differ significantly ($P < 0.05$).

¹DM is expressed in g/kg of fresh material.

²NSC = Nonstructural carbohydrate, calculated as OM – CP – NDF – fat, assuming a constant fat content of 40 g/kg DM.

³WSC = Water soluble carbohydrate.

decreased linearly ($P = 0.08$) from 20 to 16/min as the day progressed. Moreover, the proportion of bites in TGJM increased linearly ($P = 0.06$) from 73% at dawn to 79% at dusk. This result indicates that dairy cows tried to maximize their intake during the dusk grazing bout by increasing eating time and bite rate and decreasing chewing rate in preparation for the dark hours, when little grazing and much ruminating usually occur. Gibb et al. (1998) also observed a nonsignificant change in TGJM rate, which appeared to fluctuate around 78/min, and a significant increase in bite rate and the proportion of bites in TGJM as the day progressed. Moreover, Phillips and Leaver (1986) and Phillips and Hecheimi (1989) observed higher bite

rates of cows and heifers, respectively, at the dusk meal compared with other meals.

Dry matter intake was different ($P < 0.01$) among the 3 grazing bouts and increased linearly ($P < 0.01$) as the day progressed from 3 kg during the dawn grazing bout to 7 kg during the dusk grazing bout (Table 2), which was probably due to the increased eating time and bite rate during the dusk grazing bout. Assuming a constant BM at all grazing bouts, the increased eating time and bite rate accounted only for 63% of the difference in DMI between dawn and dusk. This result indicated that BM was not constant during the day and that differences in BM between the 3 grazing bouts must have occurred. When BM was cal-

Table 2. Grazing behavior parameters, DMI, intake rate, and bite mass of late lactating dairy cows at the 3 main grazing bouts during the day.

Behavior	Grazing bout			SEM	Significance of effect of		
	Dawn	Afternoon	Dusk		Bout	Linear	Quadratic
	6 to 12 h	12 to 18 h	18 to 24 h				
TET, ¹ min	132 ^a	175 ^{ab}	203 ^b	10	0.01	0.005	0.59
Bites, no.	7135 ^a	10,235 ^a	12,272 ^b	710	0.00	0.008	0.53
Chews, no.	2661	2862	3210	142	0.17	0.154	0.71
TGJM, ² no.	9796 ^a	13,097 ^{ab}	15,481 ^b	805	0.01	0.008	0.64
TGJM rate ³	74	75	76	1	0.30	0.251	0.54
Bite rate ³	54 ^a	58 ^{ab}	61 ^b	1	0.03	0.082	0.20
Chew rate ³	20 ^b	16 ^a	16 ^a	1	0.04	0.078	0.18
Bite/TGJM, ⁴ %	73 ^a	78 ^b	79 ^b	1	0.02	0.063	0.15
DMI, kg	2.9 ^a	4.2 ^a	6.9 ^b	0.6	0.00	0.006	0.27
BM, ⁵ mg per bite	401 ^a	411 ^a	563 ^b	28	0.03	0.026	0.25
IR, ⁶ g/min	22 ^a	24 ^a	34 ^b	2	0.02	0.028	0.25

^{a,b}Means in the same row with different superscripts differ significantly ($P < 0.05$).

¹TET = Total eating time (in min).

²TGJM = Total number of grazing jaw movements (bites plus chews).

³TGJM rate, bite rate, and chew rate are all expressed per minute.

⁴Bite/TGJM = Percentage of bites in the total grazing jaw movement.

⁵BM = Bite mass (mg DM per bite).

⁶IR = Intake rate (g DM/min).

culated for the 3 grazing bouts, it appeared that the average BM was different ($P = 0.03$) between the grazing bouts, and it increased linearly ($P = 0.03$) from 400 mg DM during the dawn grazing bout to 563 mg DM during the dusk grazing bout. Therefore, the much higher DMI during the dusk grazing bout can be related to the increased eating time, bite rate, and BM during this grazing bout. Other researchers (Orr et al., 1997; Gibb et al., 1998) also observed a higher BM during the dusk meal by sheep and dairy cows, respectively.

The increased BM (mg DM) during dusk time in this study can be related to the increased DM content of the grass at this time of the day (Table 1). The 40% difference in BM (mg DM) between the dawn and the dusk grazing bouts was reduced to 6% when BM was expressed in mg fresh matter, which indicates that the change in DM content of the grass as the day progressed is the main factor causing the difference in BM between the grazing bouts under continuous stocking system. Similarly Gibb et al. (1998) observed a nonsignificant change in BM as the day progressed when it was expressed as mg fresh matter and a significant increase when it was expressed in mg DM or mg OM. In that experiment, they related the lower BM at the dawn grazing bout to the lower DM content and to the higher surface moisture of the grass at dawn, which might have increased slippage between the incisors and dental pad. Intake rate (g DM/min) was different ($P = 0.02$) between the 3 grazing bouts and increased linearly ($P = 0.03$) as the day progressed from 22 to 34 (Table 2). The increased intake rate at dusk is probably related to the increased bite rate and BM at this time, as the intake rate is the product of bite rate and BM. These observations are in line with Gibb et al. (1998), who reported that intake rate increased linearly as the day progressed from 17 to 23 g DM/min.

Table 3 shows mean observed rumen pool sizes (fresh, DM, OM, N, and NDF) at 0600, 1200, 1800, and 2330 h. Rumen pool sizes were significantly ($P < 0.01$) larger at 2330 h compared with the other times during the day. This result was probably related to the longer eating time, higher bite rate, and BM during dusk time (Table 2), which resulted in a higher herbage intake at that time of the day (Table 2). Because rumen evacuations in the present study were performed at fixed time points during the day and not immediately when grazing ceased, it was important to estimate the fluctuation in rumen fill between the measured points if we want to draw valid conclusions concerning its role in regulating the cessation of grazing. To estimate rumen fill fluctuation during the day, a small dynamic mechanistic model was constructed. This model was

based on the measured TET, the exact timing of each individual grazing event, bite rate, and BM, clearance rate, and NDF content in grass and in rumen material. The model consisted of one state variable, which was the rumen NDF pool (Q_{NDFr}). In this model, Q_{NDFr} receives input from feed intake (NDF flow into the rumen), and its output is disappearance from the rumen through clearance (the sum of degradation and passage). The NDF flow into the rumen was calculated as the intake rate (kg DM/h) multiplied by NDF content in the grass (g/g DM). The intake rate was calculated from BM (kg DM/bite) and bite rate (bites/h) using the exact measured values. Both BM and bite rate were allowed to change as day progressed as shown in Table 2. Moreover, intake rate, BM, and bite rate were all set to zero when the animal was not grazing based on the observed grazing behavior patterns of each individual cow. The equations that constitute the model and the variables and parameters describing the properties of the model are listed in Table 4.

The relationship between observed and model-estimated Q_{NDFr} and the grazing behavior patterns during the day are shown in Figure 1. Model estimates of Q_{NDFr} correlated strongly ($r^2 = 0.91$) with the observed values, and the coefficient was not different from unity ($Y = 1.02 X$). The figure shows that, despite the fact that cows grazed on average 132 and 175 min during the morning and afternoon grazing bouts, respectively, Q_{NDFr} did not reach the value it reached at 2330 h, which indicates that dairy cows interrupted the first 2 grazing bouts (dawn and afternoon) before reaching their maximal rumen fill capacity. Therefore, rumen fill is less likely to play a significant role in signaling the termination of these 2 grazing bouts. Rumen DM fill at 2330 h exceeded 100 g/kg metabolic BW, calculated as BW to the power 0.75 (Table 3), and equaled that observed with silage-based winter diets, an event usually not seen under grazing, where the maximum rumen DM fill has been observed to be between 75 and 80 g/kg metabolic BW (Van Vuuren, 1993). Observed and model-estimated rumen pool size values indicate that rumen fill is more likely to play a major role in signaling the termination of the dusk grazing bout, as cows seemed to graze at dusk until their maximal rumen capacity is reached. This was evidenced by the difficulties we experienced in refilling the rumens of the cows at 2330 h because of limited space, to such a degree that some gentle force had to be used to reintroduce the last kilograms of material back into the rumens of these cows. The fact that dairy cows tend to graze longer with a higher bite rate and tend to fill their rumen to its maximal capacity at dusk time might be related to climatic or adaptive reasons. The

Table 3. Mean rumen pool sizes of grazing late lactating dairy cows at different times during the day.

Pool	Time of day				SEM	Significance of effect of		
	0600 h	1200 h	1800 h	2330 h		Time	Linear	Quadratic
	(kg)							
Rfresh ¹	80.7 ^a	83.0 ^a	86.7 ^a	106.5 ^b	5.6	0.001	0.007	0.001
RDM ²	9.5 ^a	8.9 ^a	9.9 ^a	13.1 ^b	0.7	0.001	0.006	0.005
ROM ³	8.5 ^a	8.0 ^a	8.9 ^a	11.8 ^b	0.6	0.001	0.005	0.005
RN ⁴	0.30 ^a	0.29 ^a	0.31 ^a	0.40 ^b	0.02	0.001	0.011	0.004
RNDF ⁵	4.7 ^a	4.4 ^a	5.0 ^a	6.6 ^b	0.4	0.001	0.006	0.011
	(g/kg MBW ⁶)							
RDM	76 ^a	71 ^a	79 ^a	104 ^b	7.3	0.001	0.006	0.006
ROM	67 ^a	63 ^a	71 ^a	94 ^b	6.4	0.001	0.006	0.006
RNDF	37 ^a	35 ^a	39 ^a	52 ^b	3.8	0.001	0.008	0.013

^{a,b}Means in the same row with different superscripts differ significantly ($P < 0.05$).

¹Rfresh = Total fresh rumen pool.

²RDM = Rumen DM pool.

³ROM = Rumen OM pool.

⁴RN = Rumen N pool.

⁵RNDF = Rumen NDF pool.

⁶MBW = Metabolic BW, calculated as BW to the power 0.75.

climatic reasons are related to the fact that the grazing season is mostly during summer when temperatures may be very high during the day; therefore, it is easier and less energy consuming for the cows to lose extra body heat if they are active at dusk, when temperatures are moderate. The adaptive reasons could be that the ruminants are adopting an optimal foraging strategy by taking advantage of the higher concentration of DM and photosynthetic products (sugars) in the leaves late in the day (Orr et al., 1997). This means that cows might have learned that grass quality in terms of DM and sugar improves at dusk time; therefore, they try to maximize intake at that time of the day to achieve the maximum benefit in terms of nutrients

input, with the minimum effort in terms of TGJM. It is also possible that grazing ruminants aim to finish their dusk meal with a full rumen; therefore, they start that meal at a time that ensures that their rumen is full by sunset. This relates to the fact that ruminants in temperate climates avoid (for whatever reason) grazing at night. Similarly, other researchers (Penning et al., 1991) suggested that the ruminants adopt such a strategy to ensure a high rumen fill and hence a sufficient substrate for rumen flora during the night when there is little grazing.

Table 5 shows mean rumen fermentation end product concentrations at the start and the end of a grazing bout. This was done to try to understand their role in

Table 4. Variables, constants, and equations constituting rumen NDF pool simulation model.

Variable	Type	Unit	Equation/value	If condition
Q_{NDFr} ¹	State	kg	$dQ_{NDFr}/dt = F_{NDFin} - F_{NDFout}$	No
F_{NDFin} ²	Auxiliary	kg/h	$= IR \times (NDF_{grass}/1000)$	No
F_{NDFout} ³	Auxiliary	kg/h	$= Q_{NDFr} \times Kcl$	No
IR ⁴	Auxiliary	kg/h	$= \text{Bite rate} \times \text{bite mass} \times 0.06$	$= 0$, when animal was not eating
Bite mass	Pseudo-constant	g	$= 0.40, 0.41, \text{ and } 0.56 \text{ between } 6 \text{ and } 12 \text{ h, } 12 \text{ and } 18 \text{ h, and } 18 \text{ and } 24 \text{ h, respectively}$	$= 0$, when animal was not eating
Bite rate	Pseudo-constant	/min	$= 54, 58, \text{ and } 61 \text{ between } 6 \text{ and } 12 \text{ h, } 12 \text{ and } 18 \text{ h, and } 18 \text{ and } 24 \text{ h, respectively}$	$= 0$, when animal was not eating
NDF_{grass} ⁵	Pseudo-constant	g/kg DM	$= 446, 450, \text{ and } 428 \text{ between } 6 \text{ and } 12 \text{ h, } 12 \text{ and } 18 \text{ h, and } 18 \text{ and } 24 \text{ h, respectively}$	No
Kcl ⁶	Constant	/h	$= 0.056$	No

¹ Q_{NDFr} = Rumen NDF pool.

² F_{NDFin} = Flow of NDF into the rumen through intake.

³ F_{NDFout} = Flow of NDF out of rumen NDF pool through both degradation and passage (clearance).

⁴ IR = Intake rate.

⁵ NDF_{grass} = NDF content in grass (g/kg DM).

⁶ Kcl = Clearance rate of NDF.

Figure 1. Observed (squares) and model-estimated (black line) rumen NDF pool fluctuation of a grazing dairy cow (cow no. 179) during the day coupled with the observed grazing behavior pattern during that day (on the x-axis), eating (gray), ruminating (black), and idling (white).

controlling the initiation and termination of eating behavior and, hence, feed intake in grazing dairy cows. It was proposed in many studies (Faverdin et al., 1992; Mbanya et al., 1993) that dairy cows' feed intake might be regulated by fermentation end product concentrations through receptors in the rumen. If that were true, dairy cows should have a different rumen concentration of a certain end product at the end of the grazing bout (when eating ceased) as compared with when the grazing bout starts. The results showed that concentrations of all fermentation end products at the start of a grazing bout were not significantly different from those at the end of a grazing bout. This may indicate that rumen fermentation end products may not play a major role in initiating or terminating a

grazing bout. However, NH_3 concentration had a low P value (0.13) and numerically differed between the start and the end of a grazing bout (Table 5), indicating that it might be more important than the other fermentation end products in regulating eating behavior under grazing.

Figure 2 shows rumen concentration of fermentation end products and pH during the day coupled with the observed grazing behavior pattern. The concentration of all fermentation end products fluctuated during the day in response to eating and rumination. This diurnal fluctuation was minor for total VFA, acetate, propionate, butyrate, and pH, whereas, the observed fluctuation in NH_3 concentration was major. Rumen NH_3 concentration fluctuated ($P < 0.05$) from 80 to >200

Table 5. Mean fermentation end product concentrations (mM) and pH at the start and end of a grazing bout in the rumen of dairy cows.

	Grazing bout		SEM	Significance level		
	Start	End		P (2-tailed)	Correlation ¹	P cor ²
Acetate (C2)	69.7	70.4	1.3	0.70	0.49	0.02
Propionate (C3)	22.0	22.7	0.7	0.29	0.72	0.00
C2/C3	3.3	3.2	0.1	0.08	0.86	0.00
Butyrate	13.7	14.1	0.3	0.31	0.45	0.04
Total VFA	108.7	110.8	2.0	0.49	0.46	0.04
NH_3 , mg/L	146.8	161.3	7.9	0.13	0.68	0.00
$\text{NH}_3/\text{total VFA}^3$	0.078	0.084	0.003	0.12	0.70	0.00
pH	6.18	6.13	0.05	0.28	0.74	0.00

¹Correlation between the start and end values.

² P value of the correlation between the start and end values.

³ $\text{NH}_3/\text{total VFA} = \text{NH}_3 \text{ (mM)} \div \text{total VFA (mM)}$.

Figure 2. Diurnal fluctuation in rumen NH_3 , VFA, and pH of a grazing dairy cow coupled with grazing behavior pattern (on the x-axis), eating (gray), ruminating (black), and idling (white). TVFA = total VFA.

mg/L and showed 2 peaks during the day: at 1230 h midday and at 2230 h in the evening. For a fermentation end product to play a significant role in signaling termination or initiation of a grazing bout, its concentration should fluctuate significantly rather than remain within a small range. In the present study, a huge significant fluctuation was only observed in NH_3 concentration (Figure 2A), rendering it as a main candidate for a possible role in signaling the termination

of a grazing bout. Other researchers (Chilibroste, 1999) observed a sharp increase in NH_3 concentration with time while VFA concentration exhibited a plateau during 1 h of grazing and concluded that NH_3 concentration might be more important than VFA in regulating meals under grazing. In general, NH_3 concentration seemed to increase after grazing, probably because of the ingestion of grass, which contains a high proportion of NPN and rapidly degradable protein. The

fact that the NH_3 peak after the dawn grazing bout occurring at 1230 h midday was sharper and higher than the after dusk grazing bout occurring at 2230 h is probably related to the lower protein and higher WSC content of the grass at dusk time (Table 1). Higher WSC makes more energy available for the microbial population, improving its ability to use NH_3 N available in the rumen for growth purposes and reduces the need of microbes to ferment protein to obtain energy, a process known to be the main contributor to NH_3 concentration in the rumen.

The effect of VFA (acetate, propionate, and butyrate) on intake was previously illustrated in intraruminal infusion studies (Montgomery et al., 1963; Faverdin et al., 1992; Anil et al., 1993), in which the infusion was done for a short term (3 to 5 h) under indoors situation. In these studies, the concentrations of acetate, propionate, and butyrate were almost doubled because of the infusion of 5 to 9 mol of the acids as compared with the control treatment. In the present study, under grazing, where VFA enter the rumen only through the fermentation of the ingested herbage, the concentration of all VFA fluctuated during the day in response to eating and rumination, but was never doubled (Figure 2). Total VFA and acetate concentration fluctuated slightly ($P > 0.05$) between 90 and 120 mmol/L and between 60 and 72 mmol/L, respectively, and showed only one peak during the day at 2330 h just before midnight (Figure 2, B and C). Moreover, time of day did not significantly influence the total VFA and acetate concentration, ruling them out as candidates for controlling meals under grazing. Other VFA (propionate and butyrate) seemed to increase ($P < 0.05$) gradually as the day progressed, showing a sharp rise at dusk time and reaching a peak at 2330 h just before midnight (Figure 2, D and E). In contrast, rumen pH decreased ($P < 0.05$) gradually as the day progressed from 6.5 to 6.0 (Figure 2, F), probably as a result of the increased VFA concentration during the day. The increased concentration of VFA at dusk time could be related to the higher bite rate, BM, and, hence, higher intake rate and DMI at that time of the day (Table 2). The increased concentration of propionate and butyrate as day progressed follows the pattern of WSC content of the grass and DMI, which increased linearly as the day progressed (Tables 1 and 2), resulting in higher WSC intake at dusk. The relationship between higher WSC intake and increased propionate and butyrate concentration in the rumen is well established (Lee et al., 2002). The fact that propionate and butyrate were significantly influenced by time of day only because of a difference between the last time point at 2330 h and the other time points undermines their possible role in meal control under grazing.

Except for NH_3 concentration, which showed 2 peaks during the day, other fermentation end product concentrations and rumen pools were maximal at, or shortly after, the dusk grazing bout ceased. Therefore, the multifactorial theory of meal control seems to be adequate to explain why animals interrupted the last grazing bout at dusk time but fails to adequately explain why animals interrupted the first 2 grazing bouts at dawn and afternoon. This was evidenced by the fact that, at these 2 grazing bouts, cows ceased grazing long before their rumens were full or the concentration of a certain fermentation end product or a combination of fermentation end products was maximal.

CONCLUSIONS

Under a continuous stocking system, where grass availability is not limited, late lactating dairy cows tried to maximize their DMI at dusk by increasing eating time and bite rate and decreasing chewing rate. The TGJM rate, consisting of total number of bites and total number of chews a cow can make per minute, was constant during the day at around 75/min. This indicated that cows could not maneuver much by increasing their TGJM rate. However, cows could maneuver largely by changing the composition of TGJM between bites and chews and seemed to maximize bite rate and minimize chewing rate at dusk time. Bite mass was constant during the day, as the cows seemed to ingest a similar amount of fresh herbage per bite at different times during the day. However, because of the increase in DM content of the grass at dusk, BM in mg DM was much higher at that time of the day. Dairy cows interrupted the first 2 grazing bouts (dawn and afternoon) long before reaching their maximal rumen capacity, indicating that rumen fill is less likely to play a significant role in signaling the termination of these 2 grazing bouts. However, rumen pool sizes were always maximal at the time when the dusk grazing bout ceased, indicating that rumen fill is more likely to play a major role in signaling the termination of the dusk grazing bout. The concentrations of all fermentation end products at the start of a grazing bout were not significantly different from those at the end of a grazing bout, indicating that rumen fermentation end products may not play a major role in initiating or terminating a grazing bout.

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