



## Intake rate and jaw movements of grazing dairy cows facing reduced herbage height



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### Abstract:

Grazing dairy production is limited by low herbage intake, and the characteristics of herbage affect jaw movements and intake rate of cows. The objective was to evaluate the intake rate and jaw movements of cows grazing *Avena strigosa* at three percentages of herbage height reduction (0, 50 and 70 %), as it would have been due to grazing. The experimental design was a 3 x 3 repeated Latin square and treatments were randomly assigned to 18 plots of 3 m<sup>2</sup>. Measurements were performed on six cows during three consecutive days, during each measurement day, two groups of three cows were assigned to treatments in 10 min grazing sessions. Jaw movements were measured by acoustic analysis of the 18 sound recordings of the grazing sessions. With increasing reduction in herbage height, intake rate decreased ( $P \leq 0.05$ ), while cows maintained constant ( $P \geq 0.05$ ) rates of total jaw movements (69.9 min<sup>-1</sup>) and chew movements (29.7 chews min<sup>-1</sup>) but tended ( $P = 0.057$ ) to decrease the rate of compound movements (chew-bite) and increase ( $P \leq 0.05$ ) the rate of exclusive bites. To

maintain a high intake rate at tall herbage (0 % of reduction in herbage height), cows allocated a higher proportion of compound movements, which were needed to process the higher bite mass; but were less efficient when grazing shorter pastures (70 % of reduction in herbage height) due to the increase in total jaw movements per gram of dry matter ingested.

**Key words:** Biting rate, Chewing rate, Chew-bite, Bite mass, Herbage intake.

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## Introduction

In dairy production based on grazing, low herbage intake limits production<sup>(1)</sup>, hence optimizing herbage intake of cows is one of the aims of pasture management<sup>(2)</sup>. Intake rate is a variable of interest in evaluating short-term intake and understanding plant-animal relationships in grazing systems<sup>(3)</sup>. Intake rate is controlled by the rate of jaw movements and by the capacity of cows to allot different classes of jaw movements when facing herbage with diverse physical, as well as chemical structures that affect intake<sup>(4)</sup>. In this regard, when grazing, cattle perform three classes of jaw movements: exclusive bite apprehension, chew and compound chew-bite movement i.e., chewing and apprehension with just one jaw movement<sup>(5)</sup>. These movements can be exclusively detected by means of the acoustic analysis of the sounds produced by jaws during herbage ingestion<sup>(6)</sup>.

Notwithstanding, certain studies have only evaluated bites and chew movements, due to the use of pressure sensors to monitor mandibular movements, without distinguishing compound chew-bite movements and exclusive bites<sup>(7)</sup>. For instance, Fonseca *et al*<sup>(8)</sup> found that, as herbage height increased, the rate of total jaw movements remained constant, while the rate of chewing movements increased and the rate of bite movements decreased. However, these authors did not evaluate compound movements. Nevertheless, Galli *et al*<sup>(9)</sup> highlighted that sheep allocated a higher number of compound movements in tall than in short herbage.

Bite mass and intake rate of cattle increase with the rise in height of herbage<sup>(3,10,11)</sup>, and as the bite mass rises, so does the number of jaw movements per bite. Conversely, the reduction in herbage height during a grazing session negatively affects bite mass and intake rate, due to changes in the vertical structure of the herbage that constrain bite formation<sup>(8)</sup>; facing such

situations, cattle increase the rate of bites movements and reduce the number of jaw movements per bite<sup>(12)</sup>.

Based on the above, there is evidence that cattle are adept at increasing or decreasing the rate of bite jaw movements and the number of jaw movements per bite as a function of the size of the bite they ingest. But it is important to reveal how cattle regulate the allotment of jaw movements (exclusive apprehension bites, mastication movements and compound jaw movements) in the face of the variations in bite mass and intake rate that occur with reductions in herbage height.

Therefore, it was hypothesized that cows grazing tall herbage need to allocate a greater number of compound movements, useful to be able to process and ingest large bite mass and maintain high intake rate. But in herbage height reduction situations, when cows graze in lower herbage strata dominated by stems, they must increase the number of exclusive bites apprehension and chew movements; in order to be able to shred more fibrous herbage and to compensate for the lower intake rate due to the intake of lower bite mass; bites of -fibrous herbages in turn would increase the number of chew movements per gram of dry matter consumed. Consequently, this study was aimed at evaluating the intake rate of grazing dairy cows, and bite mass, jaw movements corresponding to exclusive bite apprehension, chew and compound chew-bite movements, at three percentages of herbage height reduction (0, 50 and 70 %) representing stages of herbage depletion in a grazing session.

## **Material and methods**

### **Location**

The experiment took place between 17/01/2020 and 02/02/2020 at the Experimental Grazing Unit of the Animal Production Department of Universidad Autónoma Chapingo, Texcoco, State of Mexico, Mexico, 19 29' N, 98° 54' W, and an altitude of 2,240 m. The climate is temperate and subhumid with summer rains, annual rainfall of 636 mm and a mean annual temperature of 15.2 °C.

## Experimental site and animals

The experimental pasture consisted of black oat (*Avena strigosa* Schreb), sown at a density of 120 kg ha<sup>-1</sup> pure germinating seed; at sowing it was fertilized with 18 kg N ha<sup>-1</sup> y 46 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> and, at tillering, additional 60 kg de N ha<sup>-1</sup> were supplied. In the pasture, a portable electric fence was used to create nine strips, each measuring 46 m<sup>2</sup> (11.5 x 4 m). Within each strip, three plots measuring 5 m<sup>2</sup> (2 x 2.5 m) were defined, for a total of 27 plots separated by 1-meter-wide aisles. The aisles were designed by mowing all the herbage with a rotary mower (HRR216 PKA, Honda®, USA). Six strips (18 experimental plots) were used for the experiment, and the remainder were used to accustom the cows to short grazing sessions. Six New Zealand Holstein cows (530 ± 40 kg live weight) were used for the experiment. Prior to the experiment, the cows were accustomed to wearing muzzles, which housed the equipment that recorded their jaw movements. During the adaptation phase, the animals remained in an area adjacent to the experimental plots in a black oat pasture and received 5 kg of concentrate cow<sup>-1</sup> d<sup>-1</sup>.

## Experimental design and treatments

The experimental design was a 3 x 3 repeated Latin square. The treatments were three levels of herbage height reduction (0 %, 50 % and 70 %). The treatments were randomly assigned to the 18 experimental plots in accordance with the design. Measurements were performed over the course of three consecutive days. On each day, two groups of three cows were allotted to short grazing sessions in the treatment plots.

To reduce the height of the herbage by 50 % and 70 %, respectively, in each of the corresponding plots, 25 height measurements were taken using an adapted sward stick. The height to be reduced was calculated based on the average height of the herbage, and the herbage was subsequently cut at that height with a Homelite® USA UT44110 trimmer and removed.

## Measurements in the plots

Prior to the experimental grazing sessions, herbage height measurements were taken, and samples were collected for herbage mass and morphological composition in each plot. Herbage height (cm) was measured by taking 25 readings with the adapted sward stick.

Herbage mass, g dry matter (DM) m<sup>-2</sup>, was measured by cutting the herbage to ground level in two 1 m<sup>2</sup> (0.5 m × 2 m) sampling units. This left three m<sup>2</sup> of herbage for the grazing sessions.

To estimate the DM content, two samples per plot were weighed and dried to a constant weight at 55 °C in an oven with forced air circulation. The morphological composition was assessed by hand-separating two samples per plot into leaf blades and pseudostems and stems, including senescent material. Those morphological components were then dried to a constant weight at 55 °C in an oven with forced air circulation to determine the DM content and calculate the proportion of each component. The samples used to estimate DM content of herbage on offer were ground in a Thomas Model 4, Wiley®, USA mill with a 1 mm sieve. Afterwards in a sequential way neutral detergent fiber content (NDF) and acid detergent fiber content (ADF) were measured using a A200, Ankom® USA fiber analyzer with F57, Ankom®, USA filter bags with twenty-five microns porosity<sup>(13)</sup>. After the experimental grazing sessions, the residual herbage height was measured 25 times per plot using the adapted sward stick, the depth of the grazed horizon (cm) was calculated as the difference between the height of the herbage on offer and that of the residual herbage<sup>(14)</sup>. The residual herbage mass (g DM m<sup>-2</sup>) was assessed by cutting herbage to ground level in the 3 m<sup>2</sup> plot, DM content was estimated in the same way as that of herbage on offer.

## Response variables and animal measurements

Eighteen (18) sound recordings of herbage intake from all cows in each treatment were analyzed to quantify jaw movement classes. Each sound recording was obtained from a ten-minute grazing session in each plot. As is typical on mornings (of this time of the year at the experimental site, grazing sessions (after ~8:00) were conducted under good sunshine and clear skies with average temperatures of 17.5 °C. Before each grazing session, a voice recorder (ICD-PX470, Sony®, China) was fitted to the muzzle of each cow, along with a unidirectional microphone (MIC-290, Steren®, Mexico), which had a frequency response of 80-12500 Hz and a sensitivity of 40 dB. The microphone was attached to the animal's forehead with an elastic band that was tied to the muzzle<sup>(15)</sup>. During each grazing session, the time was recorded using a stopwatch. At the end of each session, the cows were moved to the management pen so that the equipment could be removed. Then, the cows were taken to an adjacent area of the experimental plots where they had access to black oat herbage.

The sound recordings were downloaded to computers in MP3 format and analyzed audibly and visually in the Audacity editor (version 2.3.1) by three observers. The analysis of the sound waves lasted approximately one hour per grazing session; the observers completed the

analysis within 2 wk. To distinguish the jaw movements, the sound waves corresponding to the three jaw movement classes were used as visual references. The sound waves of each recording were classified as follows<sup>(4)</sup>.

- Exclusive bite: apprehension when listening to the sound generated by tearing herbage during its removal.
- Chew movement: when the sound of grinding herbage was heard.
- Compound chew-bite jaw movement: when sounds of grinding and tearing herbage were perceived within a single jaw movement.

Each observer listened to the grazing sessions three times. In the first reproduction, total jaw movements were counted. In the second reproduction, bite jaw movements, including exclusive bites apprehension, and compound chew-bite movements, were quantified<sup>(5)</sup>, and in the third reproduction, compound movements were counted. After processing the data by difference, the following were obtained: chewing jaw movements (total jaw movements minus biting jaw movements) and exclusive biting movements (total jaw movements minus chewing and compound movements). The rates of each class of jaw movement were estimated by dividing the total jaw movements of each class by grazing time: total jaw movements per minute (jaw movements  $\text{min}^{-1}$ ), biting per minute (bites  $\text{min}^{-1}$ ), compound jaw movements per minute (chew-bites  $\text{min}^{-1}$ ), chewing per minute (chews  $\text{min}^{-1}$ ), and exclusive biting per minute (exclusive bites  $\text{min}^{-1}$ ). The proportions of each jaw movement class were also estimated<sup>(4)</sup>.

The estimates included the following: apparent herbage intake (g DM), apparent NDF intake (g NDF), intake rate (g DM  $\text{min}^{-1}$ ), bite weight (g DM), time per bite (s), jaw movements per bite, chew movements per bite, and chew movements per g DM or NDF consumed during a grazing session. Apparent herbage intake estimates were obtained in each plot and assumed to be the disappearance of herbage mass<sup>(16)</sup>; obtained by the difference between the herbage mass on offer and the mass of residual herbage. Apparent NDF intake was obtained by the product of apparent intake and the proportion of NDF in the herbage. The intake rate was obtained by dividing the herbage intake by the grazing time of each session<sup>(17)</sup>. Bite mass was estimated by dividing herbage intake by the total number of bites (exclusive bites plus chew-bites) performed in each grazing session<sup>(3)</sup>.

Time per bite, jaw movements per bite, chew movements per bite were calculated by dividing grazing time, total jaw movements and chew movements by total number of bites (exclusive bites plus chew-bites). Chew movements per g DM and NDF consumed resulted from dividing chew movements by DM and NDF intakes.

## Statistical analysis

Data analysis was performed in the SAS 9.4 program<sup>(18)</sup>. The data describing pastures were analyzed by analysis of variance with the GLM procedure, fixed effects of treatment, day of measurement and their interaction were included in the model. The total jaw movements quantified by the three observers during the acoustic analysis were subjected to analysis of variance with the GLM procedure; fixed effects of treatment, observer and their interaction were included in the model. Means were estimated with LSMEANS and compared with Tukey's test ( $P \leq 0.05$ ).

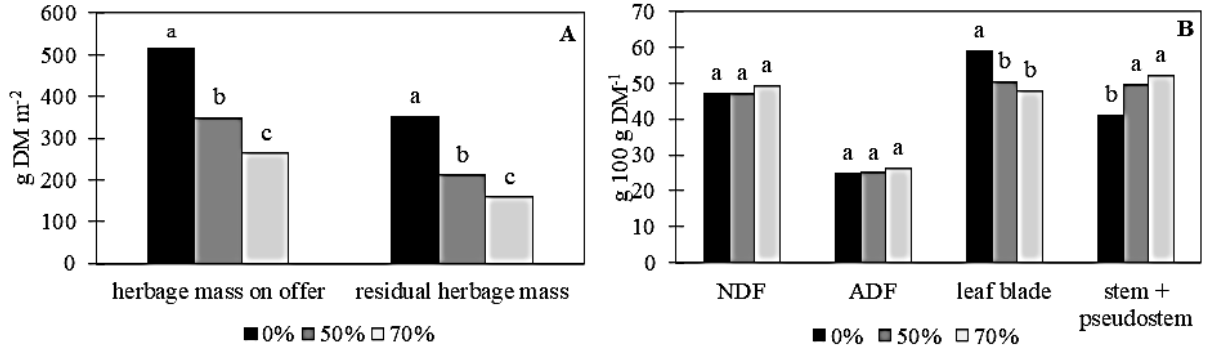
The average of the jaw movements quantified by the three observers was used for the analysis of the three classes of jaw movements. Prior to data analysis, normality tests (Shapiro-Wilks;  $P \geq 0.05$ ) were performed. The variables "chewing rate" and "number of chewings per gram of DM consumed" were transformed using the logarithmic function.

The analysis of variance was based on a 3 x 3 repeated Latin square design, with the fixed effects of square, day, cow within square and treatment included in the statistical model. The GLM procedure was used, the least squares means were estimated with PDIF and compared with Tukey's test ( $P \leq 0.05$ ). Linear regression analyses ( $Y_{ij} = a + bx + \epsilon_{ij}$ ) between selected variables were also performed using the REG procedure.

## Results

The herbage mass on offer and the residual herbage mass decreased as the herbage height reduction increased ( $P \leq 0.01$ ) (Figure 1A). The proportion of leaf lamina was similar ( $P > 0.05$ ) in plots with a 50 % or 70 % reduction in herbage height (an average of 49 g 100 g DM<sup>-1</sup>). In plots with no reduction in herbage height, the proportion of leaf lamina was 20 % higher ( $P \leq 0.05$ ) than the average of the plots with a 50 % or 70 % reduction in herbage height (Figure 1b). The proportion of stem + pseudostem was similar ( $P > 0.05$ ) in plots with a 50 % and 70 % reduction in herbage height (an average of 51 g 100 g DM<sup>-1</sup>). However, that proportion in plots with no reduction in herbage height was 19 % lower than the average of plots with 50 % and 70 % reduction in herbage height (Figure 1B). There were no differences ( $P > 0.05$ ) in the NDF (average 47.8 g 100 g DM<sup>-1</sup>) and FDA (average 25.3 g 100 g DM<sup>-1</sup>) contents among the different herbage height reduction percentages (Figure 1B).

**Figure 1:** A) Herbage mass on offer and residual of *Avena strigosa* Schreb pastures grazed at three forage height reductions (0, 50 and 70 %). B) Neutral detergent fiber (NDF), by acid detergent fiber (ADF), leaf blade, and stem + pseudostem



<sup>abc</sup> Columns with different letters are different ( $P \leq 0.05$ ).

There was no effect ( $P \geq 0.05$ ) of the interaction observer  $\times$  herbage height reduction, nor were there differences ( $P \geq 0.05$ ) in the number of exclusive bites apprehension jaw movements, chew movements and compound chew-bite movements quantified by the three observers (Table 1) within the three percentages of herbage height reduction (0, 50 and 70 %).

**Table 1:** Number of exclusive bites, chews and compound jaw movements by cows in 10 min grazing sessions on black oats pastures at three levels of reduction in herbage height (0 %, 50 % and 70 %)

RHH (%)	Observer			Mean	Level of significance ( <i>P</i> )		
	1	2	3		Observer	RHH	Observer×RHH
Exclusive bites							
0	381	392	382	385	0.919	0.421	0.999
50	370	376	388	378			
70	358	354	364	359			
Mean	370	374	378				
SEM	25						
Chews							
0	273	253	262	262	0.700	0.596	0.989
50	293	281	271	282			
70	285	282	268	278			
Mean	283	272	267				
SEM	25						
Compounds chew-bite							
0	335	313	305	318	0.697	0.002	0.963
50	302	302	301	302			
70	251	255	231	246			
Mean	296	290	279				
SEM	24						

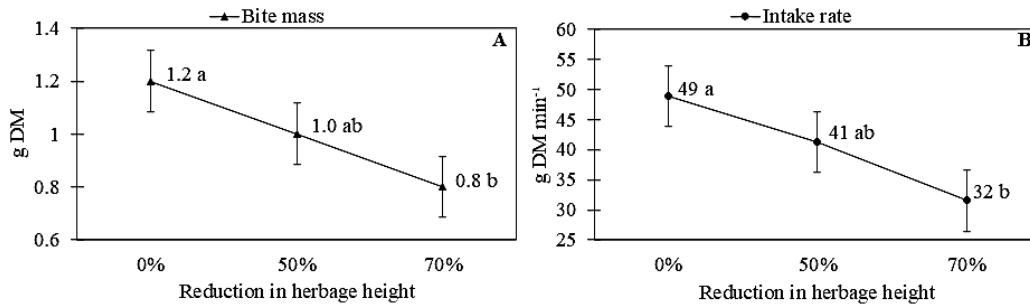
RHH=reduction in herbage height; SEM= standard error of means.

Heights of herbage on offer, residual herbage, DM and NDF intake decreased with increasing reduction in herbage height ( $P < 0.05$  Table 2), however, there was no effect ( $P > 0.05$ ) of that reduction on rates of total jaw movements (mean 69.9 jaw movements  $\text{min}^{-1}$ ), biting (mean 40.2 bites  $\text{min}^{-1}$ ) and chewing (29.7 chews  $\text{min}^{-1}$ ). Nevertheless, cows tended to reduce ( $P = 0.057$ ) the rate of compound jaw movements and to increase ( $P \leq 0.05$ ) the exclusive biting rate with increasing reduction in herbage height. Cows allocated similar ( $P > 0.05$ ) proportions of bites (exclusive bites plus chew-bites) and chew movements among percentages of reduction in herbage height; the averages were 57.7 % and 42.3 %, respectively. Still, the proportion of compound movements was 28 % higher ( $P \leq 0.05$ ) in the plots with no herbage height reduction than in those with a 70 % reduction. Conversely, the proportion of exclusive bites apprehension movements was 73 % higher ( $P \leq 0.01$ ) in plots with a 70 % herbage height reduction than in plots with no herbage height reduction.

Intake rate and bite mass decreased ( $P \leq 0.05$ ) as the herbage height reduction increased (Figure 2). Jaw movements per bite and time per bite were similar ( $P > 0.05$ ) across different

percentages reduction in herbage height, with an average of 1.77 jaw movements per bite and 1.53 s per bite (Table 2). However, the number of compound movements per bite did not differ between 0 % and 50 % reduction in herbage height (mean 0.81 compound movements per bite), which was 21 % higher than at 70 % reduction (Table 2).

**Figure 2:** A) Bite mass. B) Intake rate of cows in 10 min grazing sessions on *Avena strigosa* Schreb pastures at three forage height reductions (0, 50 and 70 %)



<sup>ab</sup> Data with different letters are different ( $P \leq 0.05$ ).

Additionally, cows increased ( $P \leq 0.05$ ) their jaw movements  $\text{g DM}^{-1}$  (Figure 3A), chew movements  $\text{g DM}^{-1}$  and chew movements  $\text{g NDF}^{-1}$  consumed (Figure 3B) as herbage height decreased. There was a negative linear relationship between jaw movements per  $\text{g DM}$  consumed and intake rate ( $y = -20.2x + 78.1$ ,  $R^2 = 0.91$ ,  $P \leq 0.01$  Figure 4A) and a positive linear relationship between jaw movements per bite and time per bite ( $y = 0.63x + 0.40$ ,  $R^2 = 0.74$ ,  $P \leq 0.01$  Figure 4B).

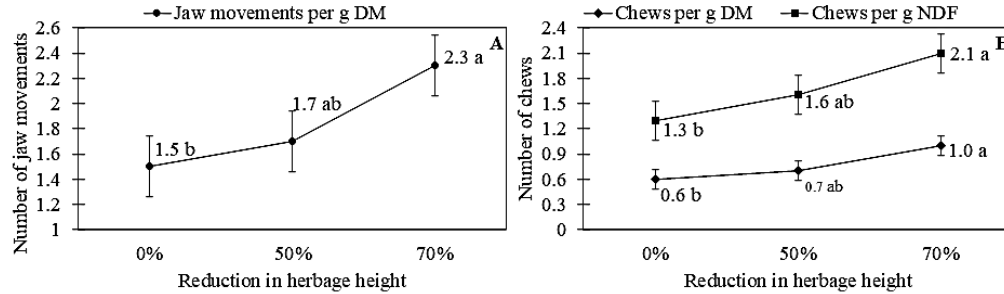
**Table 2:** Herbage heights, intake, rates, and proportions of jaw movements of cows in 10 min grazing sessions on black oats (*Avena strigosa* Schreb) pastures at three percentages of reduction in herbage height (0, 50 and 70 %)

	Reduction in herbage height (%)			SEM	P
	0	50	70		
Height of herbage on offer, cm	53.7 <sup>a</sup>	25.6 <sup>b</sup>	17.6 <sup>c</sup>	0.88	0.001
Residual herbage height, cm	23.7 <sup>a</sup>	14.1 <sup>b</sup>	10.1 <sup>c</sup>	0.63	0.001
Depth of the grazed layer, cm	30.0 <sup>a</sup>	11.5 <sup>b</sup>	7.5 <sup>c</sup>	.99	0.001
Herbage intake, g DM	489.4 <sup>a</sup>	412.4 <sup>ab</sup>	315.1 <sup>b</sup>	34.6	0.022
NDF intake, g	230.5 <sup>a</sup>	194.6 <sup>ab</sup>	155.1 <sup>b</sup>	17.6	0.047
Jaw movements rate, JW min <sup>-1</sup>	69.2	70.1	70.3	1.24	0.826
Biting rate, bites min <sup>-1</sup>	41.0	40.2	39.3	1.63	0.784
Chewing rate, chews min <sup>-1</sup>	28.3	29.9	30.9	1.21	0.341
Chew-bite compounds rate, chew-bites min <sup>-1</sup>	33.8	32.1	26.8	1.8	0.057
Exclusive biting rate, exclusive bites min <sup>-1</sup>	7.2 <sup>b</sup>	8.1 <sup>b</sup>	12.5 <sup>a</sup>	0.41	0.001
Bites, %	59.5	57.5	56.2	1.8	0.465
Chews, %	40.5	42.5	43.8	1.8	0.465
Chew-bite compounds, %	49.2 <sup>a</sup>	45.9 <sup>ab</sup>	38.4 <sup>b</sup>	2.1	0.018
Exclusive bites, %	10.3 <sup>b</sup>	11.6 <sup>b</sup>	17.8 <sup>a</sup>	0.6	0.001
Jaw movements per bite, n	1.7	1.8	1.8	0.06	0.630
Compound jaw movements per bite, n	0.8 <sup>a</sup>	0.8 <sup>a</sup>	0.7 <sup>b</sup>	0.02	0.007
Time per bite, sec	1.5	1.5	1.6	0.07	0.630

SEM= standard error of the means; P=probability of difference; DM= dry matter; NDF= neutral detergent fiber; JW= jaw movements.

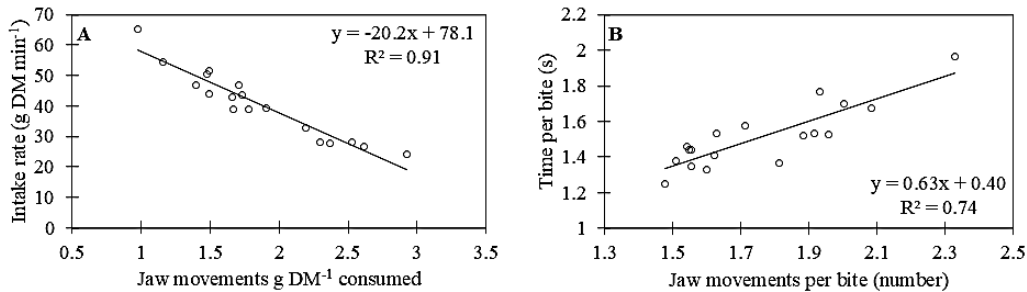
<sup>abc</sup> Means per column with different letter are different ( $P \leq 0.05$ ).

**Figure 3:** A) Jaw movements per g DM consumed. B) Chews per g DM and g NDF consumed by cows in 10 min grazing sessions on *Avena strigosa* Schreb pastures at three forage height reductions (0, 50 and 70 %)



<sup>ab</sup> Data with different letters are different ( $P \leq 0.05$ ).

**Figure 4:** A) Relationship between intake rate and jaw movements per g DM consumed. B) Relationship between time per bite and jaw movements per bite of cows in 10 min grazing sessions on *Avena strigosa* Schreb pastures at three forage height reductions (0, 50 and 70 %)



## Discussion

The observed changes in the cows' intake behavior in this study can be explained by the effect of differences in the structural characteristics of the herbage (height, mass, and morphological composition) in each treatment<sup>(3)</sup>. Reducing the height of the herbage by 0 %, 50 % or 70 % resulted in plots of herbage with high, medium, or low in height. Consequently, the mass of herbage in each treatment was also high, medium, or low (Table 2).

In taller plots where herbage height was not reduced (averaging 53.7 cm), cows had access to a leafy canopy with a higher herbage mass and a higher proportion of leaf blades. The 30 cm depth of the grazed layer indicates that cows removed 56 % of the herbage height, meaning grazing was concentrated in the upper layer of the plots' vertical profile. It is therefore possible to deduce that cows took bites of greater depth and area in the taller plots<sup>(3)</sup>, which explains the higher bite mass and consequently, the higher intake and dry matter (DM) intake rates; according to Boval and Sauvan<sup>(19)</sup>, there is a positive correlation ( $r=0.78$ ) between bite mass and intake rate. Additionally, in temperate grasslands in a vegetative state, bite size and DM intake are positively affected by herbage height<sup>(20)</sup>. Higher herbage intake has also been reported in cattle grazing on higher strata of leafy pastures with more leaves<sup>(14)</sup>.

Conversely, in plots with a 50 % or 70 % reduction in herbage height (averaging 25.6 or 17.6 cm, respectively), cows had access to grazed layers with lower herbage mass and more stems and pseudostems. The grazed layer depths in the medium-height (25.6 cm) and short (17.6 cm) plots were 11.5 and 7.5 cm, respectively. Cows consumed 45 % and 43 % of the pasture height, respectively. As the reduction in herbage height increased to 50 % and 70 %, the grazing horizons became more difficult for the cows to reach, so the depth of the grazing horizon decreased. In tall herbage, however, with no reduction in herbage height, the grazing horizon's depth was close to the estimated bite depth of cattle (close to 50 % of the pasture height<sup>(17,21)</sup>). The shallower depth of the grazed layers in the medium- and low-height plots compared to the taller plots suggests that the cows took bites of a shallower depth and smaller area. This resulted in lower bite masses, a lower intake rate, and lower dry matter (DM) intake. The main cause of reduced dry matter (DM) intake in the lower strata of the plots was the greater proportion of pseudostems and stems, which limit bite formation<sup>(17)</sup>. Similarly, Mezzalira *et al*<sup>(12)</sup> and Benvenuti *et al*<sup>(14)</sup> found that cattle grazing in lower strata dominated by stems had lower DM intake. These results confirm the relationship between intake rate, bite mass, and herbage characteristics reported by Boval and Sauvan<sup>(19)</sup>.

In this study, the rates of jaw movements, bites (exclusive bites plus chew-bites), and chew movements remained consistent across the examined herbage height reduction percentages. These values fell within the minimum and maximum ranges reported for grazing cattle<sup>(22)</sup>, with mean values of 70.7 jaw movements  $\text{min}^{-1}$ , 45.6 bites  $\text{min}^{-1}$ , and 22.8 chews  $\text{min}^{-1}$ . However, in this study, cows performed a higher proportion of compound jaw movements and tended to increase the speed of these movements in taller plots (with no reduction in herbage height), where bite mass was higher. This confirms Galli *et al*<sup>(4)</sup> approach that the allocation of compound jaw movements is an ingestive behavior strategy necessary for cows to chew and swallow higher bite masses. In this study, 82 % of the total jaw movements performed by cows in taller plots were compound jaw movements.

As Boval and Sauvan<sup>(19)</sup> stated, larger bites require more processing before the next bite can be taken. Consequently, the time between bites (handling time) increases, and the bite rate

decreases. Because cows needed to process larger bites in taller plots, they did not reduce their bite rate; however, they did reduce the rate and proportion of exclusive bites. Additionally, time per bite increased with an increase in jaw movements per bite (Figure 4b), this relationship is consistent with previous findings<sup>(12)</sup>.

Time per bite is the total time that cows spend on chewing and handling bites<sup>(19)</sup>. However, in this study, time per bite represented only the time required for chewing because exclusive bites and compound movements were grouped together in the time per bite estimate. When grazing in shorter plots (a 70 % reduction in herbage height), cows increased their rate of exclusive bites as a behavioral strategy to remedy the lower dry matter intake rate caused by collecting smaller bites<sup>(20)</sup>. Nevertheless, this strategy was unsuccessful, and DM intake decreased. Furthermore, the increase in jaw movements per gram of dry matter (g DM) due to the reduction in herbage height suggests that cows were less efficient while grazing under these conditions. A linear decrease in intake rate was observed with an increase in jaw movements per gram of dry matter consumed (Figure 4A). It has also been reported<sup>(12)</sup> that cows were less efficient as herbage height decreased progressively grazing in that case on *Cynodon* sp. and *Avena strigosa*.

The increase in chew movements per g DM consumed with progressive reduction in herbage height could not be explained by the higher contents of NDF and ADF in the herbage, as these were similar between treatments. However, fewer chew movements per g DM consumed than per g NDF consumed were observed, indicating that chewing NDF is more difficult than chewing DM (Figure 3B). In this regard, Grant and Cotanch<sup>(23)</sup> pointed out that feeds with high NDF content (values from 57.1 to 58.6 g NDF 100 g DM<sup>-1</sup>) require more chew movements per g NDF consumed (values from 2.6 to 3.5 chews per g NDF consumed); these values are higher than those found in this study, which ranged from 1.3 to 2.1 chew movements per g NDF consumed with a mean NDF content of 42.3 g NDF 100 g DM<sup>-1</sup>.

## Conclusions and implications

With taller herbage, the ingestive behavioral strategy used by cows to process the larger bites and maintain a high intake rate was to allocate a higher proportion of compound chew-bite jaw movements. When faced with shallower herbage height (as reduced by grazing), cows were less efficient due to the increase in jaw movements per gram of dry matter consumed, with the consequent reduction in intake rate because of the lower amount of herbage ingested per bite. In addition, cows had to perform more chew movements per gram of dry matter consumed in the lower pasture layer dominated by stems and pseudostems.

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## Conflicts of interests

The authors declare no conflicts of interest.

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