Chewing activities, sorting behaviour and ruminal fermentation of lactating dairy cows fed diets with similar proportions of undigested neutral detergent fibre with wheat straw substituted for alfalfa hay, corn silage or both

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ABSTRACT
Feeding behaviour and ruminal fermentation of dairy cows were evaluated when fed diets formulated to supply a similar proportion of undigested neutral detergent fibre (uNDF) after 30-h incubation (uNDF\textsubscript{30}), while wheat straw (WS) replaced for corn silage (CS), alfalfa hay (AH) or both. In a randomised block design, 32 multiparous Holstein cows (days in milk = 78 ± 11 d, milk production = 56 ± 6 kg/d) were used. AH and CS were the only forage sources in control diet (CSAH). WS was substituted for alfalfa hay (WSCS), CS (WSAH) or both (WSCSAH) on uNDF\textsubscript{30} basis. Dry matter consumption from 6 to 24 h after feed delivery was lower in WSAH than in WSCS or CSAH. No difference existed in total time spent for eating (250 min/d), rumination (460 min/d) and chewing (710 min/d). Total concentration of volatile fatty acids (VFAs) in the rumen was not different between treatments but propionate proportion was lower for cows fed WSAH than CSAH diet (19.0 vs. 24.1 mM/100 mM). Ammonia nitrogen concentration in the rumen fluid was greater for WSAH than WSCS or CSAH. With combining uNDF\textsubscript{288} and peNDF, peuNDF\textsubscript{288} was calculated and its intake had the highest correlation with chewing time (r = −0.60), sorting index of particles retained on 8-mm sieve (r = 0.42) and rumen pH (r = 0.52). Forage replacement on uNDF\textsubscript{30} basis resulted in a relatively similar response on feeding behaviours and ruminal fermentation and enabled to replace high-quality forages with low-quality forages in the dairy cow rations.

HIGHLIGHTS
- Wheat straw (WS) was substituted for alfalfa hay (AH), corn silage (CS) or both on an uNDF\textsubscript{30} basis.
- Treatments had small differences in chewing patterns and ruminal fermentation.
- Combination of uNDF\textsubscript{288} and diet particle size improved correlation coefficient with chewing, long particle intake and rumen pH.

Introduction
To achieve a balanced diet for high-producing cows and maintain chewing activity and rumen function, it is critical to include sufficient fibre in the diet (Allen 1997). Forage is an important source of fibre in dairy cow rations because of its primary contribution to the physical form of diet, which is important for optimising feed intake and stabilising ruminal fermentation, and thus preventing metabolic disorders (Van Soest 1994; Mertens 1997; Beauchemin 2018). Obtaining sufficient physical properties of diet becomes increasingly important as dietary forage level has diminished in the diet of high-producing cows (Esmaeili et al. 2016) due to several nutritional and economical constraints (Naderi et al. 2016; Nemati et al. 2020).

Feeding behaviour has an important effect on the health and production of dairy cows. Maulfair et al. (2010) reported that fluctuations in rumen...
fermentation patterns and productivity occur as a result of ration sorting in dairy cows. DeVries (2013) reported that sorting against long particles resulted in a 0.4-unit decrease in rumen pH and a 0.6% decrease in milk fat content. Fibre digestibility is an important factor in the regulation of rumination, ruminal physical fill, voluntary feed intake and productivity of dairy cows (Van Soest 1994; Nousiainen et al. 2003; Mertens 2016). Undigested neutral detergent fibre (uNDF) has recently received increased attention as a functional fibre fraction controlling rumen fill, digestion and forage passage dynamics, and is known to affect rumination behaviour and feed intake (Cotanch et al. 2014; Mertens 2016; Fustini et al. 2017; Miller et al. 2021). According to Kahyani et al. (2019b), uNDF concentration (at 30, 240 and 288 h of incubation) differs greatly between WS, beet pulp, corn silage (CS) and alfalfa hay (AH). Therefore, formulation of dairy rations on the basis of uNDF may have potential desirable effects on sustaining feeding behaviour and ruminal fermentation of high-producing dairy cows fed different forage types.

This experiment is part of a larger project targeting to quantify several nutritional, behavioural and health responses of dairy cows to the diets variable in forage type but balanced for the amount of uNDF and NDF digestibility that were determined after 30-h in situ incubation, and are termed uNDF\textsubscript{30} and NDFD\textsubscript{30}, respectively. Data on lactation performance, and nutrient digestibility were previously reported in our companion article (Kahyani et al. 2019a). In short, substituting WS for AH or CS in the diets with similar amount of uNDF\textsubscript{30} resulted in comparable milk production (49.5 kg/d), without any adverse effect on DMI and ruminal pH. For this study, we aimed to assess the substitution effects of WS for AH or CS on feed sorting, chewing patterns and ruminal fermentation in high-producing dairy cows. We hypothesised that substituting WS for AH or CS on uNDF\textsubscript{30} basis would sustain feeding behaviour required for stable rumen function. Beet pulp was incorporated into all experimental rations in order to maintain a similar concentration of NDFD\textsubscript{30}.

Materials and methods

Experimental design, treatments and animals

This study is part of a larger experiment and the detailed description on experimental design is reported in the companion article (Kahyani et al. 2019a). In brief, CS was harvested at a theoretical chop length of 25–30 mm. AH and WS were chopped at a length cut of 15 and 10 mm, respectively. Wheat straw (WS) was reconstituted to achieve a DM content of 25%. These forages along with beet pulp were subjected to an in situ procedure to quantify uNDF fraction (Kahyani et al. 2019a), and uNDF\textsubscript{30} concentration for CS, AH, WS and beet pulp averaged 37.3, 32.0, 62.4 and 7.70% of DM, respectively (Kahyani et al. 2019a). CS and AH were the only forage sources in control ration (CSAH). The remaining three diets included WS in replacement of AH (WSCS), CS (WSAH) or both (WSCSAH) to achieve similar proportion of uNDF\textsubscript{30} (~17% of diet DM). NDF digestibility after 30-h in situ incubation (NDFD\textsubscript{30}) was also similar across diets (44.5% of NDF), which was achieved by beet pulp addition to diets. However, uNDF\textsubscript{288} content was different among diets, averaging 9.4, 8.1, 10.8 and 8.9% of DM for CSAH, WSCS, WSAH and WSCSAH, respectively (Kahyani et al. 2019a). In the companion article, a detailed description of the experimental diets, including ingredients and chemical composition, was also provided (Kahyani et al. 2019a). Briefly, the DM proportion of CS, AH, WS, and beet pulp were 22.0, 18.0, 0.0 and 2.0 in CSAH diet, 22.0, 0.4, 9.04 and 8.40 in WSCS diet, 6.80, 9.20, 9.04 and 4.64 in WSAH diet, and 14.4, 9.20, 9.04 and 6.56 in WSCSAH diet, respectively. Diets were formulated to have similar energy density (NE\textsubscript{L} = 1.65 Mcal/kg of DM) and crude protein (16.4 ± 0.38% of DM). Dry matter, NDF, and forage NDF contents were similar across diets, averaging 41.7, 30.5 of DM and 20.3% of DM, respectively. However, forage-to-concentrate ratio was 40:60, 31:69, 34:66 and 33:67 for CSAH, WSCS, WSAH and WSCSAH, respectively.

The experiment involved 32 multiparous Holstein cows (body weight = 642 ± 50; days in milk = 78 ± 11 d; milk yield = 56 ± 6 kg/d; mean ± standard deviation). This experiment consisted of three phases: a 10-d covariate period, a 35-d adaptation period and a 7-d data collection phase. Cows were housed individually in pens measuring 4 × 4 m within a roofed building that had open sides. Bedding was made of wood shavings and sand that was refreshed each day. Feed was delivered twice a day at 10:00 and 18:00 h at a rate providing 10% refusals (Kahyani et al. 2019a). Diets were manually mixed and weighed into each cow’s feed trough, and refusals were manually removed daily and weighed.

Particle size and diurnal variation in DMI

Amounts of TMR delivered and refused were weighed and sampled daily for each cow from 35 to 41 d of
each period, and daily DMI for individual cows was calculated. From 35 to 41 d of experiment, TMR and refusals of individual cows were sampled and immediately frozen at −20°C until analysis for particle size separation. After thawing, particle size distributions of representative subsamples (as-fed basis) were determined (in triplicate) using the Penn State Particle Separator (PSPS; Nasco, Fort Atkinson, WI) equipped with 3 sieves (19, 8 and 1.18 mm). Each sieved fraction was oven dried (60°C for 48 h) to determine DM content. Physically effective factor (pef) was determined as the total proportion of DM retained on the 8 ± 19-mm sieves (pef8; Lammers et al. 1996) and 1.18 ± 8 ± 19-mm sieves (pef1.18; Kononoff et al. 2003). Physically effective NDF (peNDF) inclusive of particles >1.18 mm (peNDF1.18) and >8 mm (peNDF8) was calculated through multiplication of pef1.18 and pef8 by NDF content of the ration (DM basis), respectively. Physically effective uNDF (peuNDF) after 30-(peuNDF30) or 288-h (peuNDF288) in situ incubation was calculated by multiplying dietary uNDF concentration (% of DM) by pef8 and pef1.18 (Grant et al. 2018). Particle size, peNDF and peuNDF were determined in both TMR and orts samples in order to determine their actual intakes and account for sorting. From 35 to 41 d of the experiment, the whole quantity of feed remaining in the feed bunk was collected on 2, 4, 6 and 24 h after morning feed delivery, to determine diurnal variations in DMI. NDF was quantified according to the procedure of Van Soest et al. (1991), and was inclusive of a-amylase and sodium sulphite.

Chewing and sorting behaviour

Eating and rumination activities were visually monitored for each cow from 39 to 41 d of study using four trained observers. Eating and ruminating activities were noted at 5-min intervals, and each activity was assumed to persist for the entire 5-min interval (Colenbrander et al. 1991). Rumination was a series of events that occurred when a bolus was regurgitated, chewed and swallowed. Chewing activity was calculated as sum of eating and rumination activities (Maekawa et al. 2002). Meals were later calculated as the sum of at least 5 min of consecutive eating activity preceded and followed by at least 5 min of non-eating activity. Chewing activity as a function of kg of DM and NDF consumed was calculated by dividing total chewing time by the respective intakes quantified from 39 to 41 d (Kahyani et al. 2013). Eating or rumination rate was calculated as the ratio of DMI and total time spent eating or rumination per d, respectively (Beauchemin and Yang 2005). Sorting index was calculated from 35 to 41 d of the study as the proportion of the actual to expected intake of particles retained on each sieve of the PSPS (Leonardi and Armentano 2003). A value of 100% indicates no sorting. Selective refusal and preferential consumption were indicated by values less than and greater than 100%, respectively.

Ruminal fermentation

In the final day of the experiment, ruminal fluid (~3 mL) was obtained from all experimental cows at 4 h after the morning feeding from the ventral sac through rumenocentesis technique (Nordlund and Garrett 1994). The ruminal pH was immediately measured using a pH metre (HI 8318, Hanna Instruments, Romania). A portion of ruminal fluid (approximately 2 mL) was acidified with 200 μL of 25% metaphosphoric acid/mL for volatile fatty acids (VFAs) analysis. Another portion (approximately 1 mL) was acidified with 200 μL sulphuric acid (1% w/v) for ammonia-N analysis. Both samples were kept frozen at −20°C waiting analysis. The thawed ruminal samples were centrifuged at 30,000 × g for 20 min at 4°C, and supernatant was harvested for analysis of ammonia-N (Broderick and Kang 1980). Before VFA analysis, the samples were thawed and centrifuged at 10,000 × g at 4°C for 20 min. Analysis of VFA was undertaken using a gas chromatography (0.25 × 0.32, 0.3 μm i.d. fused silica capillary, model No. CP-9002 Vulcanusweg 259 a.m., Chrompack, Delft, the Netherlands), according to the procedure of Bal et al. (2000).

Data analysis

Data arranged within a randomised complete block were analysed using the MIXED Proc of SAS version 9.0 (SAS Institute Inc., Cary, NC). Block and treatment were included in the model as fixed effects. Cow was regarded as a random effect. If values from the covariate period were available and significant, they were used as a covariate in the model. Data on diet particle size were analysed using GLM model. Least-square means were reported and the difference between treatment means and contrast (CSAH vs. WSCS + WSAH + WSCSAH) was determined using the Bonferroni t-test. The CORR Proc in SAS was used to estimate the Pearson correlation coefficients. The significance level was set at $p \leq 0.05$. Trends were discussed when at 0.05 < $p < 0.10$. 


Results

Physical characteristics of diets and nutrient intakes

Data on physical characteristics of the diets are reported in Table 1. WSCS diet contained greater coarse particles (8 and 19 mm) that caused a greater amount of peNDF1.18, peuNDF288 and peuNDF30 in this diet. An inverse trend was observed for WSAH diet. Compared with CSAH diet, proportion of particles on 8-mm sieve was greater in WS-containing diets (WSCS, WSCSAH). According to the data, cows fed WS-containing diets were not different across treatments, averaging 1.78 kg DM/d (p = 0.09; data not presented).

Cows fed WSCS diet had the greatest intake of coarse particles (19 and 8 mm) expressed as kg/d or % of daily intake, which resulted in greater intake of peNDF1.18, peuNDF288 and peuNDF30 (Table 2). Starch and NDF intakes were also greatest in WSCS diet. Sorting behaviour

Data on sorting index for coarse particles (8 and 19 mm) indicated greater values for WSCS-containing diets than control diet, suggesting a lesser sorting against those long particles (Table 3). The average sorting index of 19-mm particles in WS-containing diets was 92%, while it was 76.0% in CSAH. The sorting index of 8-mm particles was greater in WS-containing diets than control diet (p = 0.03). In line with the greater sorting index of coarse particles, the sorting index for peNDF1.18, peuNDF288 and peuNDF288 > 8 fractions were greater in WS-containing diets than control diet. Cows exhibited no difference in their sorting of peNDF1.18 or peuNDF288 > 1.18.
Table 2. Diurnal dry matter (DM) intake, nutrient and particle-size consumption in dairy cows fed diets with similar concentration of undigested Neutral Detergent Fibre (NDF) after 30 h of incubation from different forage sources.

| Intake, kg/d | Diets | p Value | Treatment | Contrast |
|-------------|-------|---------|-----------|----------|
| Diurnal DM intake | | | | |
| 0–2 | CSAH | 6.77 | 7.69 | 8.76 | 7.62 | 0.61 | 0.16 | 0.07 |
| 2–4 | CSAH | 1.74 | 2.15 | 1.80 | 2.04 | 0.31 | 0.76 | 0.47 |
| 4–6 | CSAH | 1.61 | 1.74 | 0.95 | 1.71 | 0.43 | 0.55 | 0.75 |
| 6–24 | CSAH | 16.08 | 16.74 | 12.93 | 14.22 | 0.90 | 0.02 | 0.18 |
| 0–24 | CSAH | 26.32 | 28.52 | 24.63 | 25.72 | 0.79 | 0.01 | 0.95 |

Contrast probability. Contrast = effect of wheat straw substituted for alfalfa hay, corn silage or both (CSAH vs. WSCS + WSAH + WSCSAH).

Table 3. Sorting index1 of dairy cows fed diets with similar concentration of undigested Neutral Detergent Fibre (NDF) after 30 h of incubation from different forage sources.

| Item | Diets | p Value | Treatment | Contrast |
|------|-------|---------|-----------|----------|
| Diets2 | | | | |
| PSA | SEM | Treatment | Contrast |
| 19 mm | | | | |
| PSU | | | | |
| 19 mm | | | | |
| 8 mm | | | | |
| Pan | | | | |

Within a row, least squares means with different superscripts differ (p < 0.05).

A value equal to 100 indicates no sorting occurred, less than 100 indicates sorting against and greater than 100 indicates sorting for (Leonardi and Armentano 2003).

Experimental diets were combinations of different forage sources but similar dietary concentration of undigested NDF after 30 h of incubation (uNDF<sub>30</sub>). CSAH = 0% wheat straw (WS), 59% corn silage (CS) and 41% alfalfa hay (AH); WSCS = 40% WS, 59% CS and 1% AH; WSAH = 40% WS, 41% AH and 19% CS; WSCSAH = 40% WS, 39% CS and 21% AH.

Contrast probability. Contrast = effect of wheat straw substituted for alfalfa hay, corn silage or both (CSAH vs. WSCS + WSAH + WSCSAH).

peNDF<sub>30</sub> or peNDF<sub>1.18</sub> is physically effective NDF calculated as multiplication of dietary NDF content (% DM) by pef<sub>8</sub> and pef<sub>1.18</sub>, respectively.

uNDF<sub>30</sub> and uNDF<sub>288</sub> were NDF residues after 30- and 288-h in situ incubation, respectively.

peuNDF<sub>288</sub> and peuNDF<sub>30</sub> were physically effective uNDF<sub>288</sub> and uNDF<sub>30</sub> determined as uNDF<sub>288</sub> and uNDF<sub>30</sub> content (DM basis) multiplied by pef<sub>8</sub> or pef<sub>1.18</sub> (Grant et al. 2018).
Within WS-containing diets, the forage type generally did not have a considerable effect on sorting index.

**Meal patterns and chewing activity**

Number of meals per day was least with WSAH diet (8.90) in comparison to other diets (10.5) (Table 4). Treatments had no effect on meal length (24.5 ± 1.25 min/meal) and meal size of DM (2.62 ± 0.12). Cows fed WS-containing diets had a greater NDF intake in each meal and tended to have lower meal number and greater eating rate. Experimental diets had no effect on ruminating bout number (bout/d) and length (min/bout), averaging 11.5 and 40.9, respectively.

Time spent for eating, rumination, and chewing expressed as a function of min/d or min/kg of DM or NDF was not different across treatments (Table 5).

**Ruminal fermentation**

Information on metabolites concentration in the rumen is reported in Table 6. Cows fed WS-containing diets had a lower eating activity (min/d or min/kg of DM or NDF), but ruminating and total chewing did not differ.

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**Table 4.** Meal patterns of dairy cows fed diets with similar concentration of undigested Neutral Detergent Fibre (NDF) after 30 h of incubation from different forage sources.

| Item          | Diets | SEM | Treatment | Contrast² |
|---------------|-------|-----|-----------|-----------|
| Eating Meals/d | CSAH  | 10.7| 0.39      | 0.01      |
|               | WSCS  | 10.6|           | 0.07      |
|               | WSAH  | 8.90|           | 0.27      |
|               | WSCSAH| 10.3|           | 0.25      |
| Length, min/meal | CSAH  | 25.9|           | 0.32      |
|               | WSCS  | 24.0|           |           |
|               | WSAH  | 25.9|           |           |
|               | WSCSAH| 23.0|           |           |
| Rate, g of DM/min | CSAH  | 98  |           | 0.07      |
|               | WSCS  | 114 |           |           |
|               | WSAH  | 110 |           |           |
|               | WSCSAH| 110 |           |           |
| Meal size kg of DM | CSAH  | 2.46|           | 0.24      |
|               | WSCS  | 2.72|           | 0.15      |
|               | WSAH  | 2.79|           | 0.07      |
|               | WSCSAH| 2.52|           | 0.03      |
| kg of NDF      | CSAH  | 0.72|           | 0.24      |
|               | WSCS  | 0.83|           | 0.15      |
|               | WSAH  | 0.87|           | 0.07      |
|               | WSCSAH| 0.77|           | 0.03      |
| Rumination Bouts/d | CSAH  | 11.7|           | 0.64      |
|               | WSCS  | 11.6|           | 0.59      |
|               | WSAH  | 10.8|           |           |
|               | WSCSAH| 11.8|           |           |
| Min/bout       | CSAH  | 41.2|           | 0.88      |
|               | WSCS  | 39.2|           | 0.90      |
|               | WSAH  | 40.8|           |           |
|               | WSCSAH| 42.4|           |           |

¹Within a row, least squares means with different superscripts differ (p ≤ 0.05).
²Experimental diets were combinations of different forage sources but similar dietary concentration of undigested NDF after 30 h of incubation (uNDF30). CSAH = 0% wheat straw (WS), 59% corn silage (CS) and 41% alfalfa hay (AH); WSCS = 40% WS, 59% CS and 1% AH; WSAH = 40% WS, 41% AH and 19% CS; WSCSAH = 40% WS, 39% CS and 21% AH.
³Contrast probability. Contrast = effect of wheat straw substituted for alfalfa hay, corn silage or both (CSAH vs. WSCS + WSAH + WSCSAH).

**Table 5.** Chewing activity of dairy cows fed diets with similar concentration of undigested Neutral Detergent Fibre (NDF) after 30 h of incubation from different forage sources.

| Item          | Diets | SEM | Treatment | Contrast² |
|---------------|-------|-----|-----------|-----------|
| Eating Min/d  | CSAH  | 276 | 15.0      | 0.11      |
|               | WSCS  | 256 |           | 0.03      |
|               | WSAH  | 231 |           |           |
|               | WSCSAH| 235 |           |           |
| Min/kg of DM  | CSAH  | 10.5| 0.55      | 0.20      |
|               | WSCS  | 8.7 |           | 0.04      |
|               | WSAH  | 9.5 |           |           |
|               | WSCSAH| 9.3 |           |           |
| Min/kg of NDF | CSAH  | 35.6| 1.95      | 0.10      |
|               | WSCS  | 29.6|           | 0.01      |
|               | WSAH  | 30.2|           |           |
|               | WSCSAH| 30.0|           |           |
| Rumination Min/d | CSAH  | 472 | 21.1      | 0.43      |
|               | WSCS  | 446 |           | 0.52      |
|               | WSAH  | 440 |           |           |
|               | WSCSAH| 484 |           |           |
| Min/kg of DM  | CSAH  | 17.9| 19.4      | 0.14      |
|               | WSCS  | 16.0|           | 0.87      |
|               | WSAH  | 17.9|           |           |
|               | WSCSAH| 19.4|           |           |
| Min/kg of NDF | CSAH  | 60.9| 62.3      | 0.15      |
|               | WSCS  | 51.9|           | 0.33      |
|               | WSAH  | 57.7|           |           |
|               | WSCSAH| 62.3|           |           |
| Total chewing Min/d  | CSAH  | 747 | 27.7      | 0.24      |
|               | WSCS  | 702 |           | 0.11      |
|               | WSAH  | 669 |           |           |
|               | WSCSAH| 719 |           |           |
| Min/kg of DM  | CSAH  | 28.6| 28.6      | 0.19      |
|               | WSCS  | 25.1|           | 0.31      |
|               | WSAH  | 27.1|           |           |
|               | WSCSAH| 28.6|           |           |
| Min/kg of NDF | CSAH  | 96.5| 92.4      | 0.09      |
|               | WSCS  | 81.3|           | 0.06      |
|               | WSAH  | 87.8|           |           |
|               | WSCSAH| 92.4|           |           |

¹Experimental diets were combinations of different forage sources but similar dietary concentration of undigested NDF after 30 h of incubation (uNDF30). CSAH = 0% wheat straw (WS), 59% corn silage (CS), and 41% alfalfa hay (AH); WSCS = 40% WS, 59% CS and 1% AH; WSAH = 40% WS, 41% AH and 19% CS; WSCSAH = 40% WS, 39% CS and 21% AH.
²Contrast probability. Contrast = effect of wheat straw substituted for alfalfa hay, corn silage or both (CSAH vs. WSCS + WSAH + WSCSAH).
Table 6. Ruminal fermentation of dairy cows fed diets with similar concentration of undigested Neutral Detergent Fibre (NDF) after 30 h of incubation from different forage sources.

| Items                                      | CSAH  | WSCS  | WSAH  | WSCSAH | SEM  | Treatment | Contrast |
|--------------------------------------------|-------|-------|-------|--------|------|-----------|----------|
| Ruminal pH<sup>a</sup>                     | 5.74<sup>b</sup> | 6.29<sup>ab</sup> | 6.08<sup>ab</sup> | 6.03<sup>ab</sup> | 0.12 | 0.04  | 0.01     |
| Ammonia N, mg/dL                           | 10.8<sup>b</sup> | 9.50<sup>ab</sup> | 13.0<sup>b</sup>  | 11.4<sup>ab</sup> | 0.76 | 0.02  | 0.19     |
| Total VFA, mM                              | 98.8  | 95.7  | 90.5  | 91.5   | 6.80 | 0.80  | 0.42     |
| Individual VFA (mM/100 mM)                 |       |       |       |        |      |        |          |
| Acetate                                    | 64.1  | 65.8  | 67.4  | 66.0   | 0.38 | 0.43  | 0.16     |
| Propionate                                 | 24.1<sup>a</sup> | 22.0<sup>ab</sup> | 19.0<sup>ab</sup> | 21.9<sup>ab</sup> | 1.23 | 0.05  | 0.03     |
| Butyrate                                   | 9.10  | 9.48  | 10.5  | 9.53   | 0.44 | 0.20  | 0.16     |
| Isovalerate                                | 0.38  | 0.32  | 0.48  | 0.28   | 0.07 | 0.23  | 0.80     |
| Valerate                                   | 1.10  | 1.07  | 1.20  | 0.96   | 0.13 | 0.62  | 0.80     |
| Isovalerate                                | 1.18  | 1.28  | 1.31  | 1.39   | 0.14 | 0.77  | 0.36     |
| Acetate-to-propionate                      | 2.81  | 3.11  | 3.57  | 3.03   | 0.22 | 0.12  | 0.10     |

<sup>a</sup>Within a row, least squares means with different superscripts differ (p < 0.05).

<sup>b</sup>Experimental diets were combinations of different forage sources but similar dietary concentration of undigested NDF after 30 h of incubation (uNDF<sub>30</sub>). CSAH = 0% wheat straw (WS), 59% corn silage (CS) and 41% alfalfa hay (AH); WSCS = 40% WS, 59% CS, and 1% AH; WSAH = 40% WS, 41% AH and 19% CS; WSCSAH = 40% WS, 39% CS and 21% AH.

<sup>c</sup>Contrast probability. Contrast r = effect of wheat straw substituted for alfalfa hay, corn silage or both (CSAH vs. WSCS = WSAH + WSCSAH).

<sup>d</sup>The pH data were presented in the companion article (Kahya et al. 2019a), and again presented in this table for the better interpretation of the rumen fermentation metabolites.

Table 7. Pearson correlation coefficients between fibre intake variables and eating and chewing patterns, particle sorting, ruminal acetate, propionate and pH and milk fat.

| Variables | DMI | NDF | uNDF<sub>30</sub> | uNDF<sub>288</sub> | peNDF<sub>8</sub> | peuNDF<sub>288 > 8</sub> | peuNDF<sub>30 > 8</sub> |
|-----------|------|-----|-------------------|-------------------|------------------|------------------------|------------------------|
| Eating, min/d | 0.40<sup>a</sup> | 0.33<sup>a</sup> | 0.36<sup>a</sup> | 0.23<sup>a</sup> | 0.22<sup>a</sup> | 0.24<sup>a</sup> | 0.21<sup>a</sup> |
| Ruminating, min/d | 0.10<sup>a</sup> | 0.04<sup>a</sup> | 0.08<sup>a</sup> | -0.01<sup>a</sup> | 0.005<sup>a</sup> | 0.03<sup>a</sup> | -0.07<sup>a</sup> |
| Total chewing, min/d | 0.32<sup>a</sup> | 0.23<sup>a</sup> | 0.28<sup>a</sup> | 0.13<sup>a</sup> | 0.14<sup>a</sup> | 0.17<sup>a</sup> | 0.07<sup>a</sup> |
| Eating, min/kg DM | -0.17<sup>a</sup> | -0.23<sup>a</sup> | -0.19<sup>a</sup> | -0.05<sup>a</sup> | -0.24<sup>a</sup> | -0.21<sup>a</sup> | -0.27<sup>a</sup> |
| Ruminating, min/kg DM | -0.59<sup>a</sup> | -0.61<sup>a</sup> | -0.59<sup>a</sup> | -0.45<sup>a</sup> | -0.48<sup>a</sup> | -0.49<sup>a</sup> | -0.61<sup>a</sup> |
| Total chewing, min/kg DM | -0.54<sup>a</sup> | -0.60<sup>a</sup> | -0.57<sup>a</sup> | -0.41<sup>a</sup> | -0.47<sup>a</sup> | -0.49<sup>a</sup> | -0.60<sup>a</sup> |
| Sorting index of 19-mm particles, % | -0.33<sup>a</sup> | -0.19<sup>a</sup> | -0.26<sup>a</sup> | -0.04<sup>a</sup> | -0.02<sup>a</sup> | -0.08<sup>a</sup> | 0.12<sup>a</sup> |
| Sorting index of 8-mm particles, % | 0.30<sup>a</sup> | 0.27<sup>a</sup> | 0.35<sup>a</sup> | 0.29<sup>a</sup> | 0.36<sup>a</sup> | 0.35<sup>a</sup> | 0.42<sup>a</sup> |
| Acetate, mM/100 mM | 0.10<sup>a</sup> | 0.16<sup>a</sup> | 0.16<sup>a</sup> | 0.22<sup>a</sup> | 0.09<sup>a</sup> | 0.08<sup>a</sup> | 0.18<sup>a</sup> |
| Propionate, mM/100 mM | -0.004<sup>a</sup> | -0.08<sup>a</sup> | -0.09<sup>a</sup> | -0.27<sup>a</sup> | 0.02<sup>a</sup> | 0.04<sup>a</sup> | -0.10<sup>a</sup> |
| Rumen pH | 0.34<sup>a</sup> | 0.41<sup>a</sup> | 0.36<sup>a</sup> | 0.24<sup>a</sup> | 0.41<sup>a</sup> | 0.38<sup>a</sup> | 0.52<sup>a</sup> |
| Milk fat, % | 0.16<sup>a</sup> | 0.22<sup>a</sup> | 0.20<sup>a</sup> | 0.18<sup>a</sup> | 0.21<sup>a</sup> | 0.18<sup>a</sup> | 0.29<sup>a</sup> |

Correlation coefficients were significant at **p < 0.01 (>0.40 or < -0.40) and *p < 0.05 (>0.33 or < -0.33).

uNDF<sub>30</sub> and uNDF<sub>288</sub> were NDF residues after 30- and 288-h in situ incubation, respectively.

peuNDF<sub>288 > 8</sub> and peuNDF<sub>30 > 8</sub> = physically effective uNDF<sub>30</sub> and uNDF<sub>288</sub> determined as uNDF<sub>30</sub> and uNDF<sub>288</sub> content (DM basis) multiplied by peNDF<sub>8</sub> (Grant et al. 2018).

DMI: dry matter intake; NDF: neutral detergent fiber; peNDF<sub>8</sub>: physically effective NDF calculated as the multiplication of dietary NDF content (% DM) by peNDF<sub>8</sub> which is physical effectiveness factor calculated by determining the DM proportion of particles on 19- and 8-mm sieves.

**Correlation coefficients**

Table 7 lists correlation coefficients between the intake of some fibre fractions (expressed as NDF, uNDF, peNDF and peuNDF) with some animal bio-responses including chewing patterns, particle sorting, ruminal acetate, propionate, and pH and milk fat percentage. An unexpected, strong and negative correlation was observed between rumination and total chewing activities (expressed as min/kg DM) and almost all diet physical characteristics (r = -0.41 to -0.61). Sorting index of the 8-mm particles had a positive and moderate correlation with the intake of NDF, uNDF<sub>30</sub>, peNDF<sub>8</sub> and peuNDF<sub>288 > 8</sub>. Ruminal pH had similar correlations with those fibre fractions but with a slightly greater correlation coefficient. Intake of peuNDF<sub>288 > 8</sub> had the greatest correlation with most of animal bio-responses like chewing (r = -0.60), sorting of 8-mm particles (r = 0.42) and rumen pH (r = 0.52).

**Discussion**

Past studies identified the variable responses in dairy cow performance (particularly high-producing cows) when substitution of CS (high vs. low cell-wall hybrids) occurred on a NDF basis, most likely because of variation in NDF digestibility (Oba and Allen 2000; Ivan et al. 2005). Dairy cow studies have identified a link between uNDF<sub>30</sub> and fibre digestibility, digestion rate of potentially digestible NDF, as well as feed intake...
and productivity (Oba and Allen 1999; Lopes et al. 2015; Nair et al. 2016). Accordingly, Kahyani et al. (2019b) proposed that formulation of dairy rations on a similar uNDF30 basis was a successful nutritional strategy for the replacement of higher-quality forages (CS or AH) with low-quality forage (WS). The specific time point of 30 h is presumed to closely represent the feed retention time in the rumen (Jones and Siciliano-Jones 2015).

Fibre requirement is determined through achievement of gastrointestinal health and normal feeding behaviour and motility of digestive tract are two animal bio-responses for satisfaction of the requirement (Plaizier et al. 2018). As previously stated, uNDF30 has a close relationship with the amount of forage retention in the rumen (Jones and Siciliano-Jones 2015), and it has the potential to induce rumination activity. In this regard, uNDF30 and forage particle size, as important nature of physical characteristics, could have some expected common role to affect animal behaviour (eating, sorting and rumination), whereby influencing animal health and performance. This study is one of the first attempts to quantify the effect of balancing of uNDF30 in different forage types on animal feeding behaviour and rumen fermentation.

**Diurnal feed intake patterns, particle intake and sorting behaviour**

The daily pattern of feed intake within the first 6 h after feed delivery was not different among treatments, thereafter (6–24 h) cows in WSAH group consumed the lowest amount of feed DM compared with CSAH or WSCS diet. In spite of similar uNDF30 feeding WSAH diet resulted in a greater consumption of uNDF288 (2.64 kg/d) than other diets, which is known to contribute to rumen fill limitations and thus restriction of feed intake later in day (Cotanch et al. 2014; Mertens 2016). This result is in agreement with our finding suggesting a lower daily meal number of cows fed with WSAH diet. Miller et al. (2020) identified that CS with greater uNDF240 concentration (conventional vs. brown midrib-3 CS) was associated with rumen fill, feed intake reduction and less milk production in Holstein cows. The interesting point of this study was that despite the fine particle size and lowest peNDF concentration of WSAH diet, feed intake was lowest at the end of the day in this diet, indicating that the lower fibre digestibility (i.e. greater uNDF288) may overshadow the reported effect of particle size on feed intake (Nasrollahi et al. 2015).

A reduction in sorting against long particles (8 and 19 mm) was observed when WS was substituted for CS and AH, which was along with a greater intake of those particles as well as greater intake of peNDF8. Consistent with our finding, Kahyani et al. (2019b) also observed a similar pattern in sorting activity when WS incrementally supplied uNDF30 (0–100%) and replaced for CS and AH in iso-uNDF30 diets. Sorting against long particles is a typical behaviour of dairy cows and occurs to a greater extent when low-quality forages with longer particle size are present in the diet (Suarez-Mena et al. 2013; Miller-Cushon and DeVries 2017). Fine chopping has been proposed to minimise sorting against long forage particles (Nasrollahi et al. 2014), particularly when poorly digestible forages are added to the ration (Coon et al. 2018). Accordingly, Coon et al. (2018) reported that the dietary inclusion of smaller-sized WS (9% of ration DM; chopped using 2.54 vs. 5.08-cm screen) resulted in less sorting against long particles, most likely due to increased diet uniformity. Zebeli et al. (2012) discussed that the moderate particle-size reduction of forage improved fibre degradation and ration uniformity, which resulted in less sorting and better diurnal distribution of peNDF consumption, minimising the risk of rumen disorders. Increased sorting against long particles (physically effective fraction) is known to contribute to less stable ruminal fermentation and, possibly a decline of rumen pH (DeVries et al. 2008; Nasrollahi et al. 2021). It is in line with the observation of this study on lower propionate in WS-containing diets than CASH (control) diet. In our companion article, we also observed a greater ruminal pH in WS-containing diets than control (5.74 vs. 6.13), which could be interpreted as another indication of a more stable rumen fermentation in WS-containing diets (Kahyani et al. 2019a). Therefore, in forage replacement strategies, to achieve dairy cow at the optimum nutritional condition, in addition to balancing for uNDF30, diet particle size and a minimum intake of moderate length particles (i.e. 8 mm) must also be taken into account.

One key point in this study that has received less attention in other studies is that it attempted to balance the diets to have a similar moisture level, with the purpose of minimising the confounding factors affecting feed-sorting behaviour. In the current experiment, WS was reconstituted with water to achieve a DM content of 25%, which causes WS particles to adhere to the other feed particles, minimising feed-sorting behaviour (Teimouri Yansari and Primohammad 2009; Kahyani et al. 2019a). Several studies have identified moisture level as a dietary...
factor affecting feed sorting behaviour in dairy cows (Leonardi et al. 2005; Fish and DeVries 2012; Kronqvist et al. 2021). More recently, Denißen et al. (2021) reported that the reduction in DM content of dairy cow TMR below 42% by water addition resulted in diminishment of feed selection against coarse particles.

**Chewing patterns**

Generally, meal patterns and chewing activity were not affected by different forage types balanced for the amount of uNDF30. The only exception was that WS-containing diets induced a marginally lower eating time than control diet (276 vs. 241 min/d), which might be due to the greater density of WS-containing diets, which originates from their greater concentrate proportion (60 vs. 67% of diet; Kahyani et al. 2019a). Previous studies also reported a similar result of chewing activity even when WS was included in dairy cow diet in replacement to alfalfa and CS on NDF basis (Farmer et al. 2014; Omidi-Mirzaee et al. 1970).

Differences in diet particle size and peNDF intake among experimental cows did not influence rumination activity, which was an unexpected finding because greater diet particle size and peNDF intake are among the known factors controlling rumination activity in dairy cows (Mertens 1997; Nasrollahi et al. 2016). A summary of data from several dairy cow studies revealed a significant variation in chewing time as a function of kilogram of NDF (ranging from 111 to 209 min/kg of NDF; Mertens 1997). The lack of difference in chewing response when expressed per kilogram of NDF is possibly suggestive of the sensitivity of the chewing response to the chemical property of NDF fraction originating from forage sources. This may indicate that in certain range of particle size, the physicochemical properties of forage (i.e. uNDF) are more important than forage particle size, confirming our initial hypothesis that diets containing various forages but supplying a similar level of uNDF30 will provide similar rumination response.

In spite of having a coarser particle size and inducing a lower sorting against long particles (19 and 8 mm), which resulted in greater peNDF intake, WS-containing diets did not affect rumination activity and even caused a lower eating time. In addition, WS-containing diets contained a higher level of beet pulp (to balanced digestible NDF; Kahyani et al. 2019a), and because of the reconstitution of both beet pulp and WS, it is possible that a portion of the larger particle size of WS-containing diets is due to small particles of beet pulp adhering to WS particles. The beet pulp particles may not be as effective as WS particles to motivate rumination. Excluding that adhering effect, as WS particles per se had a greater particle of 8 mm than the average of AH and CS (56.0 vs. 44.9%; Kahyani et al. 2019a), still more chewing activity would be expected by feeding WS-containing diets. In the present experiment, WS-containing diets had a greater concentrate level than control diet (67 vs. 60% of diet); although we did not measure the density of diets, it is generally accepted that concentrate portion has a greater density and lower volume than forages (Macleod et al. 1983; Waldo 1986; Giger-Reverdin 2000). The lower bulk volume (or greater density) of diet is apparently responsible for a lower chewing activity for cows fed WS-containing diets than control diet, which agrees with previous reports that compared WS and conventional forages on a NDF basis (Farmer et al. 2014; Omidi-Mirzaee et al. 1970).

Overall, cows in this study exhibited minimal variations in chewing behaviour despite consuming different forage types, and they spent an average of 709 min/d for total chewing. The chewing behaviour is critical to maintain normal rumen fermentation and health, and ultimately the overall metabolic and lactational response of high-producing cows (Beauchemin 2018; Grant and Ferraretto 2018). The findings of this study add to the evidence for our companion publication, which reported that milk production was not different among cows fed diets containing different forages but formulated to provide a similar level of uNDF30 (Kahyani et al. 2019a).

**Ruminal fermentation**

Lower molar concentration of propionate in the WSAH-fed cows could possibly be explained by the higher uNDF288 intake (Table 2), which provides a lower proportion of rumen fermentable carbohydrate (Smith 2019; Miller et al. 2021). In support, Smith (2019) reported a lower proportion of propionate in cows consuming higher uNDF240 (2.40 vs. 3.0 kg/d). Furthermore, cows offered WSAH diet consumed the lowest amount of starch (6.45 kg/d). Starch fermentation in the rumen results in propionate production (Grant and Ferraretto 2018; Smith 2021). Acetate-to-propionate ratio was similar across experimental diets, averaging 3.13, which is higher than the threshold of 2.78, assumed to reflect normal ruminal fermentation (Slater et al. 2000). This is also in accordance with our data in the companion article (Kahyani et al. 2019a) reporting a lack of treatment difference on milk fat percentage (2.99% on average) and fat-to-protein ratio
Therefore, rumen fermentation data can also support the satisfactory replacement of the forages in iso-uNDF\textsubscript{30} diets. Compared with control diet, WS-containing diets had a lower propionate concentration in the rumen, which is consistent with the higher peNDF intake in these treatments. It is also in agreement with the data of rumen pH that have been presented in the companion article (5.74 vs. 6.13 in control vs. WS-containing diets; Kahyani et al. 2019a).

A higher rumen ammonia-nitrogen concentration in WSAH- vs. WSCS-fed cows suggests that a combination of WS and CS rather than WS and AH was superior in providing a better synchronisation of energy and nitrogen for microbial protein synthesis. Increased ammonia-nitrogen concentration in WSAH-fed cows could be linked to an imbalance of rumen fermentable starch and protein. Compared with AH, CS contained a greater amount of starch (Kahyani et al. 2019a), resulting in greater starch intake in WSCS diet. This starch is also immature and highly fermentable in the rumen (Jensen et al. 2005), and possibly a main factor responsible for synchronisation of energy and protein utilisation, which is associated with less ammonia formation in the rumen of cows fed WSCS diet. Eastridge et al. (2009) identified that lactating cows consuming diets containing straw but balanced to supply similar non-fibrous carbohydrates did not exhibit any difference in nitrogen efficiency (i.e. milk urea nitrogen or milk protein).

**Concept of peuNDF**

Both peNDF and uNDF are functional fibre fractions that promote rumination activity, allowing ruminal fermentation to function optimally, regardless of dietary forage level (Grant et al. 2018). Thus, peuNDF integrates both physical (peNDF) and chemical nature (uNDF) of the fibre fraction, and has recently received increased attention in dairy cow studies (Grant et al. 2020; Miller et al. 2021; Serva et al. 2021). The peuNDF metric quantifies the proportion of uNDF in the physically effective fraction, which could be chewed and subjected to particle-size reduction (Smith 2019). The correlation analysis in this study revealed that among the dietary physical characteristics, peuNDF\textsubscript{288 > 8} intake had the strongest correlation with the majority of animal bio-responses (sorting, chewing, rumen pH and milk fat). This may indicate the incremental role of uNDF-to-peNDF on supporting animal health and performance, and might be recommended to adjust diet physical characteristics with chemical concept of diet digestibility.

**Conclusions**

Replacing WS with high-quality forages had negligible effect on chewing patterns and ruminal fermentation when the uNDF\textsubscript{30} level in dairy rations remained constant, supporting our initial hypothesis. Generally, sorting against large and medium-sized particles was lesser in diets containing WS, which possibly contributed to normal ruminal fermentation. To achieve the results of this study, it is essential to follow the conditions provided such as using a finely chopped and reconstituted WS, balancing for digestible NDF, in addition to uNDF\textsubscript{30} concentration of diets. Intake of peuNDF, calculated by integration of peNDF and uNDF, was highly correlated with chewing, long particle intake, and rumen pH.

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**Ethical approval**

The experimental protocols were approved by the Institutional Animal Care Committee for Animals Used in Research. The guidelines of Iranian Council for Animal Care (1995) were followed when caring for animals.

**Disclosure statement**

The authors declare that they have no competing interest.

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**Data availability statement**

The data that support the findings of this study are available from the corresponding author, [A. Kahyani], upon reasonable request.

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