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Dry period length affects rumen adaptation in dairy cattle precalving and during the first weeks after calving

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ABSTRACT

Omitting or shortening the dry period may result in a fairly constant ration throughout the transition period of dairy cows, reducing the need for adaptation of cow metabolism and rumen function to a new lactation. The objective of this study was to determine the effect of dry period length on rumen adaptation and cow metabolic state during the transition period. Twelve pregnant, rumen-cannulated Holstein Friesian dairy cows at the end of their first lactation were assigned to one of 3 treatments: a conventional (60 d), short (30 d) or no dry period (0 d). At dry-off, cows received a dry cow ration until calving. Lactating cows received a lactation ration. Cows were monitored from 8 wk before calving until 8 wk after calving for milk yield and dry matter intake (DMI). Rumen biopsies were taken from 3 locations in the rumen at 60, 40 and 10 d before calving and 3, 7, 14, 28 and 56 d after calving to assess papillae dimensions. Blood was sampled weekly from 3 wk before until 8 wk after calving, and liver biopsies were taken at wk −2, wk 2 and wk 4 relative to calving. Prepartum, DMI and milk yield were greater for cows with a short or no dry period, compared with cows with a conventional dry period. Postpartum, DMI was greater for cows with a short dry period compared with cows with a conventional dry period. Plasma glucose concentration was greater for cows without a dry period, compared with the other dry period lengths postpartum. Plasma concentrations of nonesterified fatty acids and β-hydroxybutyrate, and liver triglyceride content, did not differ among dry period. Rumen papillae differed in size based on biopsy location, but there was no interaction between biopsy location and the effect of dry period length. Rumen papillae surface area for cows managed for a 30 d or 60 d dry period decreased toward calving. At 40 d prepartum, papillae surface area was greater for short and no dry period treatment compared with a conventional dry period. At 10 d prepartum, papillae surface area was greater for the no dry period treatment compared with both other treatments, and this difference was still present 3 d postpartum. Cows managed for a short dry period showed faster increase in papillae dimensions after calving compared with cows managed for a conventional dry period. From d 28 onwards, no differences in papillae surface area were observed. The faster rumen adaptation postpartum may be related to the increased DMI during the first weeks postpartum for cows managed for a short dry period. However, this did not result in improved metabolic status or milk yield. The results from the present study demonstrate that the dietary changes related to a conventional dry period length affected rumen papillae development, not only prepartum but also early postpartum. Further optimization of dry period length as well as dietary composition throughout the transition period may support cows in their adaptation to a new lactation.
Key Words: dairy cow, dry period length, rumen adaptation, transition period, metabolic status

INTRODUCTION

In the transition period around calving, the cow's physiological status changes dramatically which coincides with, among others, housing and dietary changes (Ingvartsen, 2006; Van Knegsel et al., 2014). High-yielding dairy cows require a large adaptive capacity to cope with the transition from late gestation to early lactation. In case this adaptation fails and feed intake decreases, the energy balance (**EB**) postpartum may become more negative, which is associated with a greater incidence of diseases such as mastitis, displaced

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abomasum, ketosis and hepatic lipidosis (Collard et al., 2000). Nutrition plays a key role in a successful transition from gestation to lactation in dairy cattle. This notion is illustrated by the well-known negative effect of excessive energy intake during the dry period on the cow's health after calving (Janovick et al., 2011). To prevent excessive energy intake during the dry period, dry cows are commonly fed diets with a low energy density. In contrast, a high energy density of the diet is required after calving to meet the cow's energy requirements related with the onset of milk production. Thus, dairy cows are subjected to dietary, housing and physiological changes around calving and the adaptation process around these changes is crucial for cow health and fertility in early lactation (Zebeli et al., 2015).

The dietary changes during the transition period require a large adaptive capacity of the rumen wall including rumen papillae and its epithelial layer (Steele et al., 2015). A main factor driving the proliferation of rumen papillae is rumen fermentable organic matter (**fOM**) intake (Dirksen et al., 1985; Dieho et al., 2016a). When fOM intake is low during the dry period, rumen papillae regress (Dieho et al., 2016a), whereas greater fOM intake by supplemental concentrate during the dry period increased papillae surface area (Dieho et al., 2017a). Total rumen papillae surface area is considered an important factor in rumen performance as it may directly be related to the capacity for VFA absorption. The evidence for a positive relationship between papillae surface area and VFA absorption capacity is ambiguous though (Bannink et al., 2008; Martens et al., 2012; Dieho et al., 2016a; Dieho et al., 2016b). To avoid significant regression of rumen papillae, total fOM intake should remain relatively high during the last weeks before calving. Continuation of milk production before calving may maintain such a fairly constant papillae surface area, due to limited dietary changes and a relatively high fOM intake to support milk production. In an earlier study, a short dry period (i.e., 35 d) tended to result in a higher ruminal pH and lower concentration of total VFA before calving and higher concentration of VFA after calving, compared with a conventional dry period (Jolicoeur et al., 2014).

Limited knowledge is available concerning the dynamics of rumen papillae size during the transition period for cows with and without a dry period. Therefore, the objective of the current study was to monitor the regression and subsequent proliferation of the rumen papillae of dairy cows from 60 d before calving until 56 d after calving with either a conventional 60 d dry period, a short dry period of 30 d, or a complete omission of the dry period. We hypothesized that omitting or shortening the dry period compared with a conventional dry period, induces a smaller decline in rumen papillae surface area prepartum, and results in greater rumen papillae surface area in the first weeks postpartum.

MATERIALS AND METHODS

Animals and Treatments

All experimental protocols and interventions were approved by the Ethical Committee on Animal Experiments of the Animal Sciences Group of Wageningen University & Research, Wageningen, The Netherlands (experimental protocol 2010026). The sample size required to detect a difference of 1.5 mm papilla length at $\alpha = 0.05$ and $\beta = 0.80$ was determined based on the results of a pilot study, exploring the effect of concentrate allowance in the periparturient period (Bannink et al., 2005). Twelve rumen-cannulated Holstein dairy cows were selected at the end of their first lactation from the Dairy Campus Research herd (Wageningen Livestock Research, Lelystad, the Netherlands). Cows were blocked in 4 groups of 3 animals, based on similarity in the 305 d milk production during the first lactation. Cows from each block were randomly assigned to one of 3 treatment groups through a random drawing process with options labeled as 1, 2 or 3. The treatment groups varied in dry period length: a conventional dry period (**CON**) of 60 d, a short dry period (**SHORT**) of 30 d or no dry period (**NODRY**) with continuous milking. All cows were monitored from 60 d before their expected calving date until 8 wk postpartum. Our study was part of a larger trial with 168 cows subjected to the same 3 treatments, monitored over 2 full lactations between 2010 and 2014 (Van Knegsel et al., 2014). All animals were housed in a cubicle shed in separate dry cow and post-calving groups. On the day of calving, cows were separated from the dry cow group and housed in a straw bedded calving pen. After calving, the cows were moved to the post-calving group. Cows were milked twice daily (around 0500 and 1630 h). The drying-off protocol for cows allocated to the groups CON or SHORT started 7 d before actual drying-off with a transition to the dry-cow ration (rations are described in Tables 1 and 2). Four days before drying-off, the milking frequency was reduced to once daily.

Rations and Feeding Management

All cows had unrestricted access to fresh drinking water. Rations and feeding management are described by Van Knegsel et al. (2014). In short, 3 forage mixtures were fed: 2 prepartum rations, viz. one for lactating cows and one for dry cows, and a postpartum ration for all lactating animals. Forage mixtures were supplied ad libitum in feed weighing troughs with indi-

Table 1. Average intake of compound concentrate as well as ingredients, chemical composition and feeding value of concentrates

Item	Concentrate A *fed in the barn*	Concentrate B *fed in the milking parlor*
Average intake (kg/d)		
Precalving, all cows[1]	1.0	—
Precalving, lactating cows[1]	—	1.0
Postcalving[2]	8.5	1.0
Ingredient (%)		
Corn	53.5	30.3
Palm kernel, expeller	—	22.4
Rapeseed meal	10.9	18.3
Soybean meal	9.1	2.5
Citrus pulp	—	10.0
Sugar beet pulp	7.4	—
Molasses	5.8	5.0
Wheat middlings	3.8	—
Rapeseed meal, formaldehyde treated	3.1	1.2
Soybean meal, formaldehyde treated	2.5	4.3
Vinasses	—	2.3
Wheat	—	0.9
Palm oil	0.1	0.2
Calcium carbonate	1.9	0.7
Sodium chloride	0.9	0.5
Magnesium oxide	0.8	0.5
Urea	—	0.6
Mineral-vitamin mixture[3]	0.2	0.3
Chemical composition (g/kg)		
DM	873	881
Crude protein	158	186
Crude fat	29	43
NDF	155	246
ADF	68	143
Starch	365	222
Sugars	68	82
Ash	70	59
Feeding value (g/kg)		
DVE[4]	106	110
OEB[5]	11	27
fOM[6]	457	480
NE_L (MJ/kg)[7]	6.78	6.77

[1]Prepartum, all cows (dry and lactating) received 1.0 kg/d of concentrate A in individual concentrate feeder in the barn, from 10 d before expected calving date. All lactating cows received 1.0 kg/d of concentrate B during milking in the milking parlor.

[2]Postpartum, concentrate A allowance in individual concentrate feeder was gradually increased for all cows from 1.0 kg/d on the day of calving, to 8.5 kg/d on d 17 postpartum.

[3]Premix 2016 (Pre-Mervo UA Cooperatie, Utrecht, the Netherlands).

[4]Intestinal digestible protein (Tamminga et al., 1994).

[5]Rumen degraded protein balance (Tamminga et al., 1994).

[6]Fermentable organic matter.

[7]Net energy for lactation calculated with the Dutch net energy evaluation (VEM) system (Van Es, 1975).

vidual transponder-controlled access gates (Roughage Intake Control system, Hokofarm Group, Marknesse, The Netherlands). The stocking density was 2 cows per trough. For each visit of a cow to a feed trough, the start and end time of the visit, as well as the start and end weight of the trough, were recorded. Daily, between 1030 and 1100 h, feed refusals were removed from the troughs and fresh forage mixture was supplied. All cows in the current study were supplemented with a glucogenic concentrate (concentrate A) (Table 1). Concentrate A was fed individually using transponder-controlled concentrate dispensers starting with 1.0 kg/d from 10 d before the expected calving date. The amount supplied was gradually increased from the day of calving up to 8.5 kg/d at d 17 after calving. The maximum level of concentrate A was maintained from d 17 until the end of the experimental period at d 56. Additionally, cows received 0.5 kg of standard concentrate B at each milking in the milking parlor (1 kg per day during lactation). The chemical composition of the different rations pre- and postcalving based on the realized total feed intake is presented in Table 2. To

calculate DMI, all forage mixtures were sampled daily. The DM concentration was determined by oven drying at 104°C during 36 h. The daily DMI of each cow was calculated by multiplying the daily fresh feed intake with the DM concentration.

Each separate ingredient of the forage mixtures as well as compound concentrates were sampled weekly and stored at −20°C until chemical analyses. Before analyses (BLGG AgroXpertus BV, Oosterbeek, the Netherlands), forage samples were pooled per batch. Briefly, crude fat concentration was determined gravimetrically as the ether extract (ISO, 1999) and crude ash content after incineration at 550°C (ISO, 2002). Concentrations of NDF and ADF were determined according to Van Soest et al. (1991) and expressed without residual ash, crude protein was calculated as 6.25 × N-Kjeldahl (ISO, 2005) and sugar concentrations were determined as described by Van Vuuren et al. (1993). Starch was released by heating in a boiling water bath in the presence of 2 N HCl (Cone, 1991) after which starch concentration was determined using the amyloglucosidase method (ISO, 2004). The values of NE_L, intestinal digestible protein (DVE), rumen degradable protein balance (OEB) and fOM were calculated from the chemical composition and according to the guidelines of the Central Bureau for Livestock Feeding (CVB, 2021).

Milk Yield and Milk Composition

Milk weights were recorded automatically at each milking. Weekly, milk samples of each cow were taken at 4 consecutive milkings (2 morning and 2 afternoon milkings). Both morning milk samples were pooled to 1 composite sample; afternoon milk samples were processed likewise. The composite morning and afternoon milk samples were analyzed for fat, protein, and lactose concentration (ISO, 2013; Qlip Zutphen, the Netherlands), using a Foss MilkoScan infrared automatic analyzer (Foss Electric, Hillerød, Denmark). Weighed means were calculated from the recorded morning and afternoon milk weights and the analyses of the composite morning and afternoon milk samples.

BW, BCS and EB

The precalving BW was recorded weekly at the same time of day. For lactating cows, BW was automatically recorded twice per day when cows left the milking parlor and averaged per week. Every 4 wk, cows were scored

Table 2. Ingredient, chemical composition and feeding value (g/kg of DM, unless otherwise stated) of prepartum and postpartum rations based on realized average feed intake

	Prepartum		Postpartum
	Dry cow diet	Lactation diet	Lactation diet
Ingredient			
Wilted grass silage	358	464	335
Corn silage	172	301	218
Soybean meal	—	60	44
Rapeseed meal	106	77	55
Wheat straw	344	22	16
Rapeseed straw	—	11	8
Mineral and vitamin premix	10	11	8
Concentrate A	10	5	277
Concentrate B	—	49	39
Chemical composition			
DM (g/kg of product)	587	487	556
Crude protein	115	157	163
Crude fat	25	33	33
NDF	531	392	333
ADF	320	227	186
Starch	68	126	206
Sugars	73	92	88
Ash	86	86	84
Feeding value			
DVE[1]	45	77	89
OEB[2]	10	25	21
fOM[3]	463	552	544
NE_L[4] (MJ/kg of DM)	5.24	6.45	6.82

[1]Intestinal digestible protein (Tamminga et al., 1994).

[2]Rumen degraded protein balance (Tamminga et al., 1994).

[3]Fermentable organic matter.

[4]Net energy for lactation calculated with the Dutch net energy evaluation (VEM) system (Van Es, 1975).

for body condition from 1 (thin) to 5 (fat) according to Ferguson et al. (1994). Energy balance was calculated according to the VEM system (Van Es, 1975; CVB, 2021) as the difference between NE_L intake with feed and the NE_L required for gestation, maintenance and milk production and 1,000 VEM = 6.9 MJ of net energy. Regarding the NE_L for gestation, 1500 VEM/d is required in the 8th month and 2700 VEM/d for the 9th month of gestation. Animal maintenance requirements are 42.4 VEM/ $kg^{0.75}$·d and requirements for milk production are 442 VEM/kg of fat and protein-corrected milk (**FPCM**), which is calculated as milk yield × (0.337 + 0.116 × milk fat % + 0.06 × milk protein %) as described by Van Es (1975).

Rumen Sampling

Rumen morphology was further investigated on d-60, d-40 and d-10 relative to the expected calving date, and on d3, d7, d14, d28 and d56 after calving. Each time, the rumen content was evacuated completely and stored in an insulated tub, covered to prevent cooling until return into the rumen. Biopsies were taken at 3 locations: the right dorsal sac, directly opposite of the rumen cannula, cranially of the dorsal coronary groove; the right wall of the caudodorsal blind sac; and the ventral wall of the caudoventral blind sac. At each location, 5–15 papillae were harvested from the rumen wall by pulling them at their base using forceps (No. 631319, Stuemer, Würzburg, Germany). Papillae damaged by the biopsy procedure were easily recognized as damaged papillae, as they showed distinctive circular cut marks, and excluded. Other papillae were gently rinsed in 0.9% NaCl solution before placing them on a clean paper tissue to measure physical dimensions (height and width). Papillae were photographed using a digital camera (Canon IXUS 130, Canon Inc., Tokyo, Japan), including a ruler in each photograph. Papilla length was measured from the tip to the base of the papilla along its axis, papilla width was measured halfway of and perpendicular to the papilla length. Rumen papilla surface area was calculated as 2 × papillae height × papillae width (Dieho et al., 2016a).

Blood Collection and Liver Biopsies

To determine the metabolic status during the transition period, blood samples and liver biopsies were taken, analyzed as described by Chen et al. (2015). In short, blood was taken weekly from wk −3 relative to expected calving date until wk 8 postpartum, decanted, aliquoted and frozen at −20°C until analysis. Plasma was analyzed for glucose content using commercial kit no. 61269 (BioMérieux, Marcy l'Etoile, France), NEFA and BHB concentrations were measured enzymatically using kits no. 994–75409 (Wako Chemicals, Neuss, Germany) and RB1007 (Randox, Ibach, Switzerland) and insulin was measured using a radioimmunoassay (RIA) with a homologous double-antibody system using bovine insulin (25.7 IU/mg; Sigma, St. Louis, MO) for standards and for iodination and guinea-pig anti-bovine insulin as described by Vicari et al. (2008). Liver biopsies were performed in wk −2, wk 2, and wk 4 relative to calving as described by Chen et al. (2015). In short, the biopsy site was clipped, disinfected and locally anesthetized with 7 mL of lidocaine-HCl 2% with adrenaline (Alfasan Nederland B.V., Woerden, the Netherlands). Liver TG was extracted using 0.5 mol/L of KOH in ethanol for 30 min at 70°C, and then 2.5 mol/L of perchloric acid was added to neutralize the mixture. Concentration of TG was determined through enzymatic colorimetric analysis (Triacylglycerols LiquiColor Mono kit, Human Gesellschaft for Biochemica und Diagnostica mbH, Wiesbaden, Germany).

Statistical Analysis

Daily feed intake, milk yield, BW and EB were averaged per cow per week relative to calving. Precalving data were available for all cows from d-59 relative to actual calving date. All plasma metabolites were normally distributed by the Shapiro–Wilk test, except for BHB. Plasma BHB concentrations were $\log_e$ transformed before statistical analysis to obtain normal distribution.

Data was analyzed separately for the pre- and postpartum period (except for liver TG content) by mixed model analysis using the REML procedure in Genstat 19th edition (2018). The model structure for all measures, except papillae characteristics, was:

$$Y_{ijk} = \mu + B_i + DP_j + T_k + DP_j \times T_k + \varepsilon_{ijk}$$

where Y_{ijk} = dependent variable; μ = overall mean; B_i = effect of block (1 to 4); DP_j = effect of dry period management (CON, SHORT or NODRY); T_k = effect of time (prepartum wk −8 to −1; postpartum wk 1 to 8); $DP_j \times T_k$ = interaction between treatment and time; and ε_{ijk} = residual error. Cow was considered as the repeated effect.

For papillae characteristics, the model structure was:

$$Y_{ijkl} = \mu + B_i + S_j + DP_k + T_l + DP_k \times T_l + \varepsilon_{ijkl}$$

where Y_{ijkl} = dependent variable; μ = overall mean; B_i = effect of blocks (1 to 4); S_j = effect of rumen site (right dorsal sac, caudodorsal blind sac, caudoventral blind sac); DP_j = effect of dry period management

(CON, SHORT or NODRY); T_k = effect of time (prepartum −60, −40 or −10 d; postpartum 3, 7, 14, 21, 28 or 56 d); $DP_j \times T_k$ = interaction between treatment and time; and ε_{ijk} = residual error. Cow was considered as the repeated effect. The necessity of an auto-regressive function as well as heterogeneity were tested and judged by the difference in deviance of each model with the change in degrees of freedom in a chi-squared distribution. Auto-regressive function improved model deviance of all parameters; heterogeneity was not relevant for most parameters, but for some parameters outside the model. Significance of effect was declared at $P < 0.05$ and trends at $0.05 \leq P < 0.10$.

RESULTS

Actual dry period length was 59.3 d (±4.6 d) for group CON and 26.5 d (±4.9 d) for group SHORT. In group NODRY, one cow dried off naturally 4 d before calving; others were milked until calving as planned. Two cows in group NODRY encountered mastitis post-calving, and milk yield was affected for one cow during wk 7 and wk 8; data of this cow were therefore taken into account until wk 6.

Feed Intake

Before calving, the experimental treatments resulted in different DM and fOM intake, with the level of these differences depending on week before calving as indicated by a significant interaction between dry period length and week before calving (Figure 1; Table 3). After calving, daily DMI and fOM were on average 2.5 and 1.4 kg/d higher, respectively, for cows with a short dry period length compared with cows with a conventional dry period, but without significant differences compared with no dry period. When DMI and fOM were expressed as a proportion of BW, treatment differences showed to be most important in early lactation (DP × wk interaction; Table 3).

Milk Production and EB

As intended by the imposed treatments, before calving, the greatest milk and FPCM yield was observed for cows without dry period and lowest for cows with a conventional dry period, with cows on a short dry period in between (Table 3); the level of this effect was dependent on week relative to calving as indicated by significant interaction between both factors. After calving, dry period length did not affect average milk yield, but FPCM was 5.6 kg/d lower for group NODRY compared with group SHORT. Milk protein content was greater, and milk fat content tended to be greater, in cows without dry period compared with cows with a conventional dry period.

Prepartum, BW was affected by an interaction between dry period length and week relative to calving ($P = 0.015$) based on a relatively lower BW of the cows with a conventional dry period at the start of the ex-

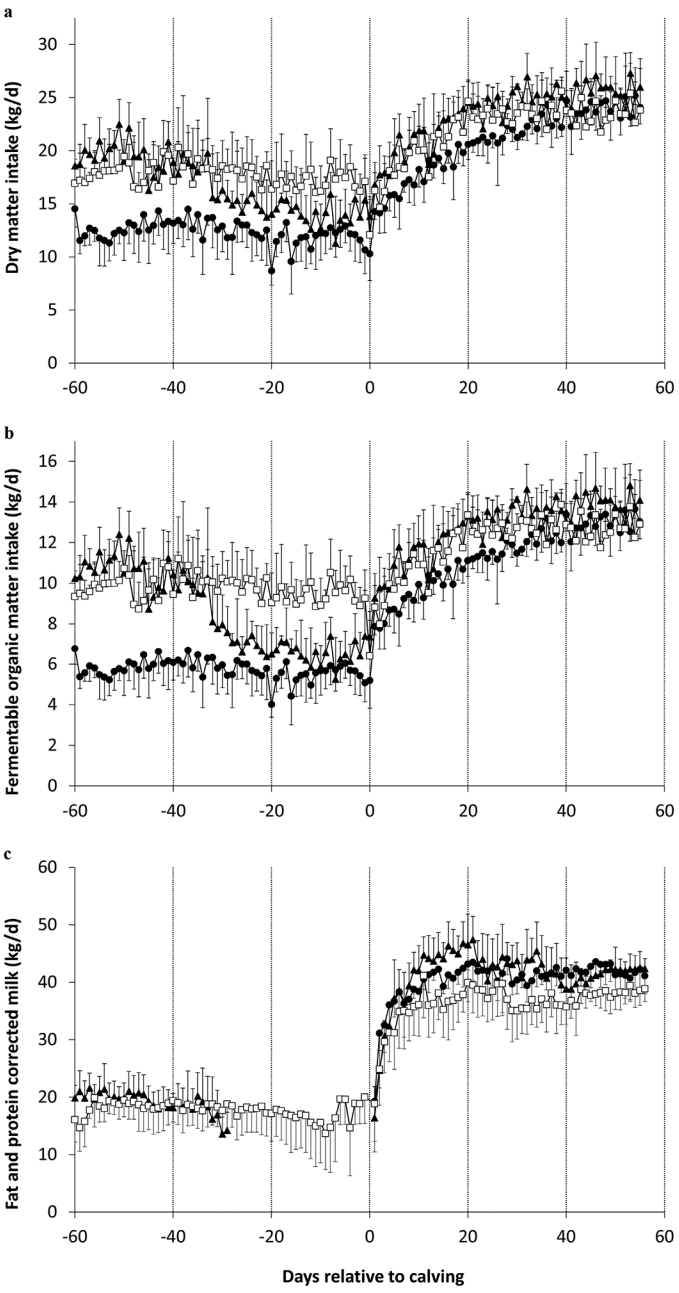

Figure 1. Average daily dry matter intake (a), fermentable organic matter intake (b) and fat- and protein correct milk (c) in kg/d for cows on a 60 d dry period (CON, black circles), 30 d dry period (SHORT, black triangles) or no dry period (NODRY, open squares) relative to the day of calving. Whiskers display the standard deviation of each group at each time point.

Table 3. Dry matter intake (DMI), fermentable organic matter (fOM) intake, milk yield, fat- and protein corrected milk (FPCM), milk components, body weight (BW), body condition score (BCS) and calculated net energy balance (EB) in the prepartum and postpartum period of cows with a dry period length of 60 (CON), 30 (SHORT) or 0 d (NODRY). Values represent predicted means by REML procedure

	Dry period length[1]				*P*-value[3]		
	CON	SHORT	NODRY	SED[2]	DP	Wk	DP × wk
Prepartum wk −8 to −1							
DMI (kg/d)	12.4[a]	16.7[b]	17.9[b]	1.04	0.005	<0.001	<0.001
DMI (% of BW)	1.87[a]	2.41[b]	2.68[b]	0.146	0.004	<0.001	<0.001
fOM intake (kg/d)	5.7[a]	8.5[b]	9.9[b]	0.62	0.001	<0.001	<0.001
fOM intake (% of BW)	0.86[a]	1.23[b]	1.49[c]	0.082	<0.001	<0.001	<0.001
Milk yield (kg/d)	0.0[a]	8.0[b]	15.7[c]	2.27	<0.001	<0.001	<0.001
FPCM (kg/d)	0.0[a]	9.6[b]	17.7[c]	2.44	<0.001	<0.001	<0.001
BW (kg)	663	693	669	31.6	0.618	<0.001	0.015
BCS	2.9	3.0	2.9	0.19	0.658	0.022	0.333
EB (kJ/kg$^{0.75}$·d)	66	89	21	57.2	0.204	0.097	0.219
Postpartum wk 1 to 8							
DMI (kg/d)	21.1[a]	23.6[b]	22.4[ab]	0.76	0.040	<0.001	0.184
DMI (% of BW)	3.44	3.58	3.55	0.159	0.704	<0.001	0.051
fOM intake (kg/d)	11.5	12.9	12.2	0.45	0.055	<0.001	0.152
fOM intake (% of BW)	1.87	1.95	1.93	0.089	0.701	<0.001	0.044
Milk yield (kg/d)	41.0	40.3	34.6	3.05	0.218	<0.001	0.610
FPCM (kg/d)	40.8[ab]	41.7[a]	36.1[b]	2.48	0.008	0.035	0.314
Milk fat (g/kg)	39.6	41.0	42.3	2.08	0.082	<0.001	0.054
Milk protein (g/kg)	34.2[a]	37.0[ab]	38.3[b]	1.48	<0.001	<0.001	0.825
Milk lactose (g/kg)	46.4	46.1	46.6	0.60	0.467	0.008	0.153
Fat yield (kg/d)	1.60[ab]	1.63[a]	1.43[b]	0.128	0.023	0.010	0.101
Protein yield (kg/d)	1.39	1.48	1.30	0.081	0.067	0.282	0.613
Lactose yield (kg/d)	1.92	1.87	1.62	0.145	0.218	<0.001	0.299
BW (kg)	613	661	636	36.5	0.474	0.053	0.236
BCS	2.1	2.4	2.6	0.40	0.586	<0.001	0.687
EB (kJ/kg$^{0.75}$·d)	−209[a]	−121[ab]	−12[b]	65.4	0.011	<0.001	0.410

[a-c]Means within a row with different superscripts differ ($P < 0.05$).

[1]Dry period length of 60 d (CON, conventional), 30 d (SHORT) or 0 d (NODRY).

[2]SED = standard error of differences.

[3]*P*-value for the effects of dry period length (DP), week (wk) or their interaction.

periment that became more similar to BW of the other groups nearer to calving (Figure 2). Prepartum, BCS was not affected by dry period length or interaction between dry period length and week relative to calving. After calving, neither BW nor BCS were affected by dry period length (Table 3). The calculated EB did not differ between the 3 treatments prepartum. In the postpartum period, the calculated EB was more negative for cows in group CON compared with group NODRY.

Plasma Metabolites and Liver TG

In the final 3 wk before calving, plasma NEFA concentrations were low and similar between groups (Table 4, Figure S1). Plasma BHB concentrations were higher for group NODRY compared with group CON or SHORT. Plasma glucose concentrations were greater for cows in group SHORT or NODRY compared with cows in group CON. Plasma insulin concentrations showed an interaction between dry period length and time, with low levels for the cows in CON, high levels for cows in NODRY and initially high but decreasing levels for cows in SHORT during the final 3 wk before calving (Figure S2). During the postpartum period

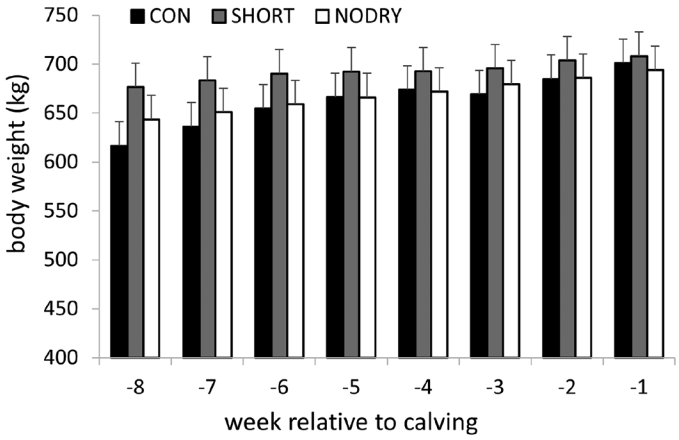

Figure 2. Average body weight precalving for cows on a 60 d dry period (CON, black bars), 30 d dry period (SHORT, gray bars) or no dry period (NODRY, open bars). Bars show predicted means by REML analysis, whiskers display the standard error of differences (SED).

Table 4. Plasma nonesterified fatty acids (NEFA), β-hydroxybutyrate (BHB), glucose and insulin and liver triacyl glycerides (TG) concentrations of cows with a dry period length of 60 (CON), 30 (SHORT) or 0 d (NODRY). Values represent predicted means by REML procedure. Plasma BHB concentrations are $\log_e$ transformed to obtain normal distribution before statistical analysis; for interpretation, back transformed results are added

	Dry period length[1]				*P*-value		
	CON	SHORT	NODRY	SED[2]	DP	wk	DP × wk
Plasma prepartum wk −3 to −1							
NEFA (mmol/L)	0.13	0.10	0.12	0.025	0.448	0.153	0.863
$\log_e$ BHB (mmol/L)	−0.98[a]	−0.93[ab]	−0.64[b]	0.136	0.057	0.305	0.267
BHB (mmol/L)	0.38	0.39	0.53				
Glucose (mmol/L)	3.42[a]	3.87[b]	3.82[b]	0.113	0.005	0.616	0.589
Insulin (μIU/mL)	15.2	21.1	20.1	4.88	0.617	<0.001	0.023
Plasma postpartum wk 1 to 3							
NEFA (mmol/L)	0.34	0.45	0.32	0.091	0.031	0.120	0.466
$\log_e$ BHB (mmol/L)	−0.74	−0.72	−0.69	0.159	0.950	0.942	0.800
BHB (mmol/L)	0.48	0.49	0.50				
Glucose (mmol/L)	3.24[a]	3.21[a]	3.57[b]	0.144	0.033	0.063	0.742
Insulin (μIU/mL)	11.5	7.0	12.8	3.38	0.249	0.372	0.651
Plasma postpartum wk 4 to 8							
NEFA (mmol/L)	0.22	0.16	0.12	0.063	0.405	0.001	0.113
$\log_e$ BHB (mmol/L)	−0.76	−0.72	−0.80	0.065	0.493	0.244	0.197
BHB (mmol/L)	0.47	0.49	0.45				
Glucose (mmol/L)	3.54[a]	3.65[ab]	3.78[b]	0.074	0.013	0.100	0.683
Insulin (μIU/mL)	12.9[a]	15.2[a]	21.8[b]	2.41	0.016	<0.001	0.004
Plasma postpartum wk 1 to 8							
NEFA (mmol/L)	0.26	0.27	0.19	0.070	0.387	<0.001	0.184
$\log_e$ BHB (mmol/L)	−0.75	−0.72	−0.75	0.087	0.903	0.556	0.482
BHB (mmol/L)	0.47	0.49	0.47				
Glucose (mmol/L)	3.43[a]	3.49[a]	3.71[b]	0.065	<0.001	<0.001	0.765
Insulin (μIU/mL)	12.3	12.2	18.5	2.56	0.075	<0.001	0.002
Liver biopsies wk −2, 2, 4							
TG (mg/g of wet weight)	27.3	25.7	17.8	8.28	0.238	0.017	0.868

[a-b]Means within a row with different superscripts differ ($P < 0.05$).

[1]Dry period length of 60 d (CON, conventional), 30 d (SHORT) or 0 d (NODRY).

[2]SED = standard error of differences.

plasma NEFA and BHB concentrations were comparable between the 3 treatment groups, except for a slightly higher NEFA level for group SHORT in the first 3 wk postcalving (Table 4). Average plasma glucose concentrations postpartum were higher for cows in NODRY, compared with cows in SHORT or CON. The effect of dry period length on plasma insulin concentrations depended on week postpartum, with low levels for the cows in CON, increasing levels for cows in SHORT from wk 4 to 8, and an even stronger increase during the same period for cows in NODRY (Figure S2). Liver TG content analyzed in wk −2, 2 and 4 relative to calving was not affected by dry period length.

Rumen papillae

An average of 8.0 (SD = 2.4) papillae per site per cow per sampling day were collected. In general, rumen papillae length and surface area differed between the 3 biopsy locations ($P < 0.001$, Figure S3). Papillae harvested from the right dorsal sac were shortest with on average 5.6 mm prepartum and 6.7 mm postpartum. Papillae from the caudoventral blind sac were longest (11.6 mm prepartum and 12.6 mm postpartum) and papillae from the caudodorsal blind sac were intermediate (7.7 mm prepartum and 9.3 mm postpartum). There was no interaction between biopsy location and the effect of dry period length in prepartum and postpartum period.

Before calving, papillae length was not affected by dry period length whereas papillae width and papillae surface area showed an interaction of dry period × day (Table 5). Cows with a dry period showed narrower papillae and a reduced papillae surface area after switching to the dry cow ration, where cows without a dry period had a relatively constant papillae width and surface area. At 40 d before the expected calving, cows in group CON had a lower papillae width and surface area than the groups with other dry period lengths. At 10 d before the expected calving date, cows in both groups CON and SHORT had a lower papillae width and surface area compared with cows in NODRY (Table 5).

After calving, papillae length, width and surface area were affected by the interaction between dry period length and day after calving (Table 6). The difference

in papillae surface area before calving was still present at 3 d postpartum: cows in NODRY had about 25 to 50% larger papillae surface area than cows in SHORT or CON (Table 6). Papillae dimensions in the NODRY group remained relatively constant, whereas papillae in the SHORT and CON group increased with day after calving. The increase in papillae surface area between d 3 and 7 was larger for cows in SHORT than in CON, reaching a papillae surface area comparable with cows in NODRY at 7 d postpartum. At 4 wk postpartum, the effect of dry period length on average papillae surface area had disappeared.

DISCUSSION

The current data indicate that shortening or omitting the dry period affects rumen papillae development not only prepartum, but also during the first 2 wk postpartum. Papillae morphology often varies between individual animals (Dieho et al., 2016a, Dieho et al., 2017a). This variation needs to be accounted for in transition trials by a repeated-measurements design (Dieho et al., 2017a). Additionally, the procedure to harvest papilla needs to be performed carefully by the same operator to prevent methodological variation. Considering the variability in papilla size on a biopsy site of an individual cow, at least 5 non-damaged papillae are required to provide a reliable average of the local papillae dimensions.

By omitting the dry period, cows received the same lactation ration throughout the transition period, not interrupted by the low-energy dry cow ration fed to cows with a shortened or conventional dry period. Prepartum papillae surface area followed the changes in fOM intake related with the differences between the dry cow and lactation ration (Figure 3). These differences in fOM intake resulted in a reduction in rumen papillae surface area for the 2 groups consuming a dry cow ration (30 d and 60 d dry period) during the final weeks before calving. Such a decline in rumen papillae surface area upon decreased fOM intake is in line with observations during the dry period by Dieho et al. (2016a). It is also in line with the decline in papillae surface area upon a reduction in NE_L intake (Dirksen et al., 1984) and upon a reduction in fOM intake during first days on fresh pasture diet compared with a total mixed ration (Schären et al., 2016). For group CON fed the dry cow ration during the entire 60 d before calving, this reduction in surface area was already apparent 40 d before calving, whereas for group SHORT cows still received the lactation ration 40 d before calving and papillae surface area at this day was not reduced compared with 60 d before calving. This absence of a decline in papillae surface area between 60 and 40 d before calving in SHORT agrees with Dieho et al. (2017a), where supplemental concentrate from 28 d before calving prevented a decline in papillae surface area between 28 and 8 d before calving. The difference in papillae surface area after a short or conventional dry period length compared with the continuously milked group was still present in the first days after calving but quickly resumed to similar values from 28 d after calving onwards.

Table 5. Main effects in rumen papillae size during the dry period as affected by dry period length (DP) of 60 (CON), 30 (SHORT) or 0 d (NODRY), by day relative to calving (day) and by the interaction between DP and day relative to calving. Values represent predicted means by REML procedure

	Dry period length[1]				*P*-value		
	CON	SHORT	NODRY	SED[2]	DP	day	DP × day
Papillae length (mm)							
d −60	8.3	8.5	8.0	0.60	0.859	0.093	0.164
d −40	8.0	8.7	9.0				
d −10	7.9	7.8	8.4				
Papillae width (mm)							
d −60	2.4^{x}	2.8^{x}	2.7	0.24	<0.001	0.521	0.001
d −40	1.9^{ay}	3.0^{bx}	2.8^{b}				
d −10	2.0^{axy}	2.3^{ay}	3.1^{b}				
Papillae surface area (mm^2)							
d −60	40.0	48.3^{xy}	46.2	6.07	0.006	0.408	0.013
d −40	31.3^{a}	54.5^{bx}	53.2^{b}				
d −10	33.8^{a}	39.0^{ay}	53.4^{b}				

[a-b]Means within a row with different superscripts show differences between treatments at the specific time point ($P < 0.05$).

[x-z]Means within a column with different superscripts show a time effect for a specific treatment ($P < 0.05$).

[1]Dry period length of 60 d (CON, conventional), 30 d (SHORT) or 0 d (NODRY).

[2]SED = standard error of differences.

Shortening the dry period relative to a conventional dry period instead of omitting the dry period subjects cows to the same rations in the final weeks before calving but with a shorter interval between the 2 dietary changes. In our study, cows without a dry period had larger papillae surface area directly after calving (at d 3) than cows in the other treatments, but cows managed for a short dry period of 30 d already reached a papillae surface area comparable to the NODRY cows at d 7 after calving. Cows managed for a conventional 60 d dry period had lowest papillae surface area after calving until 28 d after calving when all groups had comparable papillae surface area. Papillae growth can be evoked by supplemental concentrate prepartum (Dieho et al., 2017a) as well as with a faster increment of concentrate allowance postpartum (Dieho et al., 2016a). The cows participating in our study as well as in the study of Dieho et al. (2016a) were relatively young animals, transitioning from first to second parity. The precise effect of age on adaptation capacity of the rumen, however, is still unclear. Our study adds new data on papillae growth during the transition period in response to changes in dry period length and associated changes in diet composition and feed intake, showing that the duration of feeding a low-energy dry cow ration prepartum affects the size of papillae at the onset of lactation and the time required to let papillae regain their full size postpartum.

Although it was not the focus of the study, it is important to consider the effects of dry period length on milk yield postpartum and colostrum composition. Without a dry period, cows will produce less milk in the next lactation (Van Knegsel et al., 2014) and will have lower concentrations of IgG and IgM in colostrum (Mayasari et al., 2015). When feeding newborn calves from continuously milked cows, a larger volume of colostrum is required to provide sufficient immunoglobulins.

The higher DMI and fOM intake at the onset of lactation for the short or no dry period treatment relative to the conventional dry period will have stimulated papillae growth. As described earlier, the 12 primiparous cows enrolled in the current study were part of a larger trial with 60 primiparous and 108 multiparous cows subjected to the same 3 treatments (Van Knegsel et al., 2014). In the overall study, no main effect of dry period length on DMI postpartum was found during the first 14 wk after calving (Van Knegsel et al., 2014). The rumen study had fewer animals per treatment (n = 4), and monitored only primiparous cows, which may have a specific response to dry period length. Unintended systematic differences in feed intake capacity between treatment groups cannot be ruled out with a relatively small study size, despite the random assignment of cows. Body weight varied between treatments directly postpartum but when DMI and fOM intake were expressed as a proportion of BW, treatment ef-

Table 6. Main effects in rumen papillae size during early lactation as affected by dry period length (DP) of 60 (CON), 30 (SHORT) or 0 d (NODRY), by day relative to calving (day) and by the interaction between DP and day relative to calving. Values represent predicted means by REML procedure

	Dry period length[1]				*P*-value		
	CON	SHORT	NODRY	SED[2]	DP	day	DP × day
Papillae length (mm)							
d 3	8.8^{x}	8.2^{x}	9.2	0.61	0.804	<0.001	0.031
d 7	8.7^{x}	9.7^{yz}	9.4				
d 14	9.6^{xy}	9.6^{y}	9.0				
d 28	10.4^{yz}	10.2^{yz}	9.4				
d 56	10.7^{z}	10.6^{z}	9.7				
Papillae width (mm)							
d 3	2.3^{ax}	2.9^{bx}	3.4^{cx}	0.20	<0.001	<0.001	<0.001
d 7	2.3^{ax}	3.0^{bx}	3.4^{cx}				
d 14	2.4^{ax}	3.3^{by}	3.1^{bx}				
d 28	3.1^{ay}	3.7^{bz}	3.4^{abx}				
d 56	3.5^{z}	4.0^{z}	3.9^{y}				
Papillae surface area (mm^2)							
d 3	40.7^{ax}	49.6^{ax}	61.8^{bxy}	6.38	<0.001	<0.001	0.017
d 7	40.4^{ax}	60.2^{by}	64.3^{bxz}				
d 14	47.5^{ax}	64.2^{by}	56.4^{aby}				
d 28	66.1^{y}	76.4^{z}	64.8^{xyz}				
d 56	75.1^{y}	83.1^{z}	76.5^{z}				

[a-c]Means within a row with different superscripts show differences between treatments at the specific time point ($P < 0.05$).

[x-z]Means within a column with different superscripts show a time effect for a specific treatment ($P < 0.05$).

[1]Dry period length of 60 d (CON, conventional), 30 d (SHORT) or 0 d (NODRY).

[2]SED = standard error of differences.

fects remained relevant. In any case, the higher DMI in cows with a shortened dry period needs to be considered when interpreting the results on rumen performance. In general, the effect of dry period length on DMI is not consistent among studies. Some studies show a positive effect of omitting the dry period on DMI postpartum (Rastani et al., 2005), where others report no differences (Andersen et al., 2005; De Feu et al., 2009). The variation in outcome may be related to the experimental design of the rations with different dry period lengths. Rastani et al. (2005) showed an improved DMI during the first 3 wk of lactation for cows without a dry period compared with a short dry period. Interestingly, cows without a dry period as well as cows on a short dry period received the same high energy ration while cows on a conventional dry period received a low to moderate energy diet prepartum (Rastani et al., 2005). The energy balance of the cows on a short dry period was therefore highest of all treatments prepartum which increased the risk for metabolic disturbances postpartum, as shown by increased plasma NEFA and liver TG concentrations, resulting in a reduced feed intake in early lactation (Rastani et al., 2005). In other studies, continuously milked cows and cows with a conventional dry period did not have different DMI postpartum (Andersen et al., 2005; De Feu et al., 2009). In the study of Andersen et al. (2005), cows received exactly the same ration prepartum, having dry cows fed restricted to a maximum of 9 kg DM/d from dry-off to wk 3 prepartum to prevent overfeeding. Feeding the same dietary ingredients to cows with or without a dry period while preventing overfeeding at the same time, may have supported rumen adaptation differently compared with our study based on ad libitum intake of a low energy diet during the dry period. In the study of De Feu et al. (2009) no effect was found on DMI during the first 12 wk postpartum for cows with a conventional or no dry period, but unfortunately no information was given on milk yield or EB prepartum to understand the consequences of the dietary management precalving. Our results are in line with the results of Jolicoeur et al. (2014), comparing a short dry period with a conventional dry period. In the first 3 wk postpartum, DMI was highest for the cows managed for a short dry period precalving. In that study, however, cows with a conventional dry period were subjected to 3 dietary changes: 1) from lactation to far-off ration; 2) from far-off to close-up ration at 28 d before the

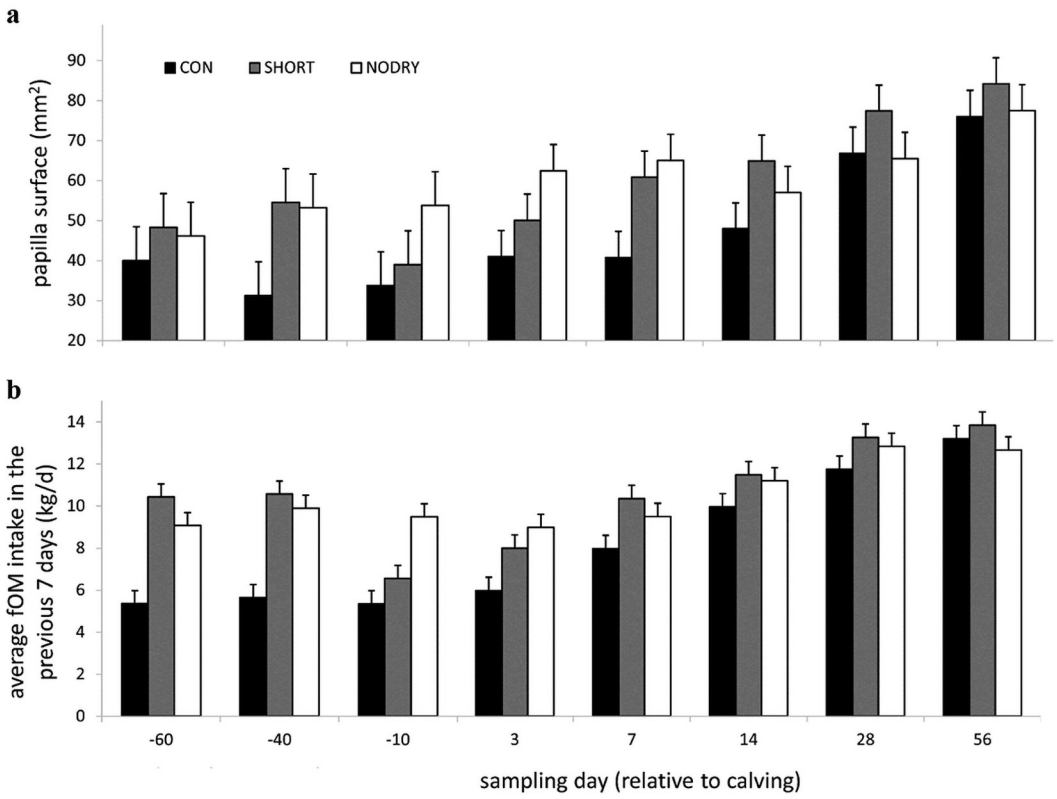

Figure 3. Average papillae surface area in mm^2 at rumen sampling days pre- and postcalving (a) with the daily fermentable organic matter intake of the 7 d preceding the rumen sampling day (b) for cows on a 60 d dry period (CON, black bars), 30 d dry period (SHORT, gray bars) or no dry period (NODRY, open bars). Bars show predicted means by REML analysis, whiskers display the standard error of differences (SED).

expected calving date; and 3) from close-up to lactation ration at calving. Cows with a short dry period did not receive the far-off ration at all, resulting in only 2 dietary changes (Jolicoeur et al., 2014), and such differences with our study hamper direct comparison.

Assuming a relationship between papillae development and nutrient absorption capacity (Schären et al., 2016), the improved papillae surface area for continuously milked cows may have improved rumen VFA absorption and thus rumen fermentation the first weeks of lactation. Papillae surface area is however not the only factor involved in nutrient absorption rate. Other rumen factors like papillary blood flow and VFA transporter expression in papillae may also be relevant (Dieho et al. 2016b, Dieho et al. 2017b), but the morphological proliferation of papillae seemed to be most associated with observed nutrient absorption rate from the rumen (Laarman et al., 2015, Schären et al., 2016; Dieho et al. 2017b). If DMI remains higher around parturition and nutrient absorption at onset of lactation is improved, this may not only support fermentation and lead to increased DMI, but may also reduce the risk for metabolic disease. In our study with second parity cows, however, no clinical cases of metabolic disease were reported; the concentrations of plasma NEFA, BHB and liver TG were generally low and comparable among treatment groups. The absence of such differences may be related to the small number of animals (n = 12) in the present study. The numerically lower NEFA concentrations of group NODRY in the subset of animals in our study is in line with the significantly lower NEFA concentrations of group NODRY compared with SHORT and CON of the main trial with a total of 168 cows as reported by Chen et al. (2015). Similarly, the numerically lower liver TG content of NODRY compared with SHORT and CON in the present study is in in line with significant differences between these groups reported by Chen et al. (2015). An effect of improved nutrient absorption with increased papillae surface area may become more relevant in a situation where cows experience more challenging conditions prone to stronger metabolic disturbances than in our study.

CONCLUSIONS

The results from the present study demonstrate that shortening or omitting the dry period, with associated dietary changes, led to a less pronounced or no decline in rumen papillae surface area precalving and to a greater papillae surface area during the first weeks after calving compared with a conventional dry period of 60 d. This may facilitate rumen adaptation and improve energy balance in early lactation. Further optimization of the combination of dry period length as well as dietary composition and associated dietary changes throughout the transition period in support of adaptation to a new lactation remains to be studied.

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