

Effect of silage dry matter content and rapeseed meal supplementation on dairy cows

2. Rumen fermentation and digesta passage rate

T. Kokkonen^{*}, M. Tuori, L. Syrjälä-Qvist

Department of Animal Science, University of Helsinki, P.O. Box 28, 00014 Helsinki, Finland

Received 15 June 1999; received in revised form 25 January 2000; accepted 10 February 2000

Abstract

The effects of direct-cut and wilted silage with or without rapeseed meal (RSM) supplementation on rumen fermentation and digesta passage rates were studied in a 4×4 balanced Latin square experiment with four multiparous cows. The dry matter (DM) and crude protein (CP) degradabilities of silages were determined in sacco. RSM supplementation replaced 16% of the oat–barley concentrate mixture. The daily concentrate amount was 10 kg. Silages were given ad libitum. The effective degradabilities of dry matter and protein (EPD) were higher ($p<0.001$) in direct-cut silage but wilted silage had higher ($p<0.001$) content of rapidly degradable protein. Rumen ammonia concentration was higher with direct-cut silage (10.16 versus 8.47 mmol/l, $p<0.01$), reflecting higher CP content and EPD. Rumen pH and total volatile fatty acid (VFA) concentration in rumen were not affected by silage type, and the differences in molar proportions of rumen VFA's were small. The proportion of propionate tended to be higher ($p<0.10$) with wilted silage, whereas the proportion of butyrate was higher (133 versus 128 mmol/mol, $p<0.01$) with direct-cut silage. The retention time of the digesta particle phase in alimentary tract was shorter ($p<0.05$ or better) with wilted silage. Pool mean retention time (PMRT), which illustrates the retention time of particles in rumen, was shorter (34.0 versus 28.3 h, $p<0.05$) with wilted silage. Similarly, retention time of particles in the rumen pool of particles small enough to leave the rumen tended to be shorter ($p<0.10$) with wilted silage. RSM supplementation tended to increase ($p<0.10$) rumen ammonia concentration and decreased the molar proportion of rumen butyrate (132 versus 127 mmol/l, $p<0.05$). The retention time of particles in pool, which illustrates the rate of particle break down in the rumen, was shorter ($p<0.10$) with RSM. In conclusion, the ruminal retention time

^{*} Corresponding author. Tel.: +358-9-191-58561; fax: +358-9-191-58379.

E-mail address: tuomo.kokkonen@helsinki.fi (T. Kokkonen)

of particles was shorter with wilted silage. This may affect silage digestibility negatively. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Grass silage; Silage degradability; Rumen fermentation; Digesta passage

1. Introduction

Many experiments have shown that silage DM intake has increased with wilted grass silage as compared to direct-cut silage (Ettala et al., 1982; Gordon and Peoples, 1986; Bertilsson, 1987). There is also some evidence that the digesta passage rate may differ between direct-cut and wilted silages (Teller et al., 1989, 1990). The lower digestibility of organic matter (OM) in a diet with wilted silage (Teller et al., 1992) may be associated with a shorter retention of digesta in the alimentary tract. As a result of lower digestibility of wilted silage, energy intake with wilted silage is not much higher than that with direct-cut silage. Consequently, the milk yield difference between silages is minor (Gordon, 1996).

The soluble fractions of the silage nitrogen are rapidly degraded in the rumen. Wilting may increase the proportion of these fractions due to proteolysis in field (Anderson, 1984). High soluble nitrogen content results in a high peak value of the rumen ammonia concentration after feeding, which in turn, may affect silage nitrogen utilization negatively.

Teller et al. (1990) reported that wilting increased the molar proportion of propionate in the rumen and decreased the proportion of acetate. This change was accompanied by an increase of milk protein concentration.

The objective of our experiment was to study the effects of direct-cut and wilted grass silage diets on rumen fermentation and digesta passage when the protein content of concentrate was altered as well as to study the degradabilities of silages.

2. Materials and methods

The design of the experiment was a 4×4 balanced Latin square with four multiparous cows (three Ayrshire, one Friesian) which had ruminal cannulas. The treatments were in a 2×2 factorial arrangement with direct-cut or wilted silage, and the concentrate was a grain mixture (oat–barley) with or without 16% rapeseed meal (RSM). Silages were given *ad libitum*, and the concentrate was provided in a fixed amount of 10 kg/day for the duration of the experiment. The experimental periods lasted 3 weeks. Feeds, feeding and feed sampling as well as the chemical analyses of feeds are described in a companion article (Kokkonen et al., 2000).

Rumen degradability of silages and concentrates (in sacco) was measured during the last week of each period. An amount of 15 g direct-cut silage, 8 g wilted silage or 5 g concentrate was weighed into the nylon bags, needleholes of which were sealed with a waterproof glue. Silage was chopped to a length of approximately 5 mm. The free surface area of the bag cloth was 33% and pore size was 40 µm. The incubation times for silages were 3, 6, 12, 24, 48, 72 and 96 h and for concentrates 3, 6, 12, 24 and 48 h. After incubation, bags were rinsed in cold water in a washing machine, oven-dried +50°C for

24 h and weighed. Silages were zero-washed for the calculation of the lag time. The dry matter and crude protein content of the remaining feed in the bag was measured as well as the particle loss and water solubility of the crude protein.

Rumen liquor was sampled 1 day in the last week of each period. The 100 ml samples were taken 0, 1, 2, 3, 4, 6, 8 and 10 h after morning feeding. The pH of the samples was measured immediately. The samples were then centrifuged and filtered through a double-layer cheese cloth. Ammonia was measured immediately from the supernatant.

A portion of the supernatant was acidified and frozen at -18°C until the VFA analysis. For determination of ruminal liquid retention time and passage rate, the cannulated cows were given 25 g CoLi-EDTA in water solution (Udén et al., 1980) through the cannula at 6:00 a.m. in 1 day in the last week of the period. Samples from rumen liquor were collected 2, 4, 6, 8, 10, 12, 14 and 16 h after marker administration. The samples were stored overnight in the refrigerator and centrifuged, filtered and diluted.

To determine digesta retention time and passage rate, the cannulated cows were given 100 g Cr-mordanted straw (Udén et al., 1980) through cannula simultaneously with CoLi-EDTA. Faecal samples were taken by rectum 4, 6, 8, 12, 20, 24, 28, 32, 36, 40, 48, 60, 72, 84, 96, 108, 120 and 132 h after marker administration. The samples were oven-dried and milled through a 1.5 mm sieve.

The VFA of ruminal samples were determined by gas chromatography (Hewlett Packard 5710A) as described by Huida (1973). Co and Cr contents of faecal samples were analysed with an atomic absorption spectrophotometer (Perkin-Elmer 5100 PC) as described by Williams et al. (1962).

2.1. Calculations

Nutritional composition of feeds was calculated using the feed analyses for each period. The dry matter degradability of silages and concentrates was calculated with NEWAY-program (McDonald, 1981) based on the equations by Ørskov and McDonald (1979), McDonald (1981) and Kristensen et al. (1982). The rate constant (k) was 0.02 for the silages, 0.03 for the cereal concentrates and 0.04 for RSM (Tuori et al., 1996). The particle loss of concentrates from nylon bags was corrected according to Weisbjerg et al. (1991).

The effect of the sampling time on rumen fermentation parameters was taken into account by fitting third-order regression equations to the data of individual cows and then calculating minimum or maximum concentration or molar proportion and the time elapsed between morning feeding and the calculated minimum or maximum concentration or molar proportion. For rumen pH, the time below pH 6 (between the morning and afternoon feedings) was calculated using the same method. Regression equations were not fitted to the data of minor volatile fatty acids.

The excretion curves of markers (Cr, Co) were drawn for each cow and each period before the calculation of retention times. Outliers and the artificial tail consisting small concentrations at the end of faecal sampling were removed before further analysis.

Retention times were calculated according to Grovum and Williams (1973), Grovum and Phillips (1973) and Thielemans et al. (1978) as described by Huhtanen (1987). Retention times were also calculated using gamma models (Moore et al., 1992) by

Table 1
Feed composition

	Direct-cut silage	Wilted silage	Oat	Barley	Rapeseed meal
DM (g/kg)	186	288	880	869	885
In DM (g/kg)					
Ash	84	95	33	24	79
Crude protein	164	155	135	135	361
Crude fat	54	44	65	35	78
Crude fibre	296	290	103	50	126
NDF	550	555	283	191	283
ADF	306	301	116	54	195
ADL	22	25	23	8.0	87
Sugars	108	89			
Lactic acid	3.0	21			
Acetic acid	3.9	3.1			
Unidentified VFA		3.5			
In total nitrogen (g/kg)					
Soluble N	440	501			
Ammonium N	20	56			
pH	3.88	4.14			

partitioning the retention of digesta in the rumen into two compartments: the fast compartment, and the slow compartment. Results were calculated using the gamma-3 model (G3G1), which gave the smallest error variance, although the difference between this model and the gamma-4 model (G4G1) was marginal.

2.2. Statistical analyses

Significance of treatment effects was determined using analysis of variance (ANOVA) with SAS statistical software (SAS, 1989).

Feed intake, milk yield, retention times, rumen fermentation parameters and degradabilities of silage dry matter and crude protein were analysed using the following model:

$$Y_{ijklm} = \mu + S_i + R_j + (S \times R)_{ij} + P_k + A_l + \varepsilon_{ijkl},$$

where S , R , P and A are the effects of silage, RSM, period and animal and ε_{ijkl} is the error term (Table 1).

3. Results

3.1. Feed intake

The feed intake is given in Table 2. The dry matter intake (DMI) of wilted silage was greater ($p < 0.001$) than DMI of direct-cut silage. Total DMI also increased ($p < 0.001$) with wilted silage. RSM supplementation had no effect on feed intake.

Table 2
Feed intake, milk yield and live weight

	Direct-cut silage		Wilted silage		SEM	Significance (<i>p</i>)		
	RSM0	RSM16	RSM0	RSM16		Silage	RSM	Interaction
(kg DM/day)								
Silage	8.6	9.4	10.7	10.9	0.49	**	NS	NS
Concentrate	7.7	7.8	7.7	7.9	0.076	NS	NS	NS
Total DMI	16.6	17.5	18.7	19.0	0.53	*	NS	NS
(g DM/kg W ^{0.75})								
Silage	72.6	80.0	90.4	91.9	3.76	**	NS	NS
Concentrate	66.0	67.0	65.0	66.5	0.53	NS	°	NS
Total DMI	141.1	149.2	157.9	160.5	4.01	*	NS	NS
Milk yield (kg/day)	20.5	22.4	20.2	22.9	0.72	NS	**	NS
Live weight (kg)	574	574	580	582	4.25	NS	NS	NS

° $p < 0.10$; * $p < 0.05$; ** $p < 0.01$.

3.2. Silage degradability

The silage degradability parameters are shown in Table 3. Soluble, easily degradable fraction (*a*) of dry matter was greater ($p < 0.01$) in direct-cut silage and nonsoluble, degradable dry matter fraction (*b*) was greater ($p < 0.10$) in wilted silage. The degradation rate (*c*) of dry matter fraction *b* was slightly higher ($p < 0.10$) in direct-cut silage. Effective degradability of dry matter in direct-cut silage was greater ($p < 0.001$) than that in wilted silage.

Table 3
Degradability of silages^a

	Direct-cut silage	Wilted silage	SEM	Significance (<i>p</i>)			
				Silage	Cow	Period	Diet
DM							
<i>a</i>	22.65	18.98	0.653	**	NS	*	NS
<i>b</i>	58.38	60.18	0.595	°	NS	NS	NS
<i>c</i>	0.053	0.050	0.0011	°	NS	*	NS
Lag time (h)	2.38	2.70	0.173	NS	NS	NS	NS
ED DM	64.98	61.84	0.0822	***	°	NS	NS
CP							
<i>a</i>	34.77	43.51	0.834	***	NS	*	NS
<i>b</i>	54.17	44.34	0.869	***	NS	°	NS
<i>c</i>	0.119	0.077	0.0037	***	NS	°	NS
Lag time (h)	2.61	2.96	0.114	°	NS	*	NS
EPD	81.31	78.72	0.103	***	NS	°	NS

^aSignificant interactions ($p < 0.05$): silage × period (effective degradability of DM, EPD).

° $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 4
Rumen fermentation

	Direct-cut silage		Wilted silage		SEM	Significance (<i>p</i>)		
	RSM0	RSM16	RSM0	RSM16		Silage	RSM	Interaction
PH	6.06	5.98	6.08	6.08	0.046	NS	NS	NS
NH ₃ -N (mmol/l)	9.43	10.88	8.32	8.62	0.58	**	°	NS
Total VFA (mmol/l)	122.12	124.33	122.77	123.44	1.08	NS	NS	NS
Molar proportions (mmol/mol)								
Acetate	669	670	664	669	4.1	NS	NS	NS
Propionate	156	160	166	168	3.6	°	NS	NS
Butyrate	135	131	128	122	2.0	**	*	NS
Isobutyrate	9.3	9.1	9.2	9.2	0.21	NS	NS	NS
Valerate	12.2	12.9	14.1	13.2	0.87	NS	NS	NS
Isovalerate	13.8	11.5	13.0	12.1	0.77	NS	NS	NS
Caproate	0.47	0.52	0.68	0.63	0.049	*	NS	NS
(Ac+Bu)/Pr	5.26	5.10	4.87	4.80	NS	°	NS	NS
NGR ^a	5.80	5.62	5.38	5.26	NS	*	NS	NS

^a NGR=Acetate+2×butyrate+valerate/(propionate+valerate) (Ørskov, 1975).

° *p*<0.10; * *p*<0.05; ** *p*<0.01.

Fraction *a* of crude protein was greater (*p*<0.001) in wilted silage, while fraction *b* was greater (*p*<0.001) in direct-cut silage. The degradation rate (*c*) of fraction *b* was higher (*p*<0.001) in direct-cut silage crude protein. The effective protein degradability (EPD) of direct-cut silage was higher (*p*<0.001). The effects of diet and cow on silage degradability were not significant (*p*<0.05).

3.3. Rumen fermentation

Silage or RSM had no effect on rumen pH and total VFA concentration (Table 4). There was a rapid increase in VFA concentration and a decrease in pH after the meal with every treatments (Fig. 1). Maximum VFA concentration or minimum pH did not differ between the treatments. Time between morning feeding and maximum VFA concentration was shorter with RSM (3.4 versus 5.0 h; *p*<0.05) (Fig. 2). Treatments had no effect on the duration of the depression of pH below 6.

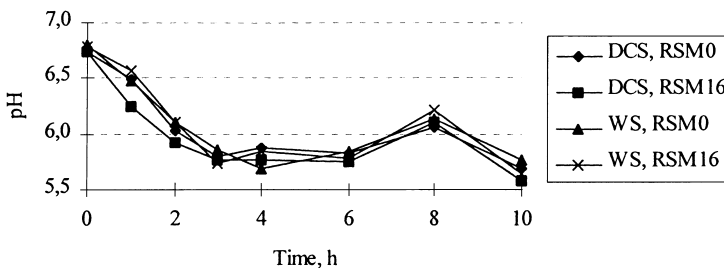


Fig. 1. Rumen pH.

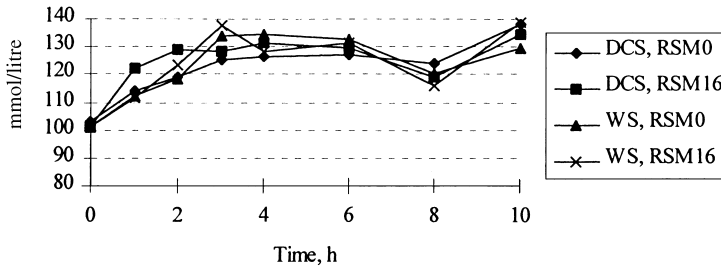


Fig. 2. Total VFA concentration in rumen.

Direct-cut silage increased ($p < 0.01$) the ammonia concentration, and there was a trend ($p < 0.10$) towards higher ammonia concentration with RSM. Rumen ammonia concentration peaked 2 h after the meal in every treatment (Fig. 3). There were no significant time \times treatment interactions in ammonia concentrations.

Silage or RSM had no effect on molar proportion of acetate and there were no time \times treatment interactions in acetate proportions. The mean and maximum proportion of propionate and mean proportion of caproate were higher ($p < 0.10$ or better) with wilted silage. Time between morning feeding and maximum proportion of propionate was longer with RSM. The proportion of butyrate was higher ($p < 0.01$) with direct cut silage and lower ($p < 0.05$) with RSM. There was a similar pattern in maximum butyrate proportions. Ratio of (acetate+butyrate)/propionate and non-glucogenic ratio (NGR) (mean and minimum values) were higher ($p < 0.10$ or better) with direct-cut silage. The minimum values of these two ratios after morning feeding was reached earlier ($p < 0.10$) with a lower protein level (Fig. 4).

3.4. Digesta passage

According to all the three models, the total mean retention time (TMRT) was shorter ($p < 0.05$ or better) with those cows which were given wilted silage (Table 5). Pool mean retention time (PMRT) and ruminal mean retention time (RuMRT, Moore et al., 1992)

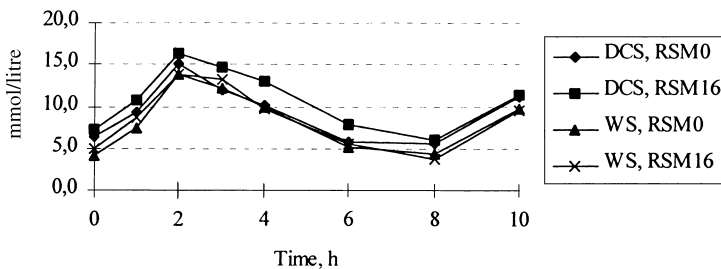


Fig. 3. Ruminal ammonia concentration.

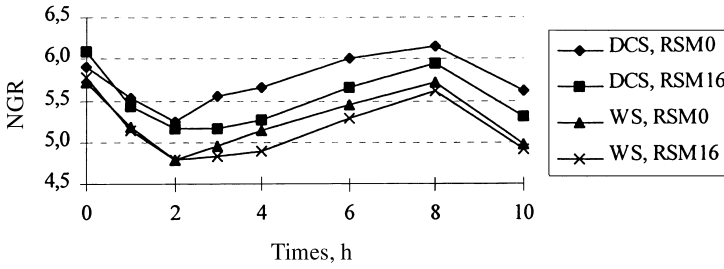


Fig. 4. Non-glucogenic ratio (NGR) of rumen VFA's.

were shorter ($p < 0.10$ or better) with wilted silage. First compartment mean retention time (FMRT) did not differ between silages, but there was a tendency ($p < 0.10$) towards decreased FMRT with RSM.

Neither silage type nor protein level had a significant effect on liquid passage rate, liquid retention times in different compartments or rumen liquid volume (Table 6). There was a tendency ($p < 0.10$) towards silage \times RSM interaction in residual mean retention time (RMRT) (Thielemans et al., 1978) and TMRT.

Table 5
Retention times of particle phase (h)

	Direct-cut silage		Wilted silage		SEM	Significance (p)		
	RSM0	RSM16	RSM0	RSM16		Silage	RSM	Interaction
TMRT ^a	41.4	40.1	37.7	35.5	0.91	**	NS	NS
PMRT ^b	34.7	33.2	29.2	27.4	1.58	*	NS	NS
RMRT ^c	6.7	6.9	8.6	8.1	0.72	°	NS	NS
TMRT ^d	40.4	38.9	34.9	34.6	1.67	*	NS	NS
TT ^e	3.9	4.1	4.1	5.9	0.56	NS	NS	NS
k_1^f	0.029	0.030	0.036	0.038	0.0023	*	NS	NS
k_2^f	0.570	0.633	0.635	0.795	0.0897	NS	NS	NS
TMRT ^g	46.8	45.8	43.0	40.6	1.43	*	NS	NS
FMRT ^g	9.5	6.3	9.1	6.6	1.19	NS	°	NS
RuMTR ^g	31.3	31.7	27.7	26.6	1.80	°	NS	NS
TD ^g	6.0	7.8	6.3	7.4	1.13	NS	NS	NS

^a Thielemans et al. (1978): TMRT — total mean retention time.

^b PMRT — pool (rumen) mean retention time.

^c RMTR — residual mean retention time.

^d Grovum and Phillips (1973): TMRT — total mean retention time.

^e TT=transit time; time for the first appearance of marker in faeces.

^f k_1 and k_2 are the rate constants of the kinetics of the marker in reticulo-rumen and hindgut.

^g Moore et al. (1992): TMRT — total tract mean retention time; FMRT — first compartment mean retention time; RuMTR — ruminal mean retention time; TD — time delay to first marker appearance.

° $p < 0.10$; * $p < 0.05$; ** $p < 0.01$.

Table 6
Retention time of liquid phase

	Direct-cut silage		Wilted silage		SEM	Significance (<i>p</i>)		
	RSM0	RSM16	RSM0	RSM16		Silage	RSM	Interaction
Liquid outflow from rumen								
(%/h)	13.45	13.29	14.44	15.26	0.0096	NS	NS	NS
(l/day)	474.3	477.4	499.6	485.9	12.68	NS	NS	NS
Liquid volume of rumen (l)	147.0	149.7	148.3	134.9	7.31	NS	NS	NS
TMRT ^a (h)	21.3	22.7	22.2	21.0	0.63	NS	NS	°
PMRT (h)	18.9	18.4	18.7	17.8	0.67	NS	NS	NS
RMRT ^b (h)	2.4	4.4	3.5	3.2	0.46	NS	NS	°
TT (h)	2.9	2.6	2.4	3.0	0.60	NS	NS	NS
TMRT ^c (h)	22.8	22.0	22.2	21.8	0.85	NS	NS	NS
<i>k</i> ₁	0.053	0.055	0.054	0.057	0.0020	NS	NS	NS
<i>k</i> ₂	0.997	1.090	1.007	1.045	0.1032	NS	NS	NS

^a Thielemans et al. (1978): TMRT — total mean retention time.

^b RMTR — residual mean retention time.

^c Grovum and Phillips (1973): TMRT — total mean retention time.

° *p* < 0.10.

4. Discussion

4.1. Silage type

4.1.1. Degradability

The DM degradation of direct-cut silage was faster at the beginning of incubation (fraction *a* was larger). This is in agreement with Makoni et al. (1991) and Teller et al. (1993). In the other experiments, there have been no differences in *a* fraction (Gordon and Peoples, 1986; Charmley et al., 1990). Teller et al. (1993) reported that OM degradation rate (*c*) of fraction *b* was higher in wilted silage, whereas in our experiment the degradation rate of direct-cut silage DM was higher, although the difference between silages was small. The effective degradability of DM was higher in direct-cut silage, consistent with the results reported by Teller et al. (1993).

Higher sugar and CP contents may explain the greater *a* fraction in direct-cut silage. Sugars and protein in silage are rapidly and highly degradable in the rumen (Setälä et al., 1985). In contrast, differences in fibre fractions were too small to explain the difference in DM degradability.

Wilted silage contained more soluble and ammonium N than direct-cut silage, resulting in faster CP degradation at the beginning of incubation (fraction *a* was larger). Faster degradation is in accord with Gordon and Peoples (1986), but contradicts the results of Morgan et al. (1980), Makoni et al. (1991) and Tamminga et al. (1991).

This contradiction is due to a difference in ensiling methods. Grasses in the three latter experiments were ensiled without additive. Using formic acid as an additive prevents protein degradation in silo. However, wilting also may prevent protein degradation in silo because higher osmotic pressure inhibits microbial activity (Tamminga et al., 1991).

Thus, when ensiled without additive, wilted silage probably has less degraded protein than direct-cut silage ensiled without additive, even taking into account protein degradation during wilting (McDonald and Edwards, 1976).

Fraction *b* in CP was smaller in wilted silage and it degraded slowly. Also, in accordance with Makoni et al. (1991), EPD was lower in wilted silage. The reasons for these two characteristics may be a partial protein denaturation during wilting which inhibits degradation and a higher CP content in direct-cut silage which increases the rate of protein degradation (Tamminga et al., 1991). The results of Nocek and Grant (1987) with timothy silage give further support to higher rumen degradability of CP in direct-cut silage. They observed that potentially degradable rumen CP tended to increase with lower silage DM concentrations. Therefore, wilting seems to increase the escape of silage protein from ruminal degradation but the nutritional value of this escaped protein to the animal may be low.

4.2. Rumen fermentation

There was no difference between silages in rumen pH variation. Rumen pH decreased to below 6 about 2 h after feeding and remained there 3–4 h (calculated with regression equations). Prior to afternoon feeding, pH rose momentarily but following feeding it fell down to 5.7. Low pH resulted from concentrate feeding regime. Rumen pH depression was not so severe that it would have altered microbial population to any great extent (Hoover, 1986).

In agreement with the results of Gordon and Peoples (1986), there was no difference in average rumen pH or VFA concentration, although Teller et al. (1990) reported that wilted silage tended to decrease rumen pH.

The molar proportions observed in our experiment are typical of a diet based on restrictively fermented silage. This rumen fermentation pattern is characterized by low proportion of propionate and high proportion of acetate and butyrate. Consequently, the ratio of acetate plus butyrate to propionate is very high (Huhtanen, 1998).

Gordon and Peoples (1986) and Peoples and Gordon (1989) did not observe any differences between wilted and direct-cut silage in molar proportions of rumen VFA. In contrast to those results, wilted silage increased the molar proportion of propionate in our experiment and decreased the proportion of butyrate. The increase of the proportion of propionate with wilted silage was also observed by Teller et al. (1993). In addition, in agreement with our results, they observed a decrease in the proportion of acetate and a decrease acetate plus butyrate:propionate ratio.

It has been established that lactic acid ferments quickly to propionate in rumen (Jaakkola, 1992). Wilted silage contained more lactic acid than direct-cut silage, which may have contributed to the higher proportion of propionate in the rumen. Direct-cut silage contained more sugars than wilted silage. This may have raised the molar proportion of butyrate in the rumen (Jaakkola, 1992).

Contradicting an earlier study (Peoples and Gordon, 1989), the concentration of ammonia was higher with direct-cut silage, which was probably due to higher CP content and protein degradability. There was no difference in curves describing ammonia concentration despite the larger fraction of rapidly degrading nitrogen in wilted silage. In

contrast to this, Teller et al. (1992) reported that rumen ammonia concentrations were higher with wilted silage, starting at 3 h post-feeding. With all the treatments, rumen ammonia concentration remained over 3.6 mmol/l, this has been suggested to be the optimal concentration for microbial synthesis (Satter and Slyter, 1974).

4.3. *Digesta passage*

TMRT of particles in our trial (40.8 h for direct-cut silage and 36.6 h for wilted silage) was near those reported by Huhtanen (1987) (36.8–37.7 h, direct-cut silage), but shorter than those of Udén (1984) (51.2 h, direct-cut silage). PMRT was longer and RMRT and TT were shorter than in Huhtanen (1987). These differences are probably related to the particle size of Cr-mordanted straw. In Huhtanen (1987), straw was milled to pass through a 1.5 mm sieve. In our experiment, the sieve size was 2.0 mm and in Udén (1984) it was 6 mm. The passage of small particles is faster than that of bigger particles. Furthermore, it is possible that smaller particles contain proportionally more marker than larger particles. Therefore, they absorb less liquid in the rumen and their density is different than that of larger particles, thus affecting passage (Bruining and Bosch, 1992). Wilting increased the silage intake in our study, as well as, in several others (e.g. Ettala et al., 1982; Bertilsson, 1987). It has been suggested that the rate of particle breakdown in rumen might be the rate-limiting step to digestion and passage thus affecting intake (Welch, 1982). Indeed, wilted silage decreased PMRT, suggesting shorter retention of particles in the rumen. Using a gamma model gave further information about particle retention. RuMRT was shorter for wilted silage, with RuMRT illustrating the retention time of particles small enough to leave the rumen. Thus, it seems that higher intake was facilitated by faster passage of small particles from the rumen. Possibly, this was due to increased number of particles leaving rumen per rumen contraction.

There was no difference in FMRT, which illustrates the rate of particle breakdown in rumen. This result is in contrast with Teller et al. (1989, 1990), who reported that particle breakdown was less effective with wilted silage. However, the rate of particle breakdown does not have a marked effect on digesta passage because most of the feed particles in rumen are small enough to pass the rumen-omasal orifice. Much more important for particle passage is their functional density, which is affected by the number of gas bubbles resulting from microbial fermentation (Lechner-Doll et al., 1991). Teller et al. (1993) also concluded that the reduction of particle size in the rumen is not limiting to voluntary grass silage intake.

4.4. *Protein content of concentrate*

Increasing the protein content of concentrate had only a marginal effect on rumen fermentation. Rumen pH and VFA concentration were not affected. However, there were some changes in the pattern of rumen fermentation. Total VFA peaked sooner, whereas propionate peak molar proportion was delayed after morning feeding with RSM. Lipogenic to glucogenic ratio in rumen VFA reached minimum earlier without protein supplement.

The molar proportions of VFA were very similar as in the earlier experiments with the same type of feeding (Mayne and Gordon, 1984; Peoples and Gordon, 1989). The high lipogenic to glucogenic ratio in rumen VFA, which is typical of diets based on restrictively fermented silage (Huhtanen, 1998), was slightly lower with RSM as a result of a lower molar proportion of butyrate.

Increasing protein supply has increased rumen ammonia concentration in earlier studies (Burgess and Nicholson, 1984; Mayne and Gordon, 1984). This tendency was seen in our experiment as well, though, without significant differences between the protein levels.

There was no difference in the shapes of curves illustrating rumen ammonia concentrations with the two protein levels. The average ammonia concentrations remained over 4.7 mmol/l, considered optimal for fibre digestion (Hoover, 1986). Only the values before feeding with wilted silage were slightly lower than that. Thus, it is unlikely that rumen ammonia concentration limited fibre digestion in any of the groups.

5. Conclusions

Wilting of silage increased the passage rate of small particles from the rumen, thus, exposing them for a shorter time to the digestion of rumen microbes. Feeding with wilted silage increased the proportion of propionate in the rumen. Differences in the degradability of silages were related to the chemical composition of silages. These differences are small provided that conditions during wilting are good and enough preservative is added during harvest.

Rapeseed meal supplementation decreased the proportion of butyrate in the rumen but had no significant effect on rumen ammonia concentration.

References

- Anderson, R., 1984. Effect of prolonged wilting on the nitrogenous constituents of silage. In: 57th Annual Report 1983–1984. Agricultural Research Institute of Northern Ireland, pp. 46–53.
- Bertilsson, J., 1987. Effects of conservation method and stage of maturity upon the feeding value of forages to dairy cows. *Swedish J. Agric. Res.* 17, 123–131.
- Bruining, M., Bosch, M.W., 1992. Ruminant passage rate as affected by CrNDF particle size. *Anim. Feed Sci. Technol.* 37, 193–200.
- Burgess, P.L., Nicholson, J.W.G., 1984. Protein level in grass silage-based total mixed rations for dairy cows in midlactation. *Can. J. Anim. Sci.* 64, 435–442.
- Charmley, E., Gill, M., Thomas, C., 1990. The effect of formic acid treatment and duration of the wilting period on the digestion of silage by young steers. *Anim. Prod.* 50, 497–504.
- Ettala, E., Rissanen, H., Virtanen, E., Huida, L., Kiviniemi, J., 1982. Wilted and unwilted silage in the feeding of dairy cattle. *Ann. Agric. Fenniae* 21, 67–83.
- Gordon, F.J., Peoples, A.C., 1986. The utilization of wilted and unwilted silages by dairy cows and the influence of changes in the protein and energy concentration of the supplement offered. *Anim. Prod.* 43, 355–366.
- Gordon, F.J., 1996. Effect of silage additives and wilting on animal performance. In: Garnsworthy, P.C., Cole, D.J. (Eds.), *Recent Developments in Ruminant Nutrition*, Vol. 3. Nottingham University Press, Nottingham, pp. 229–243.

- Grovum, W.L., Phillips, D.G., 1973. Rate of passage studies in sheep. 5. Theoretical considerations based on a physical model and computer simulation. *Br. J. Nutr.* 30, 377–390.
- Grovum, W.L., Williams, V.J., 1973. Rate of passage in sheep. 4. Passage of marker through alimentary tract and the biological relevances of rate-constants derived from changes in concentration of marker in faeces. *Br. J. Nutr.* 30, 313–329.
- Hoover, W.H., 1986. Chemical factors involved in ruminal fiber digestion. *J. Dairy Sci.* 69, 2755–2766.
- Huhtanen, P., 1987. The effect of dietary inclusion of barley, unmolassed sugar beet pulp and molasses on milk production, digestibility and digesta passage in dairy cows given grass silage based diets. *J. Agric. Sci. Finland* 59, 101–120.
- Huhtanen, P., 1998. Supply of nutrients and productive responses in dairy cows given diets based on restrictively fermented silage. *Agric. Food Sci. Finland* 7, 219–250.
- Huida, L., 1973. Haihtuvien rasvahappojen kvantitatiivinen määrittäminen pötsinsteestä ja säilörehusta kaasunestekromatografisesti. *J. Sci. Agric. Soc. Finland* 45, 483–488.
- Jaakkola, S., 1992. Silage fermentation in relation to the feeding value with special reference to enzyme-treated grass silage. Academic dissertation, Department of Animal Science, University of Helsinki, Helsinki.
- Kokkonen, T., Tuori, M., Leivonen, V., Syrjälä-Qvist, L., 2000. Effect of silage dry matter content and rapeseed meal supplementation on dairy cows. 1. Milk production and feed utilization. *Anim. Feed Sci. Tech.* 84, 213–228.
- Lechner-Doll, M., Kaske, M., von Engelhardt, W., 1991. Factors affecting the mean retention time of particles in the forestomachs of ruminants and camelids. In: Tsuda, T., Sasaki, Y., Kawashima, R. (Eds.), *Physiological Aspects of Digestion and Metabolism in Ruminants*. Academic Press, San Diego, CA, pp. 455–482.
- Makoni, N.F., Shelford, J.A., Fisher, L.J., 1991. The rate and extent of silage nitrogen degradation in the rumen as influenced by wilting and duration of regrowth. *Can. J. Anim. Sci.* 71, 245–248.
- Mayne, C.S., Gordon, F.J., 1984. The effect of type of concentrate and level of concentrate feeding on milk production. *Anim. Prod.* 39, 65–76.
- McDonald, I., 1981. A revised model for the estimation of protein degradability in the rumen. *J. Agric. Sci., Camb.* 96, 251–252.
- McDonald, P., Edwards, R.A., 1976. The influence of conservation methods on digestion and utilization of forages by ruminants. *Proc. Nutr. Soc.* 35, 201–211.
- Moore, J.A., Pond, K.R., Poore, M.H., Goodwin, T.G., 1992. Influence of model and marker on digesta kinetic estimates for sheep. *J. Anim. Sci.* 70, 3528–3540.
- Morgan, C.A., Edwards, R.A., McDonald, P., 1980. Intake and metabolism studies with fresh and wilted silages. *J. Agric. Sci., Camb.* 94, 287–298.
- Nocek, J.E., Grant, A.L., 1987. Characterization of in situ nitrogen and fiber digestion and bacterial nitrogen contamination of hay crop forages preserved at different dry matter percentages. *J. Anim. Sci.* 64, 552–564.
- Ørskov, E.R., 1975. Manipulation of rumen fermentation for maximum food utilization. *World Rev. Nutr. Dietet.* 22, 152–182.
- Ørskov, E.R., McDonald, I., 1979. The estimation of protein degradability in the rumen from incubation measurements weighted according to rate of passage. *J. Agric. Sci., Camb.* 92, 499–503.
- Peoples, A.C., Gordon, F.J., 1989. The influence of wilting and season of silage harvest and the fat and protein concentration of the supplement on milk production and food utilization by lactating cattle. *Anim. Prod.* 48, 305–317.
- SAS 1989. *SAS/STAT Users Guide, Version 6, 4th Edition, Vol. 2*. SAS Institute, Cary, NC, USA.
- Satter, L.D., Slyter, L.L., 1974. Effect of ammonia concentration on rumen microbial protein production in vitro. *Br. J. Nutr.* 32, 199–208.
- Setälä, J., Tesfa, A., Rauramaa, A., Poutiainen, E., 1985. Factors affecting in sacco degradation of dry matter and crude protein in grass silage. *J. Agric. Sci. Finland* 57, 139–146.
- Tamminga, S., Ketelaar, R., Van Vuuren, A.M., 1991. Degradation of nitrogenous compounds in conserved forages in the rumen of dairy cows. *Grass For. Sci.* 46, 427–435.
- Teller, E., Vanbelle, M., Kamatali, P., Wavreille, J., 1989. Intake of direct-cut or wilted grass silage as related to chewing behaviour, ruminal characteristics and site and extent of digestion by heifers. *J. Anim. Sci.* 67, 2802–2809.

- Teller, E., Vanbelle, M., Kamatali, P., 1990. Effects of chewing behaviour and ruminal digestion processes on voluntary intake of grass silages by lactating dairy cows. *J. Anim. Sci.* 68, 3897–3904.
- Teller, E., Vanbelle, M., Foulon, M., Collignon, G., Matatu, B., 1992. Nitrogen metabolism in rumen and whole digestive tract of lactating dairy cows fed grass silage. *J. Dairy Sci.* 75, 1296–1304.
- Teller, E., Vanbelle, M., Kamatali, P., 1993. Chewing behaviour and voluntary grass silage intake by cattle. *Livest. Prod. Sci.* 33, 215–227.
- Thielemans, M.-F., François, E., Bodart, C., Thewis, A., 1978. Mesure du transit gastrointestinal chez le porc à l'aide des radiolanthanides. Comparaison avec le mouton. *Ann. Biol. Anim. Biochem. Biophys.* 18, 237–247.
- Udén, P., 1984. Digestibility and digesta retention in dairy cows receiving hay or silage at varying concentrate levels. *Anim. Feed Sci. Technol.* 11, 279–291.
- Udén, P., Colucci, P.E., Van Soest, P.J., 1980. Investigation of chromium, cerium and cobalt as markers in digesta. Rate of passage from the rumen. *J. Sci. Food Agric.* 31, 625–632.
- Welch, J.G., 1982. Rumination, particle size and passage from the rumen. *J. Anim. Sci.* 54, 885–894.
- Williams, C.H., David, D.J., Iismaa, O., 1962. The determination of chromic oxide in faeces samples by atomic absorption spectrometry. *J. Agric. Sci., Camb.* 59, 381–385.