Comparative aspects of volatile fatty acid production in the rumen and distal fermentation chamber in Svalbard reindeer

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Abstract: Microbial fermentation end products were investigated in Svalbard reindeer at two different locations, on Nordenskiöldland (NL) (n=7) and in a marginal area on Nordaustlandet (NA) (n=11), at different seasons. The pH ranged from 6.51-6.70 in rumen contents and from 6.78-7.17 in the distal fermentation chamber (DFC=caecum and proximal part of the colon) on NL compared to 6.10-6.71 in rumen contents and 6.50-7.35 in DFC contents on NA. The ruminal volatile fatty acid concentration ([VFA]) was 84.5 ± 9.5 mmol/l compared to 63.9 ± 17.6 mmol/kg in the DFC on NL in winter. In autumn, ruminal and DFC [VFA] was high at 113.5 ± 13.0 mmol/l and 90.4 ± 10.9 mmol/kg, respectively. On NA ruminal [VFA] was 85.7 ± 12.4 mmol/l and 59.6 ± 1.3 mmol/kg in the DFC in winter, compared to 107.3 ± 18.4 mmol/l and 102.0 ± 12.7 mmol/kg in rumen and DFC, respectively, in summer. Mean acetate/propionate (A/P) ratios in the rumen indicate fermentation in favour of plant fibre digestion in winter (4.8) but not in autumn (3.0) on NL. On NA, the mean A/P ratio was 5.1 in winter, compared to 4.6 in summer. In all DFC investigated the A/P ratio was higher than 8.9. The initial ruminal [VFA] did not reflect the VFA production measured. On NL, the production rate of VFA was low or not detectable in rumen and DFC in winter, while in autumn the total production rate of VFA was 59.3 kJ/kg$W^{0.75}$/d, of which 6.5% originated from the DFC. On NA in winter, a total of 121.3 kJ/kg$W^{0.75}$/d was estimated of which 17% originated from the DFC, compared to a total of 380.4 kJ/kg$W^{0.75}$/d in summer where the DFC only contributed 2.7%. Plants (grasses and mosses) with low quality in winter do not seem to contribute significantly to the VFA production in rumen and DFC. VFA production in the DFC seems to be of significant importance in reindeer when pastures have low availability but high quality. The concenttation and the rate of VFA production in the DFC contents were not related to the size of the chamber, but to the diet eaten.

Key words: *Rangifer tarandus platyrhynchus*, volatile fatty acids, energy production.

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Introduction

Ruminants satisfy their energy requirements by utilising end products from fermentation of microorganisms living in the gastrointestinal tract (Barcroft *et al.*, 1943; Annison & Armstrong, 1970). The rumen of domestic animals has been subject of many publications and shows that ruminal volatile fatty acid (VFA) concentration and pool size are cor-

related with VFA production rate (Leng & Brett, 1966; Leng *et al*, 1968; Weston & Hogan, 1968; White & Staaland, 1983). Research on fermentation in the rumen and in the distal fermenting chamber (DFC = caecum and proximal part of the colon, before the colon enters the colon coil) in wild animals is limited. Lechner-Doll *et al.* (1991) found only small seasonal variation in the VFA concentration in African domestic ruminants which reflected the food availability and quality. The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) live under the most austere nutritional conditions on the high-arctic archipelago of Svalbard (77-81°N). Their distribution range from high quality pastures on Nordenskiöldland (NL) to that of Nordaustlandet (NA) with a marginally vegetation, characterised as an arctic desert (Staaland & Punsvik, 1980). According to Hofmann (1985; 1989), reindeer are classified as adaptable intermediate feeders based on their gastrointestinal (GI) anatomy and feeding habit which express their ability to use a mixed diet with low fibre content (Hofmann & Stewart, 1972). The wet weight of the reticulo-rumen contents in adult female Svalbard reindeer was 77.6% of the total GI content (Staaland *et al.*, 1979) in summer, 76.6% in autumn and 76.3% in winter (Sørmo *et al.*, unpubl.). The DFC (distal fermentation chamber) of adult female Svalbard reindeer is large contributing 9.8% of the GI contents in autumn and 9.0% in winter (Sørmo *et al.*, unpubl.). Orpin *et al.* (1985) and Mathiesen *et al.* (1987) found highly active microbial organisms in the rumen and caecum of Svalbard reindeer, with strong seasonal changes in the number and composition of bacteria. Svalbard reindeer are faced with seasonal changes in photoperiod and have a corresponding pattern in food intake, which is low in winter compared to summer (Larsen *et al.*, 1985). Using the predicted data from Nilssen *et al.* (1984) and from White & Staaland (1983), the ruminal production in summer on NL (575 kJ/kg $W^{0.75}$/d) contributed 80.5% more than fasting metabolic rate in Svalbard reindeer, but the importance of VFA produced in the DFC is not understood. The contribution of fermentation products from the rumen in winter is still unclear. We therefore wanted to examine the rumen and DFC contribution of VFA's, lactate and succinate to the daily energy supply in Svalbard reindeer in different locations and at different times of the year. The ruminal and DFC fermentation in Svalbard reindeer were therefore evaluated by investigating production rates of VFA using the zero-time *in vitro* technique (Carroll & Hungate, 1954; Hungate *et al.*, 1961; Hungate, 1966; White & Staaland, 1983; Olsen & Mathiesen, 1996).

Material and methods

The study area

The investigation was carried out in one lush and one marginal area of Svalbard. The rich area was located between 78°05´-78°17´N and 15°00´-17°30´E and included several locations on the peninsula Nordenskiöldland (NL). Snow covers the ground for 8-9 months in winter and the vegetation is dominated by grasses and mosses. The marginal investigation area was Nordaustlandet (NA) (79°17´-80°50´N and 17°47´-27°22´E), an island separated from Spitsbergen by the Hinlopen strait. Glaciers covers 80% of the island, and snow covers the ground for 9-10 months of the year. The vegetation is scarce and the area is characterised as an arctic desert (Staaland & Punsvik, 1980).

Animals

A total of 7 animals were investigated on NL (3 males in winter (April) 1994, 2 females in winter (April) 1995 and 2 females in autumn (October 1995)). On NA a total of 11 adult animals were investigated. Of these were two slaughtered in winter (April) 1994, one male and one female. In August 1995, 9 animals were investigated; 3 males and 6 females. All animals were shot while grazing and all samples were taken in the field immediately after killing. The whole animal and the ruminal and DFC contents were weighed and pH was recorded in the contents immediately after killing. The rumen contents also include contents from the reticulum, the DFC consisted of caecum and the proximal part of the colon, before it enters the colon coil.

Chemical analyses

Samples of rumen contents were frozen (-20 °C) after death of the animal and were brought to the laboratory in Tromsø where it was dried at 115 °C until constant weight and the dry matter content was estimated. Analyses of the plant cell wall fraction (hemicellulose, cellulose and lignin) which was calculated from values of neutral detergent fibre (NDF), acidic detergent fibre (ADF) and acid detergent lignin (ADL), were carried out using the techniques of Van Soest (1963 a; b), Van Soest & Wine (1967) and Goering & Van Soest (1970). Nitrogen contents were determined by the Kjeldahl method (Horwitz, 1980) and converted to crude protein

(CP) by multiplication by 6.25. The amount of water-soluble carbohydrates (WSC) was determined as described in Olsen *et al.* (1994). Dry samples were ashed at 550 °C for 12h to convert all measurements to an organic matter (OM) basis.

In vitro *fermentation of ruminal and DFC contents*
When obtaining the rumen and the DFC contents, standard methods for rumen microbial studies were used (Orpin *et al.*, 1985; Olsen & Mathiesen, 1996). The total rumen and DFC fluid volume was found by determining the dry matter content. To obtain the concentration and production rate of acetate, propionate and butyrate, which constitute the total volatile fatty acids (VFA), the whole rumen and the whole DFC was emptied into pre warmed thermos flasks (10 l and 5 l) which were sealed. The zero-time *in vitro* technique was used to obtain the concentration and production rate of VFA in Svalbard reindeer (Carrol & Hungate, 1954; Hungate *et al*, 1961; Hungate, 1966; White & Staaland, 1983; Olsen & Mathiesen, 1996). By incubating the rumen and DFC contents anaerobically, a curve could be constructed from the change in VFA levels in the sample during the incubation period (70-120 min). The slope of the curve represents the rate of production *in vivo,* at the time the sample was collected from the animal. By extrapolating the regression lines to zero, we could determine the concentration of VFA in the fermenting chambers at the time of death. The contents were mixed thoroughly between each sampling. A sub sample of rumen contents (about 100 g) was sieved through two layers of muslin. The filtrate (10 ml) was fixed in 5 ml 0.5M HCl and was frozen in counting tubes (-20 °C) until analysis. Individually marked and weighed counting tubes, each containing 10 ml 0.5M HCl were added approximately 5 g of DFC contents at different time intervals in the field, and were sealed and frozen (-20 °C). After arrival at the laboratory at Department of Arctic Biology at Tromsø, the tubes were weighted and the added amount of DFC contents in each tube was calculated before analysis. All samples were taken in duplicate. From the one-hour estimate of VFA production, a total 24 h production of VFA was calculated. The VFA`s produced were assumed to be absorbed in the rumen or down the gastrointestinal tract. Therefore the contribution of VFA`s from the rumen and DFC to the total energy budget could be calculated. Energy available from the VFA pool was calculated using energy values of 874, 1534 and 2190 kJ/mole for acetic, propionic and butyric acids, respectively (Blaxter, 1962).

Measurements of pH
Ruminal and DFC contents were transferred to pre-warmed thermos containers and pH was recorded in the contents with two calibrated portable pH meters (pHM 80 and pHM 201, Radiometer®, Copenhagen) with combined pH electrodes (GK 2501C and pHC 2005, Radiometer®, Copenhagen) at 10-15 min intervals for maximum 120 min after killing. By extrapolating the calculated regression lines for changes in pH to zero time, the pH at time of death could be estimated. Change in pH per unit time was used as an indicator of fermentation rate. Temperature in the ruminal and caecal contents was kept between 35 °C and 39 °C during the sampling period.

GLC analyses
Samples of ruminal and DFC contents for analyses of VFA concentration were collected at 10-15 min intervals for maximum 120 min after killing. The samples were analysed for VFA, lactate and succinate by means of GLC (Cromepack CP 9000; Crompack, Bergen op Zoom, Holland) as described in Olsen & Mathiesen (1996) and Sørmo *et al.* (1994). Each sample was homogenised and an internal standard (IS): (0.5 ml of 0.2136 g 2-ethyl butyric acid dissolved in 250 ml distilled water) and 0.6 ml 12M HCl were added to 1ml of the homogenised sample, mixed for 0.5 min and extracted with 2 ml of diethyl ether for 1 min. The sample was centrifuged in a Labofuge, speed 5 for 5 min., the ether phase was removed and collected, and the sample was extracted again for 1 min using 1 ml of diethyl ether. Again the ether phase was removed after 5 min centrifuging. N-tert-butyldimethylsilyl-N-methyltrifluoracetamide (MTBSTFA; 10µl) was added to the combined ether extract in a test tube, which was sealed. The acids were derivated by heating for 20 min at 82 °C. Samples were kept at room temperature before injecting 0.5 µl into a gas chromatograph fitted with a CP SIL 8 CB column (Cromepack no 7452, 30 m, 0.2 mm ID) containing a film (0.25 µm) of silica gel. The carrier gas was H_2 at 45 cm/s. Injector temperature was 250 °C and detector temperature was 270 °C.

Statistical analyses
The non-parametric Wilcoxon rank sum test (Bhattacharyya & Johnson, 1977) was used to deter-

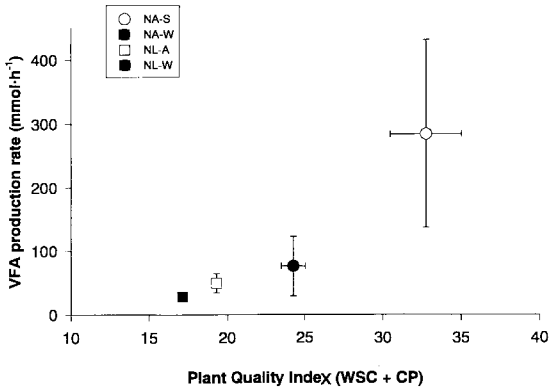


Fig. 1. Plant quality index (water soluble carbohydrares and crude protein) (mean ±SD) versus production rare of volatile fatty acids (mmol/h)(mean ±SD) in Svalbard reindeer on Nordenskiöldland (NL) and on Nordaustlandet (NA) different times of the year, ●= NL winter, ❑= NL autumn, ●= NA winter and ○ = NA summer.

mine differences among animal groups. Statistical significance was assumed to be at $P \leq 0.05$.

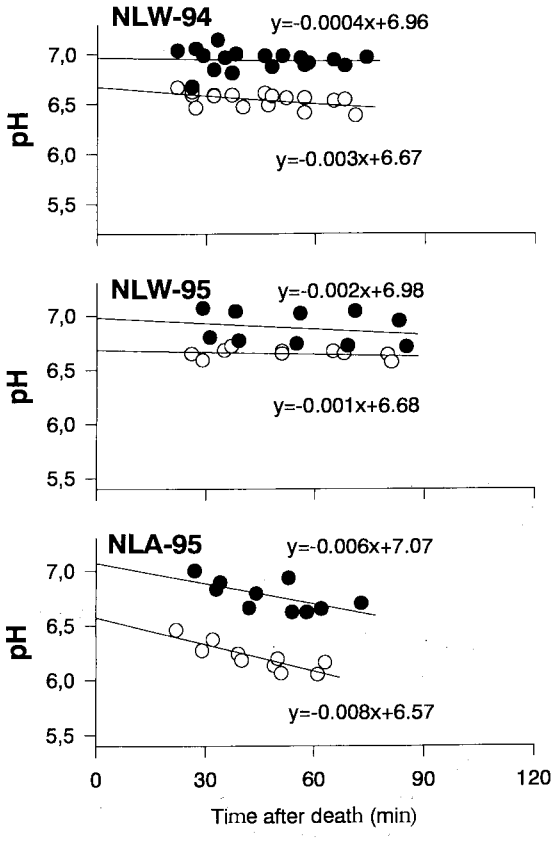
Results

Chemical composition

Chemical composition of the rumen contents of Svalbard reindeer grazing on NL and on NA is calculated from Sørmo *et al.* (unpubl.) and is shown in Table 1. The cell wall contents from the rumens of NA reindeer were lower than in NL. Both the water-soluble carbohydrates (WSC) and crude protein (CP) were concomitantly higher in NA than in NL reindeer. Highest WSC and CP and lowest cell walls were noted for NA reindeer in summer. Lowest WSC and CP were recorded in the rumens of NL reindeer in winter (Fig. 1).

pH

Ruminal and DFC pH in Svalbard reindeer from different locations and seasons are shown in Tables 2 and 3 and in Fig 2. In Tables 2 and 3 are pH at t_0 from individual animals presented, and a mean and SD for each group of animals is calculated based on the individual measurements. In Fig. 2, the slope and pH at t_0 is calculated from the regression line, which includes all measurements from each group



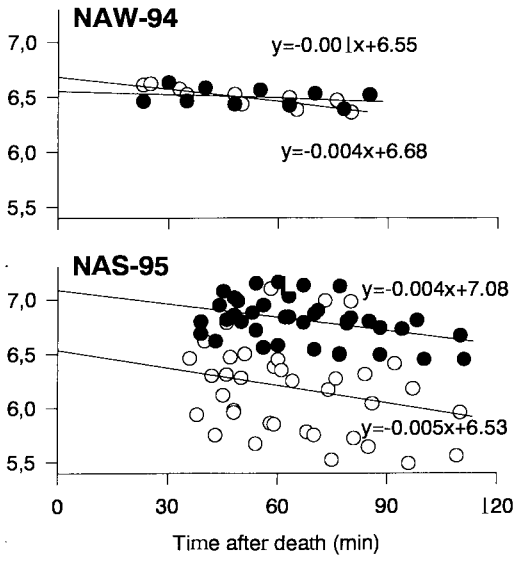


Fig. 2. Regression lines plot for the pH in the rumen (○) and in the distal fermentation chamber (●) of Svalbard reindeer at Nordenskiöldland (NL) and on Nordaustlandet (NA) different times of the year as a function of time. (W=winter. A=autumn. S=summer).

of animals. There were no significant differences ($P>0.05$) in ruminal initial pH between locations and seasons (Tables 2 and 3). There were no significant differences in initial pH in the DFC contents between animals shot in autumn and winter on NL (Table 2). Mean initial pH in DFC contents at NA in winter (6.6 ± 0.12) was significantly ($P=0.05$) lower than pH in the DFC in reindeer on NA in summer (7.0 ± 0.22) ($W_s=3$, $n_1=2$, $n_2=7$) and compared to pH measured in the DFC on NL in winter (7.0 ± 0.17) ($W_s=3$, $n_1=2$, $n_2=5$) (Table 2 and 3). In the rumen of reindeer on NL in winter, pH (mean ±SD) decreased 0.09 ± 0.04 units per hour, significantly different from autumn (-0.48 ± 0.01 units/h, $P=0.05$, W s=3, $n_1=5$, $n_2=2$). On NA the rate of pH decrease was 0.24 ± 0.08 in winter and not significantly different from summer (-0.35 ± 0.14 units/h), (Fig. 2). Rate of pH decrease in rumen contents on NL in winter was significantly lower ($P=0.05$, $W_s=3$, $n_1=5$, $n_2=2$), than on NA in winter. On NL, rate of pH decrease in DFC in winter was low (-0.12 ± 0.05 units/h), compared to -0.36 ± 0.02 units/h in autumn. On NA in winter, rate of pH decrease in DFC contents was 0.10 ± 0.03 and not different from that found in summer (-0.21 ± 0.13) ($P>0.05$), (Fig. 2).

Ruminal and DFC concentration of VFA

On NL in winter, ruminal initial mean total [VFA] (85 ± 9.5 mmol/l) was significantly lower ($P=0.05$, $W_s=3$, $n_1=5$, $n_2=2$) than in autumn (113 ± 13.0 mmol/l) (Table 2). On NA, mean initial ruminal [VFA] in summer (107 ± 18 mmol/l) was higher than in winter (86 ± 12 mmol/l) but differences were not significant (Table 3). Ruminal [VFA] in winter on NL and NA were closely similar (Tables 2 and 3). No difference in initial [VFA] in the DFC between winter and autumn on NL were observed, but on NA DFC [VFA] was significantly lower in winter (60 ± 1.3 mmol/l) compared to summer (102 ± 12.7 mmol/l) ($P=0.05$, $W_s=3$, $n_1=2$, $n_2=8$) (Table 2 and 3). There were no differences between [VFA] in females and males at NA in summer. Significant differences ($P=0.05$) in VFA pool size between winter and summer were observed on NA, but not on NL (Table 4 and 5). In addition to the

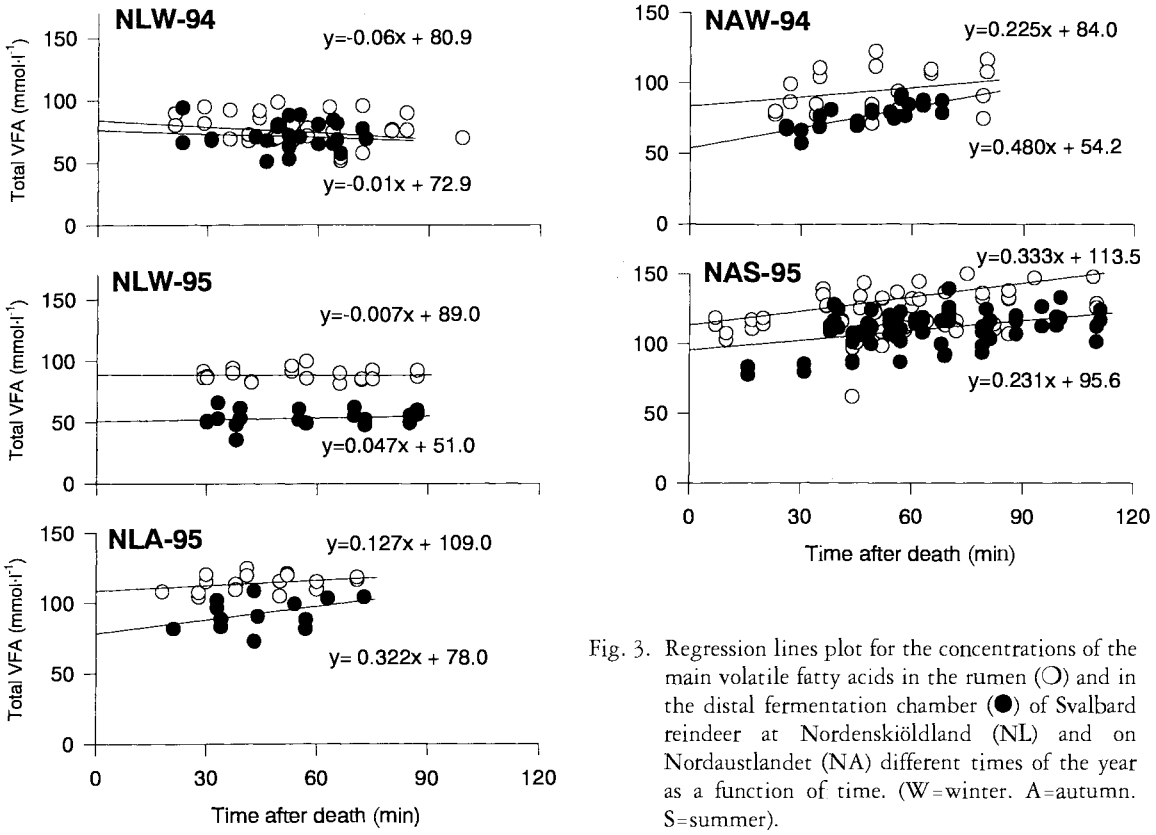


Fig. 3. Regression lines plot for the concentrations of the main volatile fatty acids in the rumen (○) and in the distal fermentation chamber (●) of Svalbard reindeer at Nordenskiöldland (NL) and on Nordaustlandet (NA) different times of the year as a function of time. (W=winter. A=autumn. S=summer).

total VFA, several other volatile fatty acids, in addition to lactate and succinate were found in the rumen and in the DFC of Svalbard reindeer (Table 6). In Tables 2 and 3 are [VFA] at t_0 from individual animals presented, and a mean and SD for each group of animals is calculated based on the individual measurements. In Fig. 3 the slope and [VFA] at t_0 is calculated from a regression line which includes all measurements from each group of animals.

Acetate, propionate and butyrate ratio

On NL in winter the ruminal mean ratio of acetate, propionate and butyrate (A/P/B) was 77:17:6 compared to 70:24:6 in autumn. On NA butyrate was a relatively more important acid and the A/P/B ratio was 76:15:9 in winter and 73:16:11 in the rumen in summer. In the DFC acetate was relatively more important than in the rumen and the A/P/B ratio was 92:6:2 in winter on NL compared to 90:8:2 in autumn. On NA in winter the A/P/B ratio in the DFC was 88:8:4 compared to 89:8:3 in summer. The major difference between VFA ratios in the rumen and DFC was the A/P ratio (Tables 2 and 3). In the rumen of NL and NA reindeer, ratios were between 3.0 to 5.1, whereas those in the DFC were 10.7 to 14.8. In the rumen, lowest A/P ratios were associated with highest [VFA].

VFA production rate

In seven of ten data sets ruminal and DFC [VFA] increased with time to give regression coefficients of 0.047 to 0.480 mmol/h/ml (Fig. 3). The lowest value was driven by one of three animals with a significant trend, therefore no seasonal VFA production was determined for the DFC of NL reindeer in the winter (Table 4). For the rumen contents of NL reindeer in winter there was an overal decline in [VFA] with time (Fig. 3), again no *in vitro* VFA production rate could be estimated (Table 4). For all NA animals [VFA] increased with time (Table 5, Fig. 3) and mean VFA production rates were determined for both winter and summer (Table 5). Thus, on NL, total ruminal and DFC VFA rate of production was low or not detectable in winter but in autumn VFA production accounted for 59 ± 6 kJ/kg$W^{0.75}$/d of metabolizable energy of which 6.5% originated from the DFC (Table 4). On NA in winter the total rate of VFA production accounted for 121.3 (69.5 kJ/kg$W^{0.75}$/d metabolizable energy of which 17% originated from the DFC. In summer VFA metabolizable energy was 380.4 ± 182.9 kJ/kg$W^{0.75}$/d, a significant increase over winter (P=0.02, W_s=3, n_1=2, n_2=9), but the DFC contributed only 2.7%. (Table 5). Initial ruminal VFA concentration was not correlated with ruminal VFA production rate (Tables 2 and 3). This was confirmed in the contents of the DFC. Rate of decrease of ruminal pH (Fig. 2) was related to increased VFA production rate (Table 4 and 5, Fig. 3), but was not significant for the DFC.

Discussion

pH

In domesticated ruminants fed a high quality diet the *in situ* pH in the rumen is usually between 5.5 and 6.7 (Hungate, 1966). Ruminal pH is dependent on the diet, the rate of salivary secretion, rate of VFA production and absorption across the rumen wall (Church, 1983). The mean initial pH measured in the rumen of Svalbard reindeer did not vary significantly between seasons and locations, ranging from 6.48 to 6.68 (Table 1 and 2, Fig. 2). These values are similar to that measured by White & Staaland (1983) but high compared to that found by Orpin *et al.* (1985) where a mean (± SD) pH of 6.19 ± 0.16 in the rumen fluid was measured in summer. In winter Orpin *et al.* (1985) observed a mean pH of 6.75 ± 0.18 in the rumen fluid. The small differences in pH observed could be due to seasonal changes in capacity of salivary secretion. The *in vitro* rate of decrease of pH in the rumen contents could indicate differences in rate of VFA production. On NA in summer, pH decreased 0.35 units/h compared to as much as 0.8 units/h on NL in summer (calculated from White & Staaland, 1983) and 0.48 units/h in autumn on NL (Fig. 2). The difference in ruminal pH rate of decrease between seasons and locations are not simply explained by differences in plant quality (Table 1). As based on WSC and CP levels, the highest rate of change should be NA in summer, NA in winter and then NL in autumn (Fig. 1). Ruminal pH also reflects VFA production. In the DFC, pH was lowest (P=0.05) in winter at NA indicating a more active microbial environment in this fermenting chamber compared to that found in the other seasons and areas (Tables 2 and 3). This is also reflected in the relatively high production rates of VFA from the DFC in this area in winter (Tables 4 and 5). On NL the DFC pH was not different in autumn and winter (Table 2). Mathiesen *et al.* (1987) found the pH in the caecum of Svalbard reindeer on NL to be low in

summer (6.81 ± 0.12) and high in winter (7.14 ± 0.26) which contrasts our findings, which could be due to local variation in plant species and plant quality. Orpin *et al.* (1985) and Mathiesen *et al.* (1987) found that the ruminal and caecal bacterial composition is strongly affected by changes in diet quality and availability which in turn is reflected in the pattern and production rate of VFA and, hence, the pH. Regulation of pH in the DFC is, however, not well understood. PH in rumen and DFC influence on absorption of VFA. The mechanism for absorption of VFA across the caecal mucosa is by simple diffusion (Myers *et al.*, 1967), but rate of absorption in the rumen and caecum of individual VFA was decreased 40-67% by increasing pH from 4.5-7.2 in the rumen (Dijkstra *et al.*, 1993), and decreased by 44% when increasing the pH from 6.2 to 7.5 in the caecum (Myers *et al* , 1967).

Concentration and production rate of ruminal VFA

The concentration and composition of VFA in the Svalbard reindeer rumen (Table 2 and 3) is comparable to that found in the rumen fluid of domestic ruminants eating a poor quality forage (Hungate, 1966) and of domestic tuminants grazing in a thornbush savannah (Lechner-Doll *et al.*, 1991). In ruminants the VFA concentration and production rate is determined by food quality and quantity (Hungate, 1966), but also of dilution rate, rumen fluid volume and absorption rate (Lechner- Doll *et al* , 1991). White & Staaland (1983) found an initial [VFA] in summer on NL at 89 ± 6 mmol/l (mean ± SD). This is low compared to that found in these experiments where the [VFA] was 107 ± 18 mmol/l in summer on NA and 114 ± 13 mmol/l in autumn on NL. In free-living Norwegian reindeer the initial total [VFA] was 79 mmol/l (Aagnes *et al* , 1995) in winter compared to 85 ± 10 mmol/l on NL and 86 ± 12 mmol/l on NA in Svalbard reindeer in winter. No positive correlation between the chemical composition of rumen contents in the animals investigated and [VFA] could be observed (Table 1, 2 and 3), even if there were differences in plant cell wall constituents. The difference in ruminal chemical composition among locations is, however, reflected in ruminal VFA production (Table 1, 4 and 5, Fig. 3., Fig. 1). White & Staaland (1983) estimated a ruminal VFA rate of production corresponding to 575 kJ/kg$W^{0.75}$/d on NL in summer. On NA in summer and on NL in autumn, ruminal VFA production represented 58 and 10%, respectively, of that found on NL in summer, which indicates a high forage quality on NL in summer (Table 4, 5 and Fig. 3). The difference probably reflects differences both in plant quality and availability (Weston & Hogan, 1968). These data support our understanding of the marginal summer and winter pasture where the availability seem to be low both summer and winter, but the quality seem to be high in NA. The low ruminal production tate on NL in winter seem to be related to a high proportion of ruminal plant cell wall and mosses (54%) (Table 1, Sørmo *et al* , unpubl.). The concentration and pool size of VFA seem to be correlated with VFA production rate in domesticated ruminants (Weston & Hogan, 1968; Leng & Brett, 1966; Leng *et al.*, 1968). This seems not to be the case in arctic ruminants like reindeer with strong seasonal changes in food intake and plant quality. Ruminal VFA concentration and pH were high in reindeer on NL in winter (Table 2), but VFA production rate was low (Table 4, Fig. 3). It is likely that VFA absorption across the rumen wall of Svalbard reindeer is low in winter when pH is high and could explain the high VFA levels measured. Lechner-Doll *et al.* (1991), observed that dilution rate, rumen fluid volume and absorption rate influenced VFA concentration far more than the production rate in seasonal Aftican domestic ruminants. Weston & Hogan (1968) also indicate that variations in diet and physiological state of the animal could influence on the blood flow supply to the rumen epithelium and could result in changes in absorption rates, pool size and rate of production of VFA relative to the VFA concentration. In Norwegian reindeer the absorptive surface of the rumen decreased between September and April with 48% determined by surface enlargement factor estimates of the rumen epithelium (Josefsen *et al.*, 1996). We assume the absorptive surface of rumen epithelium in Svalbard reindeer changes from summer to winter in a similar pattern, and the change could influence on the rate of VFA absorption.

Concentration and production rate of DFC VFA.

Large amounts of the cell wall carbohydrates like cellulose and hemicellulose partially escape rumen digestion and thus become available for fermentation by DFC bacteria (Van Soest, 1994). The proportion of hemicellulose digested in the latge intestine is higher than that of cellulose (Ulyatt *et al.*, 1975; Van Soest, 1994). This apparent resistance of hemicellulose for rumen fermentation could be an important factor limiting the rate of breakdown of cell wall carbohydrates in the rumen. Gray (1947)

found that 17% of the digestible cellulose was digested in the caecum, 70% in the rumen and 13% in the colon of sheep. Chemical analyses of the plants in the rumen contents of the Svalbard reindeer suggest that the amount of plant cell wall is high on NL and low on NA (Table 1, Sørmo *et al.*, unpubl.). Anatomical studies of Svalbard reindeer have shown that the volume of the DFC increases relative to the rumen volume when the amount of hemicellulose increases in the rumen contents (Sørmo *et al.*, unpubl.), indicating that the importance of the DFC could be related to hemicellulose fermentation. The concentration of VFA in the DFC was significantly lower in winter than in summer on NA, but no differences were observed in the ruminal hemicellulose content (Table 1 and 3, Sørmo *et al.*, unpubl.). The production rate of VFA in the DFC on NA in summer was, however, only half of that found in winter and contributed only 2,7% of the total energy produced from VFA in the GI system in summer compared to 17% in winter (Table 5). This is probably due to the botanical composition of the plants eaten, since rumen contents consisted mostly of *Saxifraga* spp. (55%) and *Draba* spp. (12%) in winter compared to grasses (53%) in summer (Sørmo *et al.*, unpubl.). Caecal volume relative to ruminal reticulum volume is higher in concentrate selectors than in grazers (Hofmann & Stewart, 1972; Hofmann, 1973; 1985; 1989). In African ruminants there is no experimental evidence to support the view that caecal digestion is relatively more important in concentrate selectors than in grazers or intermediate feeders (Hoppe, 1984). We found, however, that in the Svalbard reindeer the DFC contributes substantially (17%) to the total production of VFA in winter in an area where food is scarce and that the importance of DFC seems less when food is abundant. In sheep, caecal VFA contain a relatively higher proportion of branched chain acids compared to the rumen, indicating greater conversion of protein to VFA (Ørskov *et al.*, 1970). In the Svalbard reindeer the concentration of branched, chained VFA in the DFC did not indicate a high fermentation of protein (Table 6).

Energetics

The energy contributions from VFA from the rumen and DFC of reindeer on NA in winter and summer were 8.0 and 67.3%, respectively, more than the fasting metabolic rate of reindeer (112.3 $KJ/kgW^{0.75}/d$) predicted by Nilssen *et al.* (1984), regardless of season. On NL in summer, VFA contributed as much as 80.5% more than the fasting metabolic rate (White & Staaland, 1983; Nilssen *et al.*, 1984) but in autumn, VFA production contributed only 67.4% of fasting metabolic rate. Annison & Armstrong (1970) estimated that in ruminants 50-70% of the basal metabolic rate (BMR) originates from VFA production from the digestive system. On NL in winter, however, the VFA production rates from the rumen and DFC was very low contributing 0-45.7% to the fasting metabolic rate calculated from Nilssen *et al.* (1984). This has also been observed for other ruminants like the Klipspringer (*Oreotragus oreotragus*) where the ruminal VFA as % of BMR contributed only 11% (Hoppe, 1984). Orpin *et al.* (1985) calculated that body fat in Svalbard reindeer can only supply 10-30% of the daily energy expenditure during the winter and that the rest probably originated from the plants eaten. The mosses in the rumen contents of the NL reindeer did not seem to contribute significantly to energy production in winter.

In conclusion, the seasonal and geographical differences in diet of the Svalbard reindeer are reflected in the fermentative activity in the rumen and DFC micro-organisms. In areas with abundant vegetation with high contents of plant cell walls but low WSC and protein levels, the production rate of VFA is low both in the rumen and DFC, even though the size of the DFC is large. In areas where cell wall material is low and WSC and CP relatively high, but plant availability is low, the production rate of VFA is high both in summer and winter and the DFC contributes as much as 17% of the total VFA produced in winter.

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Appendix: Tables 1–6

Table 1. Chemical composition of organic dry matter in the rumen of Svalbard reindeer (%, mean ± SD).

	Nordenskiöldland			Nordaustlandet	
	W 1994 $n=3$	W 1995 $n=2$	A 1995 $n=4$	W 1994 $n=2$	S 1995 $n=9$
Cell wall	75.6 ± 3.2	62.3 ± 5.2	68.9 ± 3.2	45.1 ± 3.2	48.6 ± 4.1
WSC*	1.3 ± 0.4	1.0 ± 0.3	1.6 ± 0.5	5.8 ± 2.5	4.5 ± 2.1
Crude protein**	12.4 ± 1.1	14.7 ± 1.8	17.7 ± 0.8	18.5 ± 1.7	28.2 ± 2.0
Plant quality index***	13.7	15.7	19.3	24.3	32.7

W=winrer, A=autumn, S=summer. Data modified from Sørmo *et al.*, unpubl.
* WSC = warer soluble carbohydrates.
** Crude protein = total rumen nitrogen x 6.25.
***Plant quality index = WSC + crude prorein.

Table 2. PH and volatile fatty acid (VFA) concentrations estimated from zero time extrapolation, and relative molar proportions of VFA's in the rumen and distal fermentation chamber (DFC) of Svalbard reindeer on Nordenskiöldland.

SEASON	SEX	FERMENTING CHAMBER	pH (t_0)	Total VFA in rumen/DFC fluid (t_0) mmol/l or mmol/kg	Time for first sampling after death (min)	VFA concentrations in rumen/DFC fluid (mmol/l or mmol/kg)			AC/PR ratio
						Acetate	Propionate	Butyrate	
Winter	female	RUMEN	6.70	86.0	30	67.7	14.0	4.3	4.8
1995		DFC	7.11	43.6	31	39.8	3.0	0.8	13.3
	female	RUMEN	6.67	94.0	29	73.7	16.4	3.9	4.5
		DFC	6.84	58.4	29	53.0	4.3	1.1	12.3
Winter	male	RUMEN	6.69	68.6	22	48.5	12.5	5.1	3.9
1994		DFC	7.05	88.0	22	82.4	4.5	1.1	18.3
	male	RUMEN	6.55	88.5	27	70.1	13.4	4.3	5.2
		DFC	7.17	74.9	27	69.6	4.1	1.2	17.0
	male	RUMEN	6.66	85.6	26	66.8	12.0	3.9	5.6
		DFC	6.78	54.4	27	49.5	3.8	1.1	13.0
Autumn	female	RUMEN	6.51	122.7	22	85.8	29.6	7.3	2.9
1995		DFC	6.84	98.1	27	87.5	8.6	2.0	10.2
	female	RUMEN	6.58	104.3	29	72.9	24.2	7.2	3.0
		DFC	7.03	82.7	33	74.8	6.7	1.3	11.2
WINTER	MEAN ± SD	RUMEN	6.7 ± 0.06	85 ± 9.5	-	65 ± 9.8	14 ± 1.7	4 ± 0.5	4.8 ± 0.7
		DFC	7.0 ± 0.17	64 ± 17.6	-	59 ± 17.0	4 ± 0.6	1 ± 0.2	14. 8 ± 2.7
AUTUMN	MEAN ± SD	RUMEN	6.6 ± 0.05	113 ± 13.0	-	79 ± 9.1	27 ± 3.8	7 ± 0.1	3.0 ± 0.1
		DFC	6.9 ± 0.13	90 ± 10.9	-	81 ± 9.0	8 ± 1.3	2 ± 0.5	10.7 ± 0.7
SUMMER	MEAN	RUMEN*	6.5	89 ± 6.0		67	15	5	4.4

* Data calculated from White & Staaland, 1983.

Table 3. PH and volatile fatty acid (VFA) concentrations estimated from zero time extrapolation, and molar proportions of VFA's in the rumen and distal fermentation chamber (DFC) of Svalbard reindeer on Nordaustlandet.

SEASON	SEX	FERMENTING CHAMBER	pH (t_0)	Total VFA in rumen/DFC fluid (t_0) mmol or l/mmol/kg	Time for first sampling after death (min)	VFA concentrations in rumen/DFC fluid (mmol/l or mmol/kg)			AC/PR ratio
						Acetate	Propionate	Butyrate	
Winter	female	RUMEN	6.66	76.9	23	59.2	10.5	7.2	5.6
1994		DFC	6.50	60.5	23	53.4	4.9	2.2	11.0
	male	RUMEN	6.70	94.4	25	70.0	15.6	8.8	4.5
		DFC	6.67	58.6	30	51.2	4.8	2.6	10.7
Summer	female	RUMEN	6.49	146.7	38	102.6	22.9	21.2	4.5
1995		DFC	7.35	112.8	40	101.2	9.2	2.4	11.0
	female	RUMEN	6.55	84.3	44	59.9	14.9	9.5	4.0
		DFC	6.92	104.1	46	94.1	7.3	2.7	12.9
	female	RUMEN	6.26	103.8	52	75.5	17.6	10.7	4.3
		DFC	6.86	107.9	54	94.5	8.6	4.8	11.0
	female	RUMEN	6.56	119.1	36	89.3	18.7	11.1	4. 8
		DFC	6.85	108.7	39	94.3	10.1	4.3	9.3
	female	RUMEN	NM	94.1	10	69.4	15.1	9.6	4.6
		DFC	NM	NM	NM	NM	NM	NM	NM
	female	RUMEN	NM	113.7	7	78.6	22.6	12.5	3.5
		DFC	NM	78.1	15	68.4	7.7	2.0	8.9
	male	RUMEN	6.71	95.2	46	67.6	14.4	13.2	4.7
		DFC	7.24	115.8	49	103.5	9.5	2.8	10.9
	male	RUMEN	6.10	111.0	37	81.4	19.0	10.6	4.3
		DFC	6.79	99.1	39	88.4	6.8	3.9	13.0
	male	RUMEN	6.69	97.9	40	74.2	11.4	12.3	6.5
		DFC	7.11	89.2	44	82.2	4.6	2.4	17.9
WINTER	MEAN ± SD	RUMEN	6.7 ± 0.03	86 ± 12.4	-	65 ± 7.6	13 ± 3.6	8 ± 1.1	5 ± 0.8
	MEAN ± SD	DFC	6.6 ± 0.12	60 ± 1.3	-	52 ± 1.6	5 ± 0.07	2 ± 0.3	10 ± 0.2
SUMMER	MEAN ± SD	RUMEN	6.5 ± 0.22	107 ± 18.4	-	78 ± 12.6	17 ± 3.8	12 ± 3.6	4 ± 0.8
	MEAN ± SD	DFC	7.2 ± 0.22	102 ± 12.7	-	91 ± 11.3	8 ± 1.8	3 ± 1.0	12 ± 2.8

NM = not measured.

Table 4. Body mass, ruminal and DFC fluid volume (FV), pool size and production rates of VFA in Svalbard reindeer on Nordenskiöldland.

SEASON	SEX	Body mass (kg)	FERM. CHAMBER	FV (litres)	VFA pool			VFA production rate	
					mmol	kJ	kJ/kg$W^{0.75}$	mmol/h	kJ/kg $W^{0.75}$/d
Winter	female	58.0	RUMEN	9.69	833.4	867.9	41.3	28.1	33.7
1995			DFC	1.15	50.1	47.3	2.3	6.5	7.0
	female	43.5	RUMEN	8.96	842.0	879.1	51.9	0	0
			DFC	1.00	58.4	55.4	3.3	0	0
Wmter	male	52.0	RUMEN	6.47	443.8	506.0	26.1	0	0
1994			DFC	1.11	97.7	90.3	4.7	0	0
	male	62.0	RUMEN	9.36	828.1	868.4	39.3	0	0
			DFC	1.49	111.3	103.7	4.7	0	0
	male	65.0	RUMEN	7.36	630.8	976.0	42.6	0	0
			DFC	1.24	67.5	60.8	2.7	13.0	12.9
Autumn	female	56.5	RUMEN	10.18	1172.7	1300.4	63.1	38.6	49.9
1995			DFC	0.92	90.3	86.6	4.2	4.6	5.2
	female	78.5	RUMEN	7.64	796.7	890.6	33.8	60.1	61.2
			DFC	0.69	57.1	54.1	2.1	2.8	2.4
WINTER	MEAN ± SD	56.1 ± 8.56	RUMEN	8.4 ± 1.39	716 ± 175.8	820 ± 181.0	40 ± 9.3	-	-
	MEAN ± SD		DFC	1.2 ± 0.18	77 ± 26.3	72 ± 24.24	4 ± 1.1	-	-
AUTUMN	MEAN ± SD	67.5 ± 15.56	RUMEN	8.9 ± 1.80	985 ± 265.9	1138 ± 350.2	51 ± 23.7	49 ± 15.2	56 ± 8.0
	MEAN ± SD		DFC	0.8 ± 0.16	74 ± 23.5	70 ± 23.0	3 ± 1.5	4 ± 1.3	4 ± 2.0

Table 5. Body mass, ruminal and DFC fluid volume (FV), pool size and production rates of VFA in Svalbard reindeer on Nordaustlandet.

SEASON	SEX	Body mass (kg)	FERM. CHAMBER	FV (litres)	VFA pool			VFA production rate	
					mmol	kJ	kJ/kgW$^{0.75}$	mmol/h	kJ/kg W$^{0.75}$/d
Winter 1994	female	59.5	RUMEN	8.56	658.2	715.3	33.4	43.0	52.5
			DFC	0.99	60.1	58.6	2.7	18.1	19.7
	male	52.0	RUMEN	7.15	675.0	746.1	38.5	109.0	149.3
			DFC	0.90	53.0	52.3	2.7	17.3	21.2
Summer 1995	female	52.0	RUMEN	7.29	1069.9	1249.4	64.5	112.1	161.9
			DFC	0.71	80.4	76.8	4.0	5.5	6.5
	female	51.0	RUMEN	8.02	676.1	769.5	40.3	285.7	409.7
			DFC	0.87	90.7	86.6	4.5	3.7	4.4
	female	56.5	RUMEN	9.80	1017.1	1140.9	55.4	242.7	317.1
			DFC	1.12	120.4	118.6	5.8	7.3	8.3
	female	59.5	RUMEN	8.86	1054.7	1158.1	54.1	333.0	412.1
			DFC	1.02	111.1	109.8	5.1	4.2	4.6
	female	58.0	RUMEN	9.36	881.0	981.3	46.7	627.2	797.8
			DFC	0.93	NM	NM	NM	NM	NM
	female	48.0	RUMEN	7.21	819.5	942.5	51.7	227.3	344.0
			DFC	0.71	55.5	54.0	3.0	6.4	8.1
	male	73.0	RUMEN	12.61	1200.7	1388.7	55.6	158.7	176.4
			DFC	1.53	142.5	137.6	5.5	0.8	0.7
	male	57.0	RUMEN	8.74	970.2	1080.0	2.1	264.4	339.9
			DFC	1.32	131.0	127.2	6.1	20.7	23.3
	male	60.0	RUMEN	8.93	874.1	975.8	45.3	305.4	380.2
			DFC	1.26	112.1	105.8	4.9	23.5	24.7
WINTER	MEAN ± SD	55.8 ± 5.30	RUMEN	7.9 ± 1.00	667 ± 11.9	731 ± 21.8	36 ± 3.6	76 ± 46.6	101 ± 68.7
	MEAN ± SD		DFC	1.0 ± 0.06	57 ± 5.0	56 ± 4.5	2.7 ± 0.03	18 ± 0.5	21 ± 1.0
SUMMER	MEAN ± SD	57.2 ± 7.19	RUMEN	8.8 ± 1.60	952 ± 156.4	1076 ± 183.6	52 ± 7.0	284 ± 146.3	334 ± 209.6
	MEAN ± SD		DFC	1.0 ± 0.27	106 ± 28.4	102 ± 27.9	5 ± 1.0	9 ± 8.3	10 ± 8.9

NM = not measured.

Table 6 Seasonal changes in the concentration (mean ± SD) of volatile fatty acids, lactate and succinate in the rumen (mmol/l) and in the distal fermenting chamber (DFC) (mmol/kg) of Svalbard reindeer on Nordenskiöldland (NL) and on Nordaustlandet (NA).

SEASON	*n*	LOCATION	FERM. CHAMBER	ISOBUTYRIC ACID	ISOVALERIC ACID	VALERIC ACID	CAPROIC ACID	LACTIC ACID	SUCCINIC ACID
Winter	3	NL	RUMEN	0.61 ± 0.04	0.32 ± 0.04	0.27 ± 0.05	0.05 ± 0.02	0.11 ± 0.04	0.10 ± 0.04
1994	3		DFC	0.37 ± 0.05	0.24 ± 0.05	0.28 ± 0.06	0.04 ± 0.002	0.21 ± 0.15	0.30 ± 0.02
Winter	2	NL	RUMEN	0.18 ± 0.04	0.10 ± 0.003	0.35 ± 0.01	0.13 ± 0.02	0.23 ± 0.02	0.14 ± 0.05
1995	2		DFC	0.27 ± 0.02	0.13 ± 0.05	0.16 ± 0.02	0.03 ± 0.001	0.36 ± 0.03	0.17 ± 0.04
Autumn	2	NL	RUMEN	0.25 ± 0.05	0.27 ± 0.03	0.60 ± 0.12	0.16 ± 0.01	0.73 ± 0.46	0.18 ± 0.03
1995	2		DFC	0.23 ± 0.20	0.14 ± 0.09	0.22 ± 0.10	0.04 ± 0.01	1.20 ± 0.80	0.83 ± 0.40
Winter	2	NA	RUMEN	0.41 ± 0.31	0.27 ± 0.16	0.41 ± 0.32	0.23 ± 0.24	0.15 ± 0.06	0.46 ± 0.12
1994	2		DFC	0.03 ± 0.006	0.09 ± 0.07	0.20 ± 0.05	0.05 ± 0.01	0.30 ± 0.12	0.37 ± 0.05
Summer	9	NA	RUMEN	0.60 ± 0.30	0.47 ± 0.21	0.64 ± 0.13	0.38 ± 0.19	0.27 ± 0.12	0.27 ± 0.13
1995	8		DFC	0.25 ± 0.12	0.22 ± 0.11	0.39 ± 0.10	0.04 ± 0.02	1.31 ± 1.67	0.56 ± 0.55