APPLIED AND ENVIRONMENTAL MICROBIOLOGY, Jan. 1987, p. 114–118
0099-2240/87/010114-05$02.00/0

Vol. 53, No. 1

Seasonal Changes in the Cecal Microflora of the High-Arctic Svalbard Reindeer (*Rangifer tarandus platyrhynchus*)

SVEIN D. MATHIESEN,[1]* COLIN G. ORPIN,[2] YVONNE GREENWOOD,[2] AND ARNOLDUS S. BLIX[1]

Department of Arctic Biology and Institute of Medical Biology, University of Tromsø, 9001 Tromsø, Norway,[1] and Agricultural and Food Research Council, Institute of Animal Physiology and Genetics, Babraham, Cambridge CB2 4AT, United Kingdom[2]

Received 24 April 1986/Accepted 1 September 1986

The dominant cecal bacteria in the high-arctic Svalbard reindeer were characterized, their population densities were estimated, and cecal pH was determined in summer, when food quality and availability is good, and in winter, when it is very poor. In summer the total culturable viable bacterial population was (8.9 ± 5.3) × 10^8 cells ml^{-1}, whereas in winter it was (1.5 ± 0.7) × 10^8 cells ml^{-1}, representing a decrease to 17% of the summer population density. Of the dominant species of cultured bacteria, *Butyrivibrio fibrisolvens* represented 23% in summer and 18% in winter. *Streptococcus bovis* represented 17% in summer and 5% in winter. *Bacteroides ruminicola* represented 10% in summer and 26% in winter. In summer and winter, respectively, the proportion of the viable population showing the following activities was as follows: fiber digestion, 36 and 48%; cellulolysis, 10 and 6%; xylanolysis, 33 and 48%; and starch utilization, 77 and 71%. The most abundant cellulolytic species in summer was *Butyrivibrio fibrisolvens*, representing 62% of the total cellulolytic population, and in winter it was *Ruminococcus albus*, representing 80% of the total cellulolytic population. The most abundant xylanolytic species in summer was *Butyrivibrio fibrisolvens*, and in winter it was *Bacteroides ruminicola*, representing 59 and 54% of the xylanolytic isolates in summer and winter, respectively. The cecal bacterial of the Svalbard reindeer have the ability to digest starch and the major structural carbohydrates of the diet that are not digested in the rumen. The cecum in these animals has the potential to contribute very substantially to the digestion of the available plant material in both summer and winter.

Svalbard reindeer (*Rangifer tarandus platyrhynchus*) survive under the most austere nutritional conditions on the high-arctic archipelago of Svalbard (77° to 81° N) (see Orpin et al. [19]). To survive under such conditions it is imperative for the animals to digest the poor-quality, fibrous plants which are available in winter as well as to make maximum use of the summer forage rich in seed heads (21, 23). Recently, Orpin et al. (19) have shown that a highly specialized rumen microflora, which is particularly effective in fiber digestion, probably contribute substantially to this end.

During the summer these animals feed for more than 50 to 60% of the 24-h day (18), and it is likely that the flow rate of digesta from the rumen is high, containing plant tissues which are not digested in the rumen. Indeed, we have observed large fragments of plant tissues, including nearly intact mosses, in the cecal contents of Svalbard reindeer in summer.

The cecum and the colon of the ruminant contain fermentative microorganisms which generate volatile fatty acids from plant material not digested in the rumen and the higher alimentary tract (14). These acids can be utilized by the host animal as carbon and energy sources and may contribute 30% of the total volatile fatty acids entering the bloodstream (6). In domestic ruminants, 5 to 30% of the digestible cellulose and 6 to 15% of the digestible starch may be fermented in the ceca (20, 27), depending on the diet and animal species.

To provide information on the potential contribution of the cecum to plant digestion in Svalbard reindeer, we characterized the dominant culturable cecal bacteria in these animals in both summer and winter and investigated their ability to digest starch and plant cell wall polysaccharides.

* Corresponding author.

MATERIALS AND METHODS

Animals. The animals were obtained in Adventdalen, Svalbard (78° N). Adult Svalbard reindeer of both sexes were shot: six animals in September (high-arctic summer) and six in April (high-arctic winter). These animals were those used by Orpin et al. (19) in a study of seasonal changes in rumen bacterial populations, and cecal samples and pH values were obtained by the same methods.

Enumeration of viable bacteria. The total viable bacterial population in filtered cecal fluid was determined with the habitat-simulating medium of Henning and van der Walt (7) incorporating 20% rumen fluid from sheep. Anaerobic serial dilution to 10^9 in 10-fold steps was made in the same medium without the carbohydrates and agar (the basal medium). Incubations were performed in Hungate-type anaerobic culture tubes fitted with a screw cap and butyl rubber septum and incubated at 39°C under CO_2. Estimates of the population densities of cellulolytic bacteria were made by the dilution method described by Mann (12), in basal medium with Whatman no. 1 filter paper strips and 0.01% cellobiose as carbon sources.

Numbers of lactate-utilizing bacteria were determined in winter by counts of colonies in the basal medium supplemented with 1.4% sodium lactate and 2% agar. Methanogens were measured after serial dilution in the medium of Edwards and McBride (4), using the modification of Orpin et al. (19).

Each medium was made up in bulk and dispersed into anaerobic culture tubes under CO_2. The tubes were then sealed and autoclaved at 115°C for 20 min. Filter-sterilized

TABLE 1. Cecal bacterial population densities and pH in Svalbard reindeer in September (high-arctic summer) and in April (high-arctic winter)

Bacteria and pH	Mean population density/ml of cecal content (±SD) in:		
	September	April	April as % of September
Viable bacteria	$(8.9 \pm 5.3) \times 10^8$	$(1.5 \pm 0.7) \times 10^8$	17
Total cellulolytic bacteria	$(8.7 \pm 3.2) \times 10^7$	$(9.9 \pm 3.8) \times 10^7$	11
Total fiber-digesting bacteria	$(3.2 \pm 0.6) \times 10^8$	$(7.5 \pm 3.2) \times 10^7$	23
Lactate-utilizing bacteria	ND[a]	$(1.1 \pm 0.3) \times 10^6$	
Methanogenic bacteria	10^7	10^5	
pH	6.81 ± 0.12	7.14 ± 0.26	

[a] ND, Not determined.

vitamins were then added to each tube with a syringe after the medium had cooled to about 60°C. Each measurement was performed in quadruplicate for each animal, and the mean for each group of animals was determined.

Isolation of bacteria. Bacterial colonies were selected at random from tubes of viable count medium containing 10 to 50 colonies per tube, and strains of bacteria were isolated after streaking onto agar-containing habitat-simulating medium in petri dishes. A total of 60 colonies were picked to represent the bacterial population of the cecum of each animal in summer, and 30 were picked for the population in winter.

The procedure was carried out in an anaerobic chamber (Coy Laboratory Products, Ann Arbor, Mich.) under an atmosphere of 95% N_2 and 5% H_2. Further purification was made by repeated streaking from single colonies onto fresh habitat-simulating medium at intervals of 48 h, until the isolates were pure.

Identification. The isolates were identified by standard tests for rumen bacteria, based on morphology, Gram stain, carbohydrate utilization patterns, and fermentation products (8, 9). Fermentation products were measured as described by Pethick et al. (22) and Bergmeyer (2, 3). Substrate utilization patterns were determined by replica plating 40 isolates per petri dish from a master plate of basic medium containing 2% agar, supplemented with 0.2% each of glucose, maltose, and cellobiose; replicas were formed on the basal medium as a control and on the same medium containing the respective substrate being investigated at a concentration of 0.5%. Potentially cellulolytic bacteria, except the ruminococci, were identified after an initial screening by plating on to the basal medium with 0.1% carboxymethyl cellulose (DP 7-9; BDH, Poole, England) and 0.01% cellobiose added. After 24 to 48 h of 39°C incubation, the carboxymethyl cellulose plates were stained with Congo red (26). The potentially cellulolytic isolates showed zones of clearing. All isolates giving a positive result were tested for growth on phosphoric acid-treated filter paper cellulose (29). The strains digesting the cellulose were regarded as cellulolytic. The isolates having the ability to grow on either cellulose or xylan (from oats) were defined as fiber digesters.

Statistics. Results are given as means ± standard deviations. The percentages were calculated from the absolute figures and corrected to one decimal place. Significance was calculated by the Student *t* test.

RESULTS

Microscopy. Light microscopy of the diluted strained cecal contents showed an absence of ciliated protozoa, chytridiomycete fungi, and large bacteria. The only groups of organisms positively identified by microscopy were bacteria and low numbers of flagellated protozoa. The flagellated protozoa were present at 10^2 to 10^4 cells ml^{-1}.

Viable count and species distribution. Results from the viable bacterial counts are shown in Table 1, and the species distribution and their percent proportion are shown in Table

TABLE 2. Culturable cecal bacteria of Svalbard reindeer[a]

Bacteria	Mean population density/ml of cecal content (10^7) ± SD (%)		
	September	April	April as % of September
Butyrivibrio fibrisolvens	20.7 ± 3.1 (23)	2.8 ± 1.3 (18)	14
Selenomonas ruminantium	8.9 ± 1.8 (10)	1.2 ± 1.7 (8)	14
Succinivibrio dextrinosolvens	1.8 ± 1.3 (2)	ND[b]	
Lachnospira multiparus	0.7 ± 0.7 (1)	ND	
Lactobacillus sp.	0.7 ± 0.7 (1)	1.0 ± 0.7 (7)	143
Megasphaera elsdenii	1.8 ± 1.3 (2)	0.4 ± 0.7 (3)	22
Bacteroides ruminicola	8.9 ± 2.3 (10)	4.0 ± 1.8 (26)	45
Bacteroides amylophilus	6.0 ± 1.3 (7)	0.8 ± 0.3 (5)	13
Ruminococcus albus	2.9 ± 1.5 (3)	0.8 ± 0.3 (5)	28
Ruminococcus bromii	2.9 (3)	0.2 ± 0.3 (1)	7
Streptococcus bovis	14.8 ± 0.9 (17)	0.8 ± 0.8 (5)	5
Streptococcus faecium	4.5 ± 1.5 (5)	1.0 ± 0.6 (7)	22
Streptococcus faecalis	8.9 ± 7.5 (10)	1.0 ± 0.7 (7)	11
Others	6.0 ± 1.5 (7)	1.2 ± 1.6 (8)	20

[a] Species composition and population densities in absolute numbers and percentage of total in September (high-arctic summer) and in April (high-arctic winter), together with the April population densities expressed as percentages of September values.

[b] ND, Not detected.

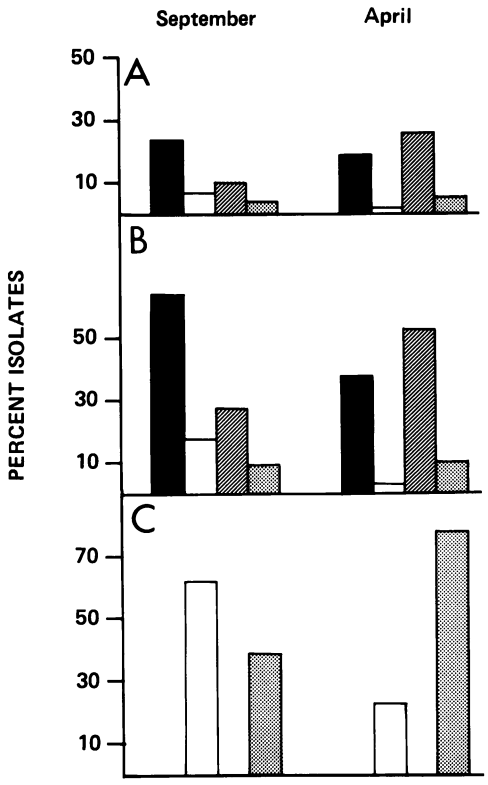

FIG. 1. Seasonal changes in population densities of the dominant fiber-digesting cecal bacteria in the high-arctic Svalbard reindeer in September (high-arctic summer) and April (high-arctic winter), expressed as a percentage of total viable bacteria (A), as a percentage of total fiber digesters (B), and the cellulolytic species expressed as a percentage of the total cellulolytic population (C). Symbols: ■, *Butyrivibrio fibrisolvens*; □, *Butyrivibrio fibrisolvens* cellulolytic; ▨, *Bacteroides ruminicola*; ▩, *Ruminococcus albus*.

2. Not all the isolates were identified in each season, and the majority of those not identified grew poorly in the culture media used. About 70% of those not positively identified were morphologically similar to *Bifidobacterium* spp., but were not further characterized. The population density of culturable bacteria in winter was 17% of the summer value. All the cultured species decreased in population density in winter compared with summer, but not all species decreased to the same extent. Two species, *Lachnospira multiparus* and *Succinivibrio dextrinosolvens*, present in summer were not detected in winter. Of the other more abundant species, population densities in winter ranged from 5% of the summer value for *Streptococcus bovis* to 45% for *Bacteroides* ruminicola.

Fiber digestion. The cultured species of bacteria capable of fermenting xylan or cellulose were *Butyrivibrio fibrisolvens*, *Bacteroides ruminicola*, and *Ruminococcus albus* (Fig. 1). The combined population densities of fiber-fermenting species decreased in winter to 26% of the summer population density, representing a proportion of the viable population of 36 and 48% in summer and winter, respectively. *Butyrivibrio fibrisolvens* was the dominant fiber-digesting species in summer (65% of the total fiber digesters), decreasing to 38% in winter. In contrast, *Bacteroides ruminicola* increased from 27% of the fiber digesters in summer to 52% in winter, although in absolute numbers its population density in winter was comparatively high, at 45% of the summer value (Table 2).

Cellulose digestion. Only two species of cellulolytic bacteria were identified. These were cellulolytic strains of *Butyrivibrio fibrisolvens* and *R. albus*, representing 7 and 3% of the total viable bacterial population densities, respectively, in summer and 1 and 5%, respectively, in winter. Total cellulolytic species in winter were present at 11% of the summer value. Of the *Butyrivibrio fibrisolvens* population, 28 and 8% showed cellulolytic activity in summer and winter, respectively. The cellulolytic population expressed as a percentage of total viable bacterial population was 10% in summer and 6% in winter. Dilution counts of cellulolytic bacteria showed between 10^6 and 10^8 cells ml^{-1} ($n = 3$) in the cecal fluid in summer and between 10^4 and 10^7 cells ml^{-1} ($n = 6$) in winter.

Xylan digestion. The total xylan-digesting population was 33% of the total viable bacterial population in summer and 48% in winter. *Butyrivibrio fibrisolvens* was the dominant xylan-utilizing bacterium in summer, making up 59% of the total xylan-digesting population, and *Bacteroides ruminicola* was dominant in winter, making up 54% of the total xylan-digesting bacterial population (Table 3).

Starch digestion. Bacteria possessing starch-digesting ability accounted for 77% of the total viable population in summer and 71% in winter. This represents a decrease in absolute number to 16%, from 6.8×10^8 to 1.1×10^8 cells ml^{-1}. The dominant bacteria digesting starch was *Butyrivibrio fibrisolvens* in summer and *Bacteroides ruminicola* in winter (Fig. 2). In both seasons, starch-digesting *Streptococcus bovis*, *Selenomonas ruminantium*, *Bacteroides amylophilus*, and *Ruminococcus bromii* were identified. Each of these species decreased considerably in population density in winter compared with summer. *Streptococcus bovis* showed the greatest decrease, falling from 17% of the total viable bacteria in summer to 5% in winter.

Methanogenic bacteria were found at 10^7 cells ml^{-1} in summer ($n = 2$) and 10^5 cells ml^{-1} ($n = 6$) in winter.

Bacteria utilizing lactate were not estimated in summer, but were detected in concentrations of 1.1×10^6 cells ml of cecal $fluid^{-1}$ in six animals in winter.

pH. Cecal pH increased from 6.81 ± 0.12 in summer to

TABLE 3. Seasonal changes in population densities in absolute numbers and percentage of xylan-digesting bacteria in the cecum of Svalbard reindeer in September (high-arctic summer) and April (high-arctic winter)

Bacteria	Mean population density/ml of cecal content (10^7) ± SD (%)		
	September	April	April as % of September
Butyrivibrio fibrisolvens	17.2 ± 3.0 (59)	2.6 ± 1.5 (35)	15
Bacteroides ruminicola	8.9 ± 2.3 (31)	4.0 ± 1.8 (54)	45
Ruminococcus albus	2.9 ± 1.5 (10)	0.8 ± 0.3 (11)	28
Total	29.0 ± 6.8	7.4 ± 3.6	26

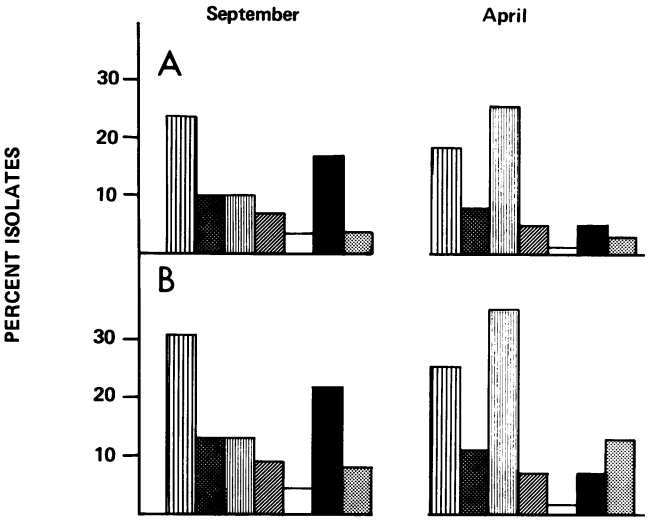

FIG. 2. Seasonal changes in population densities of the following starch-digesting bacteria in the cecum of the high-arctic Svalbard reindeer in September (high-arctic summer) and April (high-arctic winter), expressed as a percentage of total viable bacteria (A) and as a percentage of the total starch-digesting population (B). Symbols: ▥, *Butyrivibrio fibrisolvens*; ▩, *Selenomonas ruminantium*; ▤, *Bacteroides ruminicola*; ▨, *Bacteroides amylophilus*; □, *Ruminococcus bromii*; ■, *Streptococcus bovis*; ▩, other isolates.

7.14 ± 0.26 in winter (Table 1). These values are significantly different ($P < 0.05$).

DISCUSSION

It is recognized that the cecum and the proximal colon are important sites of microbial fermentation in the ruminant, yielding 4 to 26% of the total digestible energy available from the diet (1, 15, 27), but few studies of the cecal microorganisms have been published. Population densities of viable cecal bacteria of 2×10^6 to 2.5×10^7 cells g^{-1} have been found in cattle (25), 5×10^7 to 12×10^8 cells ml^{-1} in sheep (13), and 6.3×10^8 cells g^{-1} in sheep on an all-hay diet (10), using techniques similar to those employed here. The use of rumen fluid in the medium seems not to limit the cecal microbial growth (11). The population density of culturable bacteria in the Svalbard reindeer cecum showed seasonal changes, the winter value being only 17% of the summer value. This is about the same decrease as found for the rumen viable bacterial population in the same animals (19). The summer population density (nearly 10^9 cells ml^{-1}) was about 80 times higher than the mean value of 1.1×10^7 cells g^{-1} in cattle (25) and about 10 times higher than that in sheep fed cubed dried grass. In individual sheep, however, up to 11.8×10^8 cells of culturable bacteria ml^{-1} were found (13), and in sheep fed 80% concentrate and 20% hay an average of 4.9×10^{10} cells g^{-1} were found (10), being higher than the average found in summer in the Svalbard reindeer.

Most of the dominant bacterial species in the cecum of the Svalbard reindeer were species that were found in the rumen of the same animals in both seasons (19). *Butyrivibrio fibrisolvens*, the most abundant species in the rumen in both seasons, was also the most abundant cecal species in summer. *Butyrivibrio fibrisolvens* and *Ruminococcus flavefaciens* were the two cellulolytic species found in the sheep cecum (10), with *Butyrivibrio fibrisolvens* only found in animals fed hay. In winter *Bacteroides ruminicola*, present at only 1% of the rumen population of Svalbard reindeer, made up 26% of the cecal population and was the most abundant cultured bacterium. In the rumen and cecum, *Streptococcus bovis* was present in both seasons at the same proportion of the population: 17% in summer and 4 to 5% in winter. *Selenomonas ruminantum* represented 16% of the rumen population in both seasons, but only 10 and 8% of the cecal population in summer and winter, respectively. This is rather less than that found in the ceca of cattle (29%) (25).

It is not surprising that the bacteria which were found in the cecum were the same as those found in the rumen of Svalbard reindeer, since in gnotobiotic lambs (11) the establishment of a defined rumen microflora was followed by the establishment of the same species in the cecum. The cecal *Butyrivibrio fibrisolvens* strains found by Lewis and Dehority (10) were also closely related to rumen strains of the same species.

As in the rumen (19), the dominant fiber-digesting bacterium was *Butyrivibrio fibrisolvens* in summer, but *Bacteroides ruminicola* was dominant in the cecum in winter. The major cecal cellulolytic isolates were strains of *Butyrivibrio fibrisolvens* and *R. albus*. No strains resembling *Bacteroides succinogenes* and *Ruminococcus flavefaciens* were detected in the cecum, although these species were found in the rumen and the *R. flavefaciens* has been identified in the sheep cecum (10).

The population density of cellulolytic bacteria was considerably smaller, both in absolute numbers and when expressed as a percentage of the total population, in the cecum than in the rumen (19). In the rumen, the cellulolytic species increased from 15% of the population in summer to 35% of the population in winter, while in the cecum the population of cellulolytic bacteria decreased from 10% in summer to 6% in winter. In contrast, the proportion of the population with a xylanolytic capacity increased from 33% in summer to 42% in winter. These results suggest that xylanolysis may be more important than cellulolysis in the cecum in winter. This is in agreement with results from domestic ruminants in which hemicellulolysis in the cecum may be more extensive than cellulolysis (27). In sheep, less than 0.2% of the viable population in the cecum was cellulolytic (10). The values for cellulolytic species represent a minimal value, since only filtered cecum liquor was examined and not the solid phase of cecum contents.

Starch fermentation was a common ability in the cecal *Butyrivibrio fibrisolvens* and *Bacteroides ruminicola* from Svalbard reindeer. Mann and Ørskov (13) found that most of their isolates of *Bacteroides ruminicola* from the sheep cecum could also hydrolyze starch but that the *Butyrivibrio fibrisolvens* did not. In addition to these species, *Streptococcus bovis* was common in the cecum of Svalbard reindeer in summer. *Streptococcus bovis* is a lactate producer, and the lactate-utilizing *Megasphaera elsdenii* was also found both in summer and winter. Other starch-fermenting species isolated in both seasons were *R. bromii* and *Selenomonas ruminantium*. *Selenomonas* spp. were more common in the ceca of cattle, making up 29% of isolates (25) compared with 14% from the Svalbard reindeer cecum.

Two species of pectinolytic bacteria, *Succinivibrio dextrinosolvens* and *Lachnospira multiparus*, were found in both the rumen (19) and the cecum of the Svalbard reindeer. These species have not been reported from the cecum before.

Because of the very harsh climate and poor nutritional conditions during much of the year at Svalbard, it is essential for the Svalbard reindeer to maximize the utilization of the

diet particularly during the short summer, when huge amounts of body fat are deposited (24). Data on digesta flow rates through the alimentary tract are lacking, but observations of feeding behavior show that the animals eat for 50 to 60% of the day during summer (18). It is therefore likely that quantities of dietary components are not fully digested in the rumen, but are subjected to secondary fermentation in the cecum.

It has been suggested that fat is crucial for survival of these animals during winter (24). We calculated using the data of Nilssen et al. (16, 17) that this fat provides 10 to 30% of the daily energy expenditure during four months in winter depending on activity. We suggest that optimal utilization of the feed, particularly in winter, by the presence of a high ruminal and cecal fiber-digesting bacterial population could be more important (19).

Cecal pH is usually close to neutrality in domestic animals, ranging from 6.6 to 7.8 in sheep fed lucerne (5, 28) from 5.7 to 7.2 in sheep fed grain diets (10, 28). The cecal pH of the Svalbard reindeer is therefor similar to that of domestic animals.

The results presented here strongly indicate that the cecal bacteria may contribute substantially to the utilization of forage in the Svalbard reindeer. The exact contribution from the cecum cannot be determined until data on digesta composition and flow rates from the rumen and into the cecum are available.

LITERATURE CITED

1. **Beever, D. E., J. F. Coelno da Silva, J. H. D. Prescott, and D. G. Armstrong.** 1972. The effect in sheep of physical form and stage of growth on the sites of digestion of a dried grass. I. Sites of digestion of organic matter, energy and carbohydrates. Br. J. Nutr. **28**:347–356.
2. **Bergmeyer, H. U.** 1974. Methods of enzymatic analysis, vol. 3, p. 1464–1468. Academic Press, Inc. (London), Ltd., London.
3. **Bergmeyer, H. U.** 1974. Methods for enzymatic analysis, vol. 3, p. 1551–1555. Academic Press, Inc. (London), Ltd., London.
4. **Edwards, T., and B. C. McBride.** 1975. New method for the isolation and identification of methanogenic bacteria. Appl. Microbiol. **29**:540–545.
5. **Faichney, E. J.** 1968. Volatile fatty acids in the caecum of sheep. Aust. J. Biol. Sci. **21**:177–180.
6. **Harfoot, C. G.** 1978. Anatomy, physiology and microbiology of the ruminant digestive tract. Prog. Lipid Res. **17**:1–19.
7. **Henning, P. A., and A. E. van der Walt.** 1978. Inclusion of xylan in a medium for the enumeration of total culturable rumen bacteria. Appl. Environ. Microbiol. **35**:1008–1011.
8. **Holdeman, L. V., E. P. Cato, and W. E. C. Moore (ed.).** 1974. Anaerobe laboratory manual, 2nd ed. Virginia Polytechnic Institute and State University, Blacksburg.
9. **Hungate, R. E.** 1966. The rumen and its microbes. Academic Press, Inc., New York.
10. **Lewis, S. M., and B. A. Dehority.** 1985. Microbiology and ration digestibility in hindgut of the ovine. Appl. Environ. Microbiol. **50**:356–363.
11. **Lysons, R. J., T. J. L. Alexander, P. N. Hobson, S. O. Mann, and C. S. Stewart.** 1971. Establishment of a limited rumen microflora in gnotobiotic lambs. Res. Vet. Sci. **12**:486–487.
12. **Mann, S. O.** 1968. An improved method of determining cellulolytic activity in anaerobic bacteria. J. Appl. Bacteriol. **31**:241–246.
13. **Mann, S. O., and E. R. Ørskov.** 1973. The effect of rumen and post rumen feeding of carbohydrates on the caecal microflora of sheep. J. Appl. Bacteriol. **36**:475–484.
14. **McBee, R. H.** 1977. Fermentation in the hindgut, p. 185–222. *In* R. T. J. Clarke and T. Bauchop (ed.), Microbial ecology of the gut. Academic Press, Inc. (London), Ltd., London.
15. **McRae, J. C., and D. G. Armstrong.** 1969. Studies on intestinal digestion in the sheep. II. Digestion of some carbohydrate constituents in hay, cereal and hay-cereal rations. Br. J. Nutr. **23**:377–387.
16. **Nilssen, K. J., H. K. Johnsen, A. Rognmo, and A. S. Blix.** 1984. Heart rate and energy expenditure in resting and running Svalbard and Norwegian reindeer. Am. J. Physiol. **246**: R963–R967.
17. **Nilssen, K. J., J. A. Sundsfjord, and A. S. Blix.** 1984. Regulation of metabolic rate in Svalbard and Norwegian reindeer. Am. J. Physiol. **147**:R837–R841.
18. **Nyholm, E. S.** 1976. Monthly general rhythm pattern variations in the Nordenskiøld-Saline land population of the Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Nor. Polarinst. Årbok **1974**:129–138.
19. **Orpin, C. G., S. D. Mathiesen, Y. Greenwood, and A. S. Blix.** 1985. Seasonal changes in the ruminal microflora of the high arctic Svalbard reindeer. (*Rangifer tarandus platyrhynchus*). Appl. Environ. Microbiol. **50**:144–151.
20. **Ørskov, E. R., C. Fracer, V. C. Manson, and S. O. Mann.** 1970. Influence of starch digestion in large intestine of sheep on caecal fermentation, caecal microflora and faecal nitrogen excretion. Br. J. Nutr. **24**:671–682.
21. **Persen, E., Ø. Holand, A. B. Leifseth, and H. Staaland.** 1983. Reindeer grazing on Brøggerhalvøya, Svalbard. Acta Zool. Fenn. **175**:35–37.
22. **Pethick, D. W., D. B. Lindsay, P. J. Barker, and A. J. Northrop.** 1981. Acetate supply and utilization by tissues of sheep *in vivo*. Br. J. Nutr. **46**:97–110.
23. **Punsvik, T., A. Syvertsen, and H. Staaland.** 1980. Reindeer grazing in Adventdalen, Svalbard, p. 115–124. *In* E. Reimers, E. Gaare, and S. Skjenneberg (ed.), Proceedings of the Second International Reindeer and Caribou Symposium. Direktoratet for Vilt og Ferskvannsfisk, Trondheim, Norway.
24. **Reimers, E., T. Ringberg, and R. Sørumgaard.** 1982. Body composition of Svalbard reindeer. Can. J. Zool. **60**:1812–1821.
25. **Sharpe, N. E., M. J. Latham, and B. Reiter.** 1975. The immune response of the host animal to bacteria in the rumen and caecum, p. 193–204. *In* I. W. McDonald and A. C. I. Warner (ed.), Digestion and metabolism in the ruminant. The University of New England Publishing Unit, Armidale, Australia.
26. **Teather, R. M., and P. J. Wood.** 1982. Use of Congo red polysaccharide interactions in enumeration and characterization of cellulolytic bacteria from the bovine rumen. Appl. Environ. Microbiol. **43**:777–780.
27. **Ulyatt, M. J., D. W. Dellow, C. S. W. Reid, and T. Bauchop.** 1975. Structure and function of the large intestine of ruminants, p. 119–133. *In* I. W. McDonald and A. C. I. Warner (ed.), Digestion and metabolism in the ruminant. The University of New England Publishing Unit, Armidale, Australia.
28. **Williams, V. J.** 1965. Microbial metabolism in the forestomachs and the large intestine of sheep. Aust. J. Agric. Res. **16**:77–91.
29. **Wood, T. M.** 1970. Cellulose and cellulolysis. World Rev. Nutr. Diet. **12**:227–265.