ON THE QUALITY OF SVALBARD REINDEER PASTURE IN THE SUMMER AND AUTUMN

Om kvaliteten av reinbeite på Svalbard sommer og høst

STAALAND, HANS, Department of Zoology, Agricultural University of Norway, 1432 Ås-NLH, Norway.

Staaland, H. 1984. On the quality of Svalbard reindeer pasture in the summer and autumn.

Abstract: Late summer and autumn reindeer pasture plants from Adventdalen, Svalbard were analyzed for contents of fatty acids, energy content, protein, fibre, ether extract as well as content of macro minerals. Food intake of grazing reindeer in Adventdalen was estimated from fecal production. Large intake of high quality food seems to account for the growth and fattening of Svalbard reindeer during summer.

Key words: Reindeer, Svalbard, pasture quality, fatty acids, Minerals, food intake.

***Rangifer** 4 (1): 16 - 23*

Staaland, H. 1984. Om kvaliteten på reinbeite av reinbeite på Svalbard sommer og høst.

Sammendrag: Innholdet av fettsyrer, energi, protein, fiber, eterekstrakt og makromineraler ble analysert i reinbeiteplanter fra Adventdalen på Svalbard. Plantene ble samlet på ettersommeren. Fôrinntaket hos beitende rein i Adventdalen ble estimert ut fra fecesproduksjonen. Et stort inntak av fôr med høy kvalitet synes å kunne forklare vekst og fettlagring hos Svalbard-reinen om sommeren.

***Rangifer** 4 (1): 16 - 23*

STAALAND, H. 1984. Eläintieteellinen laitos, Norjan maatalouskorkeakoulu, 1432 Ås - NLH, Norja. Huippuvuorten poronlaidunten laadusta kesällä ja syksyllä.

Yhteenveto: Rasvahappojen, energian, fiiberin, eetteriuutteen ja makromineraalien sisältöä analysoitiin poronlaidunkasveissa Huippuvuorten Adventtilaaksosta. Kasvit kerättiin loppukesällä. Adventtilaaksossa laidunta-vien porojen rehun kulunki arvioitiin lannan määrästä. Korkealaatuisen rehun suuri kulutus näyttää vovan selittää Huippuvuorten porojen kasvun ja rasvakerrostuman kesällä.

***Rangifer** 4 (1): 16 - 23*

INTRODUCTION

The summer grazing season for the Svalbard reindeer is short. The snow cover the ground to the end of May or early June, and permanent snow cover can be expected from the end of September. In the period 1957-65 mean monthly temperatures in June, July, August and September were only above zero; 2.6, 6.0, 5.3 and 1.0°C (Steffensen 1969). Thus both the period of plant growth and the period reindeer can graze fresh vegetation is short. Nevertheless the Svalbard reindeer through this short period manage to restore their depleted body reserves of nutrients and to accumulate fat to an extent unknown in most other ruminants (Reimers et al. 1982).

The quality of the range is apparently good, giving a high production rate of volatile fatty acids (White and Staaland 1983), and the vegetation has high levels of protein and macro as well as micro minerals (Staaland et al. 1983). Studies on grazing behaviour and plant selection have shown that Svalbard reindeer extensively feed on grasses with high nutritional value like *Dupontia* sp. *Alopecurus alpinus* and *Poa* sp. through late summer and autumn. A highly selected food seems also to be the seeds of the viviparous grasses of *Poa*, *Deschampsia* and *Festuca* (Punsvik et al. 1980, Persen et al. 1983).

This study aims at examining the nutritional quality of some selected forage plants grazed by reindeer in Adventdalen, Svalbard, and further more to give some estimates of food intake in the grazing period July to September.

MATERIAL AND METHODS

Some of the important forage plants utilized by the Svalbard reindeer during late summer and autumn were collected in August and September 1981 in Adventdalen on western Spitsbergen. Further samples for comparative analyses of fatty acid composition were collected in July 1982 at Slettrust near Tyin in alpine areas of South Norway. Deposite fat (rump fat) from Svalbard reindeer was collected from animals shot near Isfjord also on western Spitsbergen in the fall of 1982. All samples were frozen as soon as possible and kept frozen at -20° till prossessed. Samples of dehydrated fat and ground, dehydrated plant material were boiled at 80°C in a solution of 2% concentrated sulfuric acid in methanol. Hexane was added to the solution before injection into the gass chromatograph for determination of fractional concentrations of long chained fatty acids.

These analyses were carried out at the Analytical laboratory of the Department of Animal nutrition, Agricultural University of Norway. Energy content (Cal/g D.M.) was determined by bomb calorimetry, and dry matter in vitro digestibility was determined according to the methods described by Tilley and Terry (1963). Inoculum from rumen fistulated sheep fed hay and pelleted rations was used for the in vitro studies. All other analyses were carried out by standard methods used at the Chemical research laboratory at the Agricultural University of Norway (see Staaland et al. 1983).

Fecal production was measured by following the reindeer at close range, counting their fecal droppings and collecting and weighing them. Also frequency of urination as well as resting and grazing time was recorded. Size of animals *i.e.* likely range of body weight, was estimated from experience. Dry matter content of feces was determined after drying at 105°C for 12 hrs.

RESULTS

Fatty acids

The dominating fatty acids in plant material from Svalbard is palmitic acid; C:16.0 (15-21%) and linolenic acid; C:18.3 (13-36%). In *Luzula confusa* linoleic acid; C:18.2 is found in highest concentration. In mosses the C:18 acids are less dominating and there is a large rest of non identified acids. There seems to be no major difference between Svalbard plant and mountain plants from Norway in content of fatty acids (Fig. 1).

As would be expected a large proportion of the unsaturated acids are apparently saturated when passing through the rumen (Church 1976). Thus linoleic and linolenic acids are only small fractions of the back fat acids. Contrary stearic, C:18.0, and oleic acid C:18.1 are found in high concentrations. Also the unidentified rest fraction is small compared to in plant material. The dominance of palmitic, stearic and oleic acids in fat deposits is typical for ruminants (see Church 1976) and has also previously been demonstrated in Svalbard reindeer (Ringberg et al. 1980).

Proximate food analyses

High protein content was found in *Polygonum viviparum* and in *Alopecurus alpinus.* Also the viviparous grass seeds had high levels of protein (Table 1). *Luzula confusa* had very low protein and sugar levels, and high crude fibre content. Seeds and the two grasses *Dupontia pelligera* and *Alopecurus alpinus* had the highest energy content. The viviparous grass seeds had also very high dry matter digestibility, above 80%. *Luzula confusa* had the lowest digestibility, about 40%.

Mineral content

The mineral content of the plants agrees with previous studies (Staaland et al. 1983). As shown before, Svalbard vegetation is particularely high in Na and CI compared to some Norwegian plants. Viviparous grass seeds are apparently relatively low in Ca, whereas *Equisetum arvense* is a generally good mineral source, particularely high in S (Table 2).

Fecal production and food consumption

The frequency of defecation and urination on summer and fall pasture is high (Table 3), giving a high production of feces pr. day. In large animals (100 kg) the rate of fecal production is in the order of 1.6 to 2.0 kg dry matter pr. day. In smaller animals the fecal production is lower. If the dry matter digestibility is assumed to be about 60% the dry matter food consumption in adult large reindeer would be in the order of 4-5 kg pr. day (Table 3) which again, when taking into consideration the water content of fresh vegetation, would indicate an intake of 14 - 18 kg fresh vegetation pr. day. Average dry matter content of plants analysed (Table 1) is 28 ± 8%.

Table 1. Chemical composition of forage plants collected in Adventdalen, Svalbard, medio September 1981.

Tabell 1. Kjemisk sammensetning av beiteplanter samlet i Adventdalen, Svalbard, i midten av september 1981.

Species	DM (%)	g/100 g D.M.							
		Ash	C.P	E.E.	C.F.	NFE	Total sugar	Cal/ g D.M.	In vitro digestibility (%D.M.)±S.D, n=3
Polygonum viviparum	21.0	9.35	17.14	2.61	14.19	56.71	11.95	4295	60.1±2.6*
Stellaria crassipes	37.6	8.45	12.63	2.18	24.20	52.54	5.53	4342	44.1±1.1
Cerastium arcticum**	23.4	40.47	8.28	1.75	11.97	37.53	5.81	3909	50.6±0.0
Poa alpigena (vivip. seeds)	31.5	4.67	15.67	2.48	17.46	59.72	15.75	4472	80.2±1.2
Poa alpina (vivip. seeds)	29.8	4.63	17.62	2.32	15.44	59.99	11.48	4538	83.1±0.2
Deschampsia alpina (vivip. seeds)	29.7	4.48	15.78	2.16	18.18	59.40	17.31	4492	—
Festuca rubra (seeds)	39.3	6.31	10.18	—	25.46	—	11.32	4545	58.5±1.2
Poa alpigena	30.2	7.25	11.18	1.85	22.51	57.21	12.78	4328	66.3±2.3*
Poa alpina	29.1	5.67	13.96	1.86	19.59	58.92	12.85	4375	—
Deschampsia alpina	27.3	5.57	13.74	2.56	27.83	50.30	12.09	4221	60.4±1.0
Deschampsia brevifolia	28.3	6.61	11.70	2.16	30.03	49.50	13.07	4301	61.9±1.6
Festuca rubra	27.6	9.48	12.89	2.17	22.08	53.38	14.55	4369	69.4±3.3*
Calamagrostis neglecta**	19.9	6.78	15.08	2.21	25.12	50.81	13.42	4384	58.2±1.6
Dupontia pelligera	21.0	4.76	7.44	2.43	26.19	59.18	12.29	4450	57.5±2.2
Alopecurus alpinus**	14.5	11.03	23.27	3.52	20.00	42.18	10.41	4519	74.2±1.3*
Luzula confusa	49.9	5.41	3.13	1.42	31.05	58.98	3.11	4243	40.2±0.6
Equisetum arvense	21.1	22.61	17.48	—	10.90	—	9.72	3659	73.9±1.4*

* Based on samples collected ultimo July 1983; ** Collected medio August 1981.

Table 2. Mineral concentrations (mM/kg D.M.) of forage plants collected in Adventdalen, Svalbard, medio September 1981.

Tabell 2. Mineralkonsentrasjoner (mM/kg tørrstoff) i beiteplanter samlet i Adventdalen i midten av september 1981.

Species	Ca	Mg	P	Na	K	Cl	S
Polygonum viviparus	386	130	106	27	480	169	104
Stellaria crassipes	126	72	63	16	354	61	64
Cerastium arcticum*	139	83	66	26	350	66	147
Poa alpigena (vivip. seeds)	50	30	90	15	382	80	63
Poa alpina (vivip. seeds)	33	32	93	26	421	80	88
Deschampsia alpina (vivip. seeds)	34	44	86	26	319	117	65
Festuca rubra (seeds)	60	33	73	22	247	—	—
Poa alpigena	116	35	41	8	373	171	114
Poa alpina	54	37	60	12	387	111	61
Deschampsia alpina	36	39	237	19	418	172	67
Deschampsia brevifolia	56	32	68	29	461	163	86
Festuca rubra	117	43	65	12	454	—	113
Calamagrostis neglecta*	54	43	67	31	501	193	66
Dupontia pelligera	97	33	54	18	390	161	40
Alopecurus alpinus*	100	74	100	33	935	362	146
Luzula confusa	70	44	58	16	241	84	44
Equisetum arvense	319	166	78	35	1224	—	443

** Collected medio August 1981.

DISCUSSION

Reindeer in Adventdalen through late summer and autumn graze largely on forbs and grasses, Graminae. Sedges, Cyperaceae and rush, Juncaceae, with the exception of two species; *Eriophorum scheuchzeri* and *Luzula confusa*, usually grow in small and scattered stands and may appear unimportant as summer forage. The wet meadows with *Dupontia pelligera* and *Eriophorum scheuchzeri* as well as areas with *Alopecurus alpinus* and other *Graminae* are however, heavily grazed. In between this grasses are also found *Equisetum arvense* which is also used by the reindeer (Punsvik et al. 1980, Persen et al. 1983). Further observations have also revealed that the seeds of the viviparous grasses, *Deschampsia alpina*, *Poa* spp. and *Festuca vivipara* are selected by the reindeer. In late autumn grasses with viviparous seeds can often only be found in localities not reached by the reindeer. The importance of Graminae in the reindeer diet in Adventdalen have been confirmed by botanical analyses of rumen content (Staaland et al. 1983). Both in summer and winter mosses are ingested in large quantities.

In a recent paper, Prins (1982) argue that mosses are eaten by animals in cold environments because of high content of the poly-unsaturated arachidonic acid. Some of the positive effects in cold climate would be lowering the melting points of fat in the extremities and protection of cell membranes against cold. However, Svalbard reindeer, one of Prins' examples, even though consuming, large amount of mosses (Staaland et al. 1983) may have little benefit in this respect from eating mosses, since unsaturated fatty acids usually are hydrogenated when passing through the rumen. These acids will therefore enter the small intestine in a saturated form. This seems to be confirmed in the present study since the rest fraction, several long chained unsaturated fatty acids as well as C:18.3 (linolenic) and C:18.2 (linoleic) are almost absent from back fat deposits. This is in contrast to non ruminants like e.g. Willow and Rock ptarmigans (*Lagopus lagopus* and *L. mutus*), where both linolenic, linolic and arachidonic acids constitutes large fractions of body fats (Tanhuanpää and Pulliainen 1969). Linoleic acid is the only truly essential fatty acid in the diet (McDonald et al. 1978). There seems to be no major difference in fractional content of this acid between Svalbard plants and mountain plants from Norway (Fig. 1). Scarcity of this component in the diet of Svalbard reindeer seems unlikely.

In particular the viviparous seeds from grasses are

Table 3. Fecal production of reindeer grazing native vegetation in Adventdalen during July and August 1977 and 1983. Food-intake estimated on the basis of assumed 60% D.M. digestibility.

Tabell 3. Fecesproduksjonen hos beitende rein i Adventdalen i juli - august 1977 og 1983. Beregning av förinntak er basert på en antatt tørrstoff-fordøyelighet på 60%.

Type of animal	Total period of observation (min.)	Number of observation periods (n)	Number of defecation/ 24 hr	Number of* fecal groups 24 hr	Number of urinations/ 24 hr	Kg wet feces/ 24 hr	% Dry matter in feces	Kg dry feces 24 hr	Estimated food intake (kg/day)
Adult males 80-120 kg (1977)	1067	12	130±65	215±79	51±32	9.3±2.5	20.5±2.9	1.97±0.51	4.9
Adult males 80-120 kg (1983)	644	6	104±15	134±32	56±27	9.1±1.9	17.8±2.3	1.58±0.12	4.0
Adults (male or female) (1977) 50-60 kg	741	9	111±59	194±71	36±26	5.4±3.1	21.7±2.7	1.20±0.51	3.0
Calves (yearling) 30-40 kg (1977)	86	2	90±43	140±40	48±68	2.7±0.4	22.7±1.3	0.61±0.12	1.5

* In one defecation, feces was collected as 1-3 groups on the tundra.

of high quality with very high digestibility and high energy and protein content. Some grasses, in particular *Alopecurus alpinus* seem to be high quality forage. Also plants like *Oxyria digyna* and *Equisetum arvense* can be important forage because of their high mineral and protein content (Staaland et al. 1983; tables 2 and 3). In contrary the abundant Northern Woodrush, *Luzula confusa* is very low in protein, sugar and digestibility, but high in fibre. E.g. low sugar could be a reason for not selecting this species (Arnold and Dudziński 1978).

The food intake of wild grazing reindeer is difficult to estimate. Because of the apparent tameness of the Svalbard reindeer, they can relatively easily be followed for hours at close distance and urination and defecation observed. During such observation periods they continue grazing, lie down ruminating and apparently behave normally. They may even sometimes come close (5-10 m) to have a good look at the biologist. After defecation the fecal droppings are usually easy to find, due to the open landscape and short vegetation. By this method it is therefore relatively easy to obtain a good estimate of fecal production in Svalbard reindeer during summer (Table 3). The main error encumbered is that the body weights of the animals have to be judged by experience from the weight of shot animals. From the amounts of feces produced food intake can be estimated provided the digestibility is known. From studies on in vitro digestibility (Table 1; Staaland et al. 1983) and from feeding trials (Staaland and Øritsland in prep.) 60% dry matter digestibility might be a fairly good estimate on summer pasture. The dry matter intake of adult bucks would then be in the order of 4-4.9 kg or, at a medium body weight of 100 kg, 126-155 g/BW$^{0.75}$ per day. For the 50 - 60 kg animals (medium body weight 55 kg) 148 g/BW$^{0.75}$ and for the yearlings (35 kg body weight) 104 g/BW$^{0.75}$ (Table 3). These values are lower than previous estimates made by measuring the ruminal VFA production in summer grazing Svalbard reindeer, 187 g/BW$^{0.75}$ (White and Staaland 1983). However, a small increase in dry matter digestibility to e.g. 65% would increase the calculated dry matter intake to 178 g/BW$^{0.75}$ per day. The obtained values are in good agreement with data obtained from pen-fed Svalbard reindeer, about 3.0 kg/dry matter, i.e. approximately 112 g/BW$^{0.75}$ per day (Nilssen and Ringberg 1980). The food intake for Svalbard reindeer thus appears considerably higher than estimates made for

Norwegian reindeer at Lødingen in Northern Norway and for caribou at Prudhoe Bay in Alaska; 68 and 33 g/kg per day (White and Staaland 1983).

If these values are accepted it can also be calculated that the intake of energy and nutrients are high in summer grazing reindeer on Svalbard; due to high quality forage and large intake. The mean energy content of all plant samples from Svalbard (Table 1) is 4320 cal/g dry matter. If the diet of adult reindeer, body weight 100 kg, is similarely composed the gross energy intake of grazing reindeer would be in the order of 17 000 - 21 000 Kcal/day. If approximately 60% of the energy is digested net assimilated energy would be 10 000 - 12 600 Kcal/day. Metabolizeable energy is assumed to about 80% of apparently digested energy, *i.e.* in the order of 8000 - 10 000 Kcal/day or 253 - 316 Kcal/$BW^{0.75}$ per day. Reimers (1980) estimated the maintenance energy of Svalbard reindeer during summer to be 1.49 x fasting metabolic rate; 97 Kcal/$BW^{0.75}$ per day (McEwan 1970) or 145 Kcal/$BW^{0.75}$ per day. Thus in the order of 110 - 170Kcal/$BW^{0.75}$ per day would be available for growth and fattening. This is considerably higher than estimates made for caribou at Prudhoe Bay, Alaska, 26 - 58 Kcal/$BW^{0.75}$ per day (White et al. 1975), i.e. in the order of 3500 - 5400 Kcal per day in a 100 kg animal. With an efficiency of fattening of 0.39 and an energy content of new tissue of 3.6 Kcal/g (White et al. 1975) the body weight gain would bee 380-585 g/day. If the season for growth and fattening last for about 116 days in Svalbard (Reimers 1980) this would amount to 44-68 kg body weight gain. These data are in good agreement with data from weighing of carcasses throughout the year. It has been estimated that a male reindeer may lose as much as 50% of their maximal body weight during winter, i.e. a buck with body weight of 120 kg in the fall would lose 60 kg to spring (Reimers et al. 1982). The possible daily body weight gain in reindeer on Svalbard might be higher than expected if they consume more highly digestible material i.e. viviparous seeds from grasses (Table 1).

Although these calculations are based on several assumptions and judgements, they seem to indicate that the increase of body weight and fattening is based on a large intake of high quality food, *i.e.* a food of high digestibility and high nutrient content.

There are several factors both in the habitat and in the behaviour of the Svalbard reindeer which may enhance growth and fattening processes.

The wet meadows of Svalbard, which are prime summer habitats are more dominated by Graminae than by sedges and rush than in similar wet areas (bogs) in Norwegian reindeer habitats. Also the apparent large intake of forbs and viviparous seeds in Svalbard reindeer appears important. Available plants are furthermore high in nutrient. The Svalbard reindeer habitat may be more resistent towards grazing and trampling than Norwegian habitats since lichens are less important and mosses more important (Klein 1970; Rønning 1976 & 1979; Punsvik et al. 1980; Staaland et al. 1983).

The Svalbard reindeer apparently lives a more sedentary life than continental reindeer/caribou. This is obviously an effect of several factors. The lack of predators and insect harassment, as well as a cool summer climate make movements to snow patches and high altitude less important. Since the Svalbard reindeer graze singularely or in small groups and are spaced out over the available grazing terrain, each area can support the same group og animals through prolonged periods of time or throughout the whole year. This may reduce intraspecific competition, reduce the need of migration and ultimately save energy and increase available grazing time.

Thus although the primary production may seem low (Brzoska 1976; Brattbakk and Rønning 1978) the high quality of the forage together with the sedentary behaviour of the Svalbard reindeer may explain these animals capability to grow new tissue and store fat during summer and to maintain high density populations (Reimers et al. 1980).

Acknowledgement. This study was supported by the Norwegian MAB programme. Fatty acid composition analyses of back fat and plant samples were kindly carried out by Per Lindstad at the Analytical laboratory of the Department of Animal nutrition, Agricultural University of Norway.

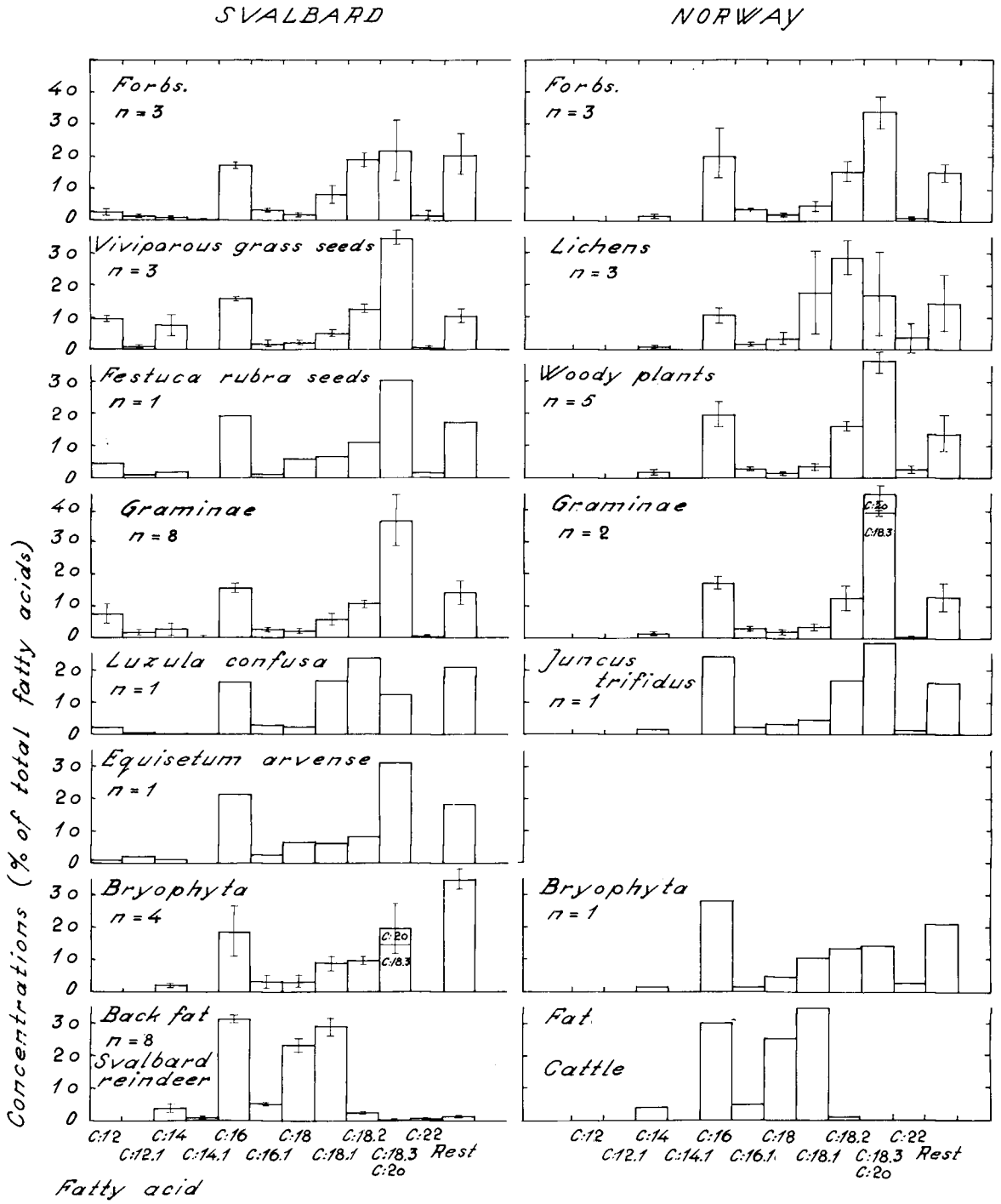

Fig. 1. Relative (percent) concentrations of fatty acid from forage plants and from back fat of Svalbard reindeer. Data on cattle fat from Church (1979).

Fig. 1. Relative (prosent) konsentrasjoner av fettsyrer i beiteplanter og ryggfett hos Svalbard-reinen. Data om fett fra kyr er tatt fra Church (1979).

REFERENCES

ARNOLD, G. W. & DUDZINSKI, M. L. 1978. Ethology of free-ranging domestic animals. - Elsevier Scientific Publishing Company, Amsterdam - Oxford - New York. 198 pp.

BRATTBAKK, I. & RØNNING, O. 1978. Rikt planteliv langt mot nord. - Forskningsnytt 23: 44-51.

BRZOSKA, W. 1976. Produktivität und Energiegehalte von Gefässpflanzen im Adventdalen (Spitzbergen). - Oecologia 22: 387-398.

CHURCH, D. C. 1976. Digestive physiology and nutrition of ruminants. Vol. I - O. & B. Books, Corvallis Oregon. 350 pp.

CHURCH, D. C. 1979. Digestive physiology and nutrition of ruminants. Vol. 2 - O. & B. Books, Corvallis Oregon. 452 pp.

KLEIN, D. R. 1970. Tundra ranges north of the boreal forest. - J. Range Manage. 23: 8-14.

McDONALD, P., EDWARDS, R. A. & GREENHALGH, J. F. D. 1978. Animal Nutrition. - Longman Inc., New York. 479 pp.

McEWAN, E. H. 1970. Energy metabolism of barren ground caribou (*Rangifer tarandus*). - Can. J. Zool. 48: 391-392.

NILSSEN, K. J. & RINGBERG, T. 1980. Seasonal changes in body weight, food intake and thyroxine in free ranging and captive Svalbard reindeer, *Rangifer tarandus platyrhynchus*. - Proc. 2nd. Int. Reindeer/Caribou Symp., Norway 1979, 329-332.

PERSEN, E., HOLAND, Ø., LEIFSETH, A. B. & STAALAND, H. 1983. Reindeer grazing on Brøggerhalvøya, Svalbard. - Acta Zool. Fennica 175: 35-37.

PRINS, H. H. 1981. Why are mosses eaten in cold environments only? - Oikos 38, 374-380.

PUNSVIK, T., SYVERTSEN, A. & STAALAND, H. 1980. Reindeer Grazing in Adventdalen. - Proc. 2nd Int. Reindeer/Caribou Symp., Norway 1979.

REIMERS, E. 1980. Activity pattern; the major determinant for growth and fattening in Rangifer? - Proc. 2nd. Int. Reindeer/Caribou Symp., Norway 1979. 466-474.

REIMERS, E., RINGBERG, T. & SØRUMGÅRD, R. 1982. Body composition of Svalbard reindeer. - Can. J. Zool. 60: 1812-1821.

RINGBERG, T., NILSSEN, K. & STRØM, E. 1980. Do Svalbard reindeer use their subcutanous fat as insulation? - Proc. 2nd. Int. Reindeer/Caribou Symp., Norway 1979. 392-395.

RØNNING, O.I. 1976. Vegetasjonslære. - Universitetsforlaget Oslo - Bergen - Tromsø. 101 pp.

RØNNING, O. I. 1979. Svalbards flora. - Norsk Polarinstitutt, Oslo. 128 pp.

STAALAND, H., BRATTBAKK, I., EKERN, K. and KILDEMO, K. 1983. Chemical composition of reindeer forage plants in Svalbard and Norway. - Holarctic Ecol. 6: 109-122.

STEFFENSEN, E. 1969. The climate and its recent variations at the Norwegian Arctic Stations. - Meteorologiske annaler, 5: 215-349.

TANHUANPÄÄ, E. & PULLIAINEN, E. 1969. Major fatty acid composition of some organ fats in the willow grouse (*Lagopus lagopus*) and the rock ptarmigan (*Lagopus mutus*). - Ann. Aca. Sci. Fenn. Ser. A, IV. Biologica 141: 1-14.

TILLEY, J. M. A. & TERRY, R. A. 1963. A two-stage technique for the in vitro digestion of forage crops. - J. Brit. Grassl. Soc. 18: 104-111.

WHITE, R. G., THOMSON, B. R., SKOGLAND, T., PERSON, S. J., RUSSEL, D. E., HOLLEMAN, D. F. & LUICK, J. R. 1975. Ecology of Caribou at Prudhoe Bay, Alaska. - Biol. Papers. Univ. Alaska. Special Rep. No. 2, pp. 150-201.

WHITE, R. G. & STAALAND, H. 1983. Ruminal volatile fatty acid production as an indicator of forage quality in Svalbard reindeer. - Acta Zool. Fennica 175: 35-37.

Manuscript received December 19, 1983