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Kristina Warenberg

Reindeer forage plants in the early grazing season

Growth and nutritional content in relation to climatic conditions

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Contents

Abstract

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The aims of this investigation were to elucidate how plants grazed by reindeer in the early spring survive the winter and develop their shoots and leaves, to study the environmental factors, mainly the local climate, which influence the early development of new biomass, and to determine the contents of nutrients (protein, sugar and minerals) in spring and autumn material. The area of investigation was the reindeer range at Ottfjället, the Lapp community of Handölsdalen, W Jämtland, Sweden, where a large enclosure was operated partly for experimental purposes during the 1970's. Two sub-areas were studied, one in the forest and one in the alpine heathland.

Local meteorology included year-long temperature determination above ground and in soil profiles and observation of snow conditions and the remarkably low intensity of soil frost under the sometimes very deep snow. Most forage plants showed some winter development beneath the snow but grew most rapidly during and after the thaw. Some plants were regarded as semi-evergreen. Quantitative investigations were made on the available above-ground biomass of four species before, during and following the snow-melt. The nutrient content and other results and their importance to reindeer are discussed at the end of the paper.

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Варэнберг, Кристина, 1982. ***Кормовые растения для оленей в весеннем пастбищном сезоне. Их рост и питательные свойства в зависимости от климатических условий.***

В работе ставится цель объяснить, каким образом растения, на которых пасутся олени ранней весной, переживают зиму и каким образом развиваются их побеги и листья; изучить факторы окружающей среды, прежде всего местный климат, влияющий на развитие биомассы; исследовать содержание питательных веществ/протеина,сахара и минеральных элементов/ в весеннем и осеннем материалах. Исследования проводились на оленей ферме Хаидэльсдаленс Самэбы в провинции Зап. Емтлянд в Швеции, где в 1970 г. была создана крупная изгородь, частично для экпериментальных целей. Исследования были проведены на двух подучастках-в лесном и горном выресковом районах.

Местные метереологические исследования были направленые на изучение температуры воздуха и почвы, а также на наблюдения глубоких слоев снега и мезлоты под иногда очень глубоким снегом. У болшинства кормовых растеий наблюдалось некоторое развитие в зимних условиях под снегом, но, они росли, однако, быстрее во время и после таяния снега. Некоторые виды можно отнести к процветающим эмой /вечнозеленым/. Были проведены количественные исследования поверхностной биомассы у четырех видов растений перед, во время и после таяния снега. В заключительной части диссертации рассматриваются питательные и другие результаты, а также их значение дла оленей.

1. Introduction

Since the spring of 1970 I have studied the grazing by reindeer on the Ottfjället reindeer range, Handölsdalen Lapp community. The aims of earlier investigations were to make a vegetation map in order to study where the most attractive types of reindeer pasture were situated. A study of the semi-evergreen plants from which the reindeer obtain their food requirement during the late winter and early spring was undertaken during the spring of 1972. The results of the investigation during 1970—1974 were published in Warenberg (1977).

The later investigations concerned the shoot development of several species grazed by the reindeer. The primary aim was to elucidate the development in such species that produce new shoots early in the spring while still covered by snow. I have called these plants semi-evergreen but the transition to evergreen is diffuse. The new shoots are believed to provide the reindeer with valuable protein and carbohydrate during the critical period in the late winter and early spring. The availability of these nutrients is of particularly great importance for the female as calving approaches. The investigations also include chemical analyses of the content of crude protein, sugar (inredos) and minerals in the plants.

Aims of the investigation

(1) How do the plants prepare for the winter? Is there shoot development beneath the snow and how do the shoots develop during and following the snow-melt?
(2) Which environmental factors influence the development of the plants?
(3) How does the biomass change during the period of snow-melt?
(4) How large are the contents of protein, sugar and minerals in spring and autumn material?

At the start I had intended to extend my investigations outside the Ottfjället reindeer range so as to enable the results to become of greater practical use to the reindeer herders. However, this could not be achieved in the time available. Instead, the investigations concentrated on the shoot's rate of growth following the snow-melt.

The intention had also been to investigate how much of the plant's biomass over-wintered, but this was modified to comprise the changes in the biomass of certain species during and after the snow-melt.

Nomenclature

The nomenclature for vascular plants follows Lid (1974) and for lichens Dahl & Krog (1973).

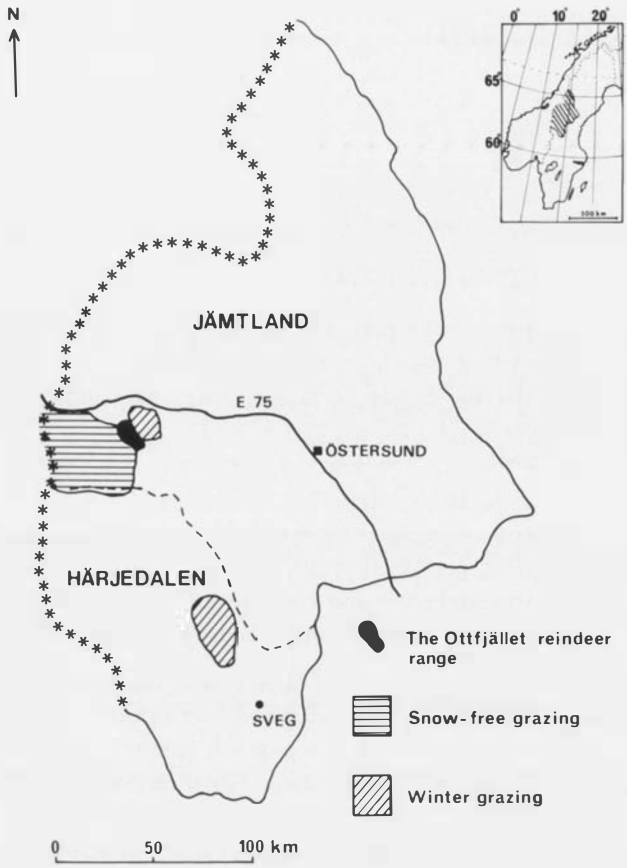


Fig. 1. Site of the investigation area and the reindeer grazing areas for the Handölsdalen Lapp community, Jämtland and Härjedalen.

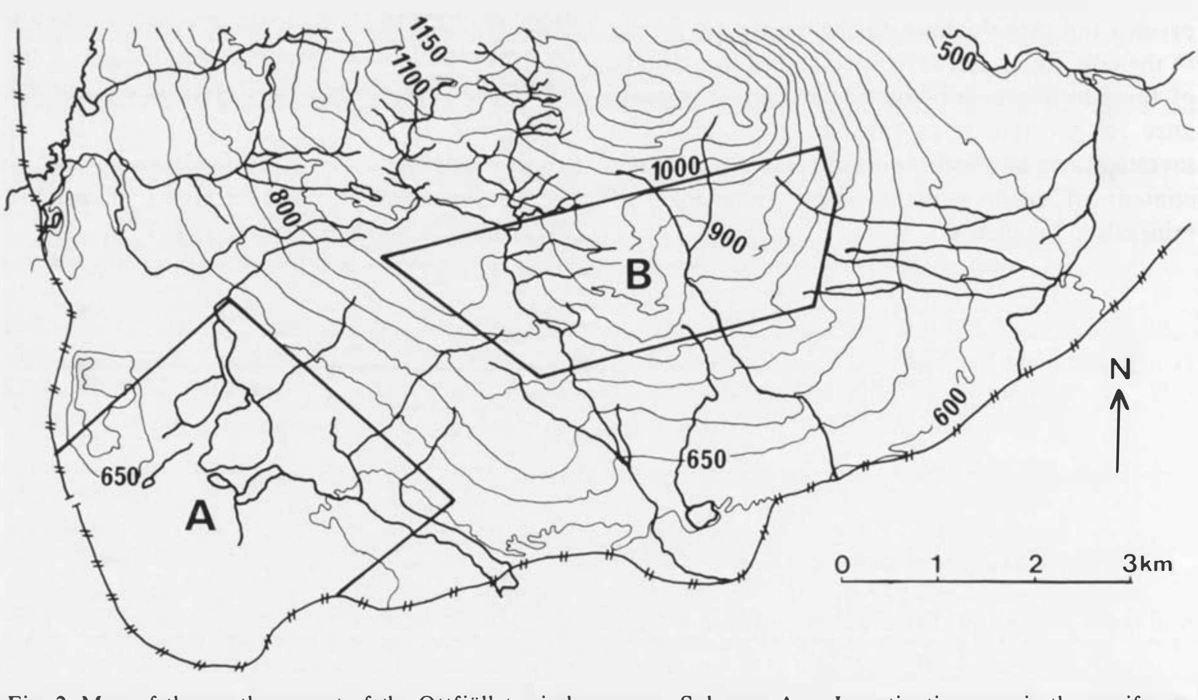


Fig. 2. Map of the southern part of the Ottfjället reindeer range. Sub-area A = Investigation area in the coniferous forest. Sub-area B = Investigation area above tree limit (cf. Warenberg 1977).

2. Area of investigation

The investigations were conducted at the Ottfjället reindeer range, Handölsdalen Lapp community in western Jämtland (Fig. 1). The reindeer range was started in 1970 but ceased its activities in 1979 when most of the stock was sold to Norwegian interests (Warenberg 1980).

The investigations upon which the present paper is based were conducted between 1974 and 1979 and cover parts of the reindeer range (A and B in Fig. 2). A number of complementary investigations were conducted during the spring of 1980. The investigations have been concentrated on such parts of the range where the reindeer are usually present during the period of snow-melt.

A closer description of topography, bedrock, and soil types of the entire Ottfjället reindeer range, together with a detailed description of plant communities in the area (including a vegetation map) are given in Warenberg (1977).

2.1 Survey of vegetation

Two sub-areas were investigated, one situated below the tree limit (A in Fig. 2), and the other within the low alpine belt (B in Fig. 2). The sub-area of investigation below the tree limit, 842 m a.s.l., mostly comprises a *Vaccinium myrtillus - Picea abies* forest, which is the dominating forest type within the Ottfjället reindeer range (Fig. 3). *Vaccinium myrtillus* is dominant in the field layer in this plant community. The field layer also contains *Deschampsia flexuosa*. In the forest there are open places with birches and willow species (Fig. 4). Locally there are areas more densely covered by herbs, e.g., *Aconitum septentrionale, Calamagrostis purpurea, Geranium sylvaticum, Lactuca alpina, Solidago virgaurea.* The sub-area also includes pine forest where *Calluna vulgaris* and *Empetrum hermaphroditum* dominate in the field layer. The bottom layer contains dominant lichens such as *Cladonia mitis* and *Stereocaulon paschale.*

There are numerous fens in the sub-area (map in Warenberg 1977). The most common type is the *Eriophorum* fen (Fig. 5) with many pines and abundant *Alectoria nigricans*, and *A. ochroleuca.* The *Eriophorum* fens are important as they contain abundant *Carex* spp., *Eriophorum* spp., and *Scirpus caespitosus*, all of which are grazed by the reindeer. On parts of the fens the reindeer can find *Menyanthes trifoliata* and fairly large quantities of *Comarum palustre.*

Most of the sub-area above the tree limit (B in Fig. 2), belongs to the low alpine belt but partly also to the middle alpine belt. The last-mentioned belt begins at the upper limit of *Vaccinium myrtillus.* A *Carex bigelowii* heath dominates here. Frequent species are *Carex*

Fig. 3. Sub-area A, below the tree limit on Mt. Ottfjället, with Lake Stora Nulltjärn in the background. The sub-area comprises *Vaccinium myrtillus - Picea abies* forest. This is the most dominating forest type within the Ottfjället reindeer range. Note the abundant birch. Several fens can be seen in the picture. July 1977.

Fig. 4. A fen near the tree limit with *Molinia caerulea* and *Scirpus caespitosus. Betula pubescens* in the foreground and old spruce forest in the background. The forest has open places, both fen areas and areas with birches and willow species. These places are important as grazing areas for the reindeer. Photo: Bengt Pettersson.

Fig. 5. *Eriophorum* fens within the reindeer range are often colonized by pine with abundant *Alectoria nigricans* and *A. ochroleuca.* These lichens are an important reserve for reindeer during periods of deep snow.

Fig. 6. *Vaccinium myrtillus* - *Empetrum* heath comprises the largest area within the low alpine belt. *Carex bigelowii* also occurs here. The most common lichens are *Cetraria nivalis* and *Cladonia mitis.*

bigelowii and *Juncus trifidus*. Within the low alpine belt on the other hand the *Vaccinium myrtillus* - *Empetrum* heath covers the largest area. *Carex bigelowii* also occurs here. The most frequent lichens are *Cetraria nivalis* and *Cladonia mitis* (Fig. 6). It is interrupted here and there by a *Loiseleuria-Empetrum* heath. There are many windswept patches in the sub-area, which are small but have importance due to the occurrence of *Juncus trifidus*. Their slopes are covered with *Vaccinium myrtillus* and *Betula nana*. In addition to *J. trifidus* in these patches, *Loiseleuria procumbens* is common.

Within the sub-area above the tree limit there are abundant *Betula nana*, *Salix glauca*, and *S. lapponum*. The grasses *Deschampsia caespitosa* and *D. flexuosa* also occur here.

2.2 The reindeer range

When the reindeer enterprise started in 1970 an enclosure was built around the range. An agreement was reached that the number of reindeer should not fall below 500 animals. The range was run during the years 1970—1975 by two Lapps, Olle Blind and Ingemar Kråik. The number of reindeer kept referred to breeding animals with restriction of the winter population. Consequently some of the calves were slaughtered. Calf mortality was large on the range (50 % in 1974/1975), the reason being discussed by Franzén & Bjärvall (1976). The reindeer were present on the range from about April 15 to early October. From late 1975 onwards the range was run by Ingemar Kråik alone. As mentioned earlier the range ceased its activities in 1979. This was in connection with the tragic death of Ingemar Kråik in a snow-scooter accident. During the period when the range was in operation a maximum of about 600 reindeer were kept.

A new attempt to open the range within the enclosed area was planned for the spring 1981. However, the experiment has been postponed to the spring 1982 as the reindeer could not be driven into the range. The experiment will cover a three-year period. Agreement has been reached between the Lapp who will run the range and the Lapp community. This agreement implies that the reindeer are immediately released from the range and returned to the community herds if the experiment should fail.

The intention is that at least 500 reindeer will be on the range during the snow-free period (cf. Svensk författningssamling 1971:437). It is planned to move the reindeer in good time before calving. Hopefully, they should be on the range by about 15—20 April 1982.

2.3 General climate conditions

The area of investigation is characterized by a "local maritime" temperature climate, its relative maritimity caused by the Storlien depression open to the Atlantic winds. The values given in Figs. 7—9 have been prepared by Haldo Vedin, meteorologist at the Swedish Meteorological and Hydrological Institute (SMHI), and represent mean values for the period 1931—1960.

The mean monthly air temperature (Fig. 7) has been calculated from values for neighbouring stations (Mo, Undersåker, Åre, Duved, Storlien, Blåhammaren, Sylstationen, Storsjö kapell, and Höglekardalen). They are

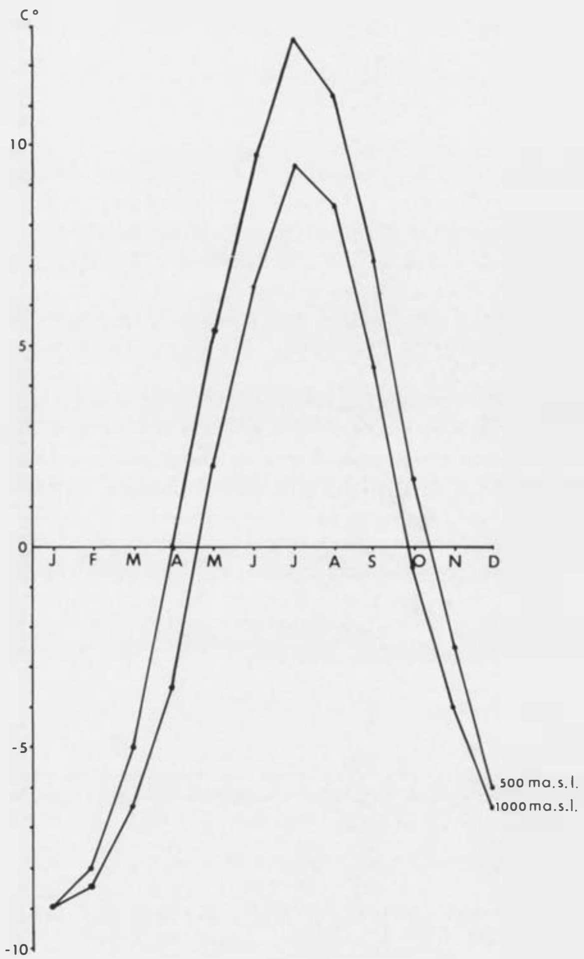


Fig. 7. Mean monthly air temperatures for the Ottfjället area (normal period 1931—1960) estimated by SMHI from several neighbouring stations (see text).

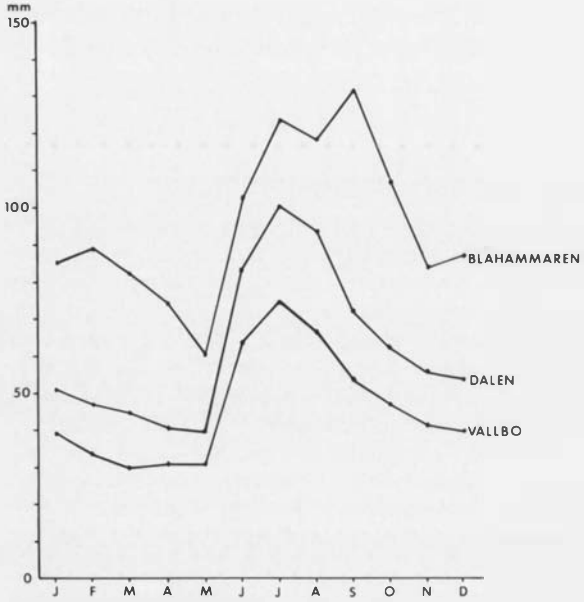


Fig. 8. Mean monthly precipitation values for the three meteorological stations closest to the Ottfjället area (normal period 1931—1960).

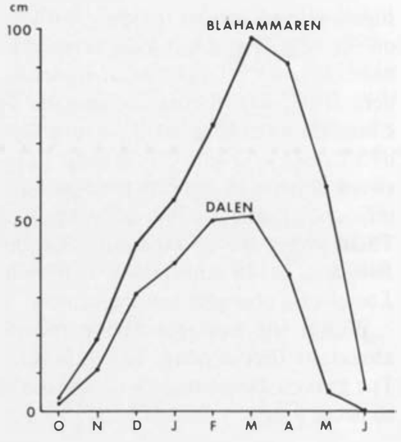


Fig. 9. Mean depth of snow at the Dalen and Blåhammaren stations (measured on the 15th of each month, normal period 1931—1960).

probably relatively reliable for the summer months whereas the values for the winter months are considerably less relevant as during the winter terrain conditions are of decisive importance for temperature and consequently make the local variations larger.

The mean precipitation for Vallbo (575 m), Dalen (480 m, about 15 km NE of Ottfjället) and Blåhammaren (1090 m) is given in Fig. 8. The values indicate that the annual precipitation at Ottsjön and in the northeastern part of the Vålöjan valley is about 550 mm whereas that within the higher situated areas is about twice as much. Higher situated areas are often subjected to mists or low-lying cloud. The lower values for Vallbo (ca. 5 km SE of Ottfjället) with an annual mean precipitation of 578 mm, and for the Vålöjan valley with 550 mm probably depend on these places being in the rain shadow of Ottfjället. The highest monthly precipitations are in June—September (October).

The mean snow depth for Dalen and Blåhammaren is given in Fig. 9. According to Pershagen (1969 p. 35) the mean number of days at Ottfjället with snow cover varies between 175 and 200. Local frost may occur during the growing period and occasionally there may be snow.

The snow cover above the tree limit largely depends on local factors. In wind-exposed areas the snow cover is relatively thin whereas it is deeper and more durable in sheltered localities.

Within the Ottfjället area snow normally falls during the last days of September but generally melts. Snow precipitation during October generally remains on the highest parts of the mountain. During the years when measurements were made the snow that fell in October did not remain at levels below 1000 m, apart from that in drifts.

Data on sunshine hours and relative humidity are taken from the meteorological station at Storlien-Visjövalen, situated at 640 m, at the tree limit and at the transition between a relatively steep NW slope and the higher situated less sloping mire plateau. The vegetation consists of scattered birches and pines. The meteorological station is consequently situated about 160—170 m

Table 1. Sunshine hours at Storlien – Visjövalen, monthly mean values for 1961–1975, monthly means 1974–1979, year sums and percent of mean value 1961–1975 and 1974–1979.

Year	J	F	M	A	M	J	J	A	S	O	N	D	Year, no. of hours	% of normal
1961–1975	28	62	123	160	211	200	170	162	106	65	34	11	1332	100
1974	31	59	205	126	320	233	139	160	124	34	43	15	1489	112
1975	31	48	131	178	180	187	229	173	86	66	30	0	1339	101
1976	15	97	186	119	281	164	217	195	135	67	30	22	1527	116
1977	15	90	95	152	173	159	181		117	47	22	15	1611	121
1978	18.1	75.5	158	162	267	212	194	127	111	43	33	39	1444	108
1979	41	69	155	136	208	180	109	127	86	117	33.6	23.4	1285	96

Table 2. Monthly means of relative humidity (%) at 13.00 hrs, and daily means for 1931 1960 at Storlien (from Tæsler 1972), from June 1976 May 1977 at Storlien Visjövalen and Ottfjället. The meteoro logical station at Storlien was moved about 2.5 km in 1962.

	Storlien 1931 1960	Storlien Visjövalen 1976 1977	Ottfjället 1976 1977
June			
13.00	66	67	66
daily mean	72	74	73
July			
13.00	68	67	66
daily mean	78	74	74
August			
13.00	70	65	61
daily mean	80	76	70
September			
13.00	76	72	72
daily mean	86	83	79
October			
13.00	82	74	75
daily mean	89	79	81
November			
13.00	87	83	80
daily mean	89	84	83
December			
13.00	88	86	84
daily mean	89	87	85
January			
13.00	87	85	85
daily mean	88	87	87
February			
13.00	85	85	82
daily mean	87	86	84
March			
13.00	82	79	74
daily mean	86	83	82
April			
13.00	77	76	75
daily mean	83	80	78
May			
13.00	68	66	68
daily mean	78	74	72

lower than measurement station 3 (the fenced-in area, see Chapter 3) on Mt. Ottfjället. This station is exposed to the south and is treeless. Despite these differences, the meteorological station at Storlien-Visjövalen is the best for comparisons with my values. The station's values for sunshine (Table 1) and relative humidity (Table 2) should be applicable to my area. Visjövalen, however, lies in an area with considerably more precipitation, and also is slightly more maritime.

As shown by Table 1, more sunshine than normal was registered during 1974, 1976, and 1977. During March 1977, when maximum temperatures within the area of investigation were exceptionally high, Storlien-Visjövalen had only 95 sunshine hours compared with normally 123. At the military air base of Frösön a total of 146 sunshine hours were registered during this month. According to the SMHI monthly report for March 1977, Storlien-Visjövalen had unusually many days with cloudy weather and consequently fewer sunshine hours than normal whereas the area around Storsjön had unusually many sunshine hours.

The relative humidity was measured during the period June 1976 to June 1977 at station 3. The difference between the area of investigation and Storlien-Visjövalen during this period was negligible. However, March 1977 had lower relative humidity at 13.00 h in comparison with Storlien-Visjövalen in the same year. The divergence from the normal year 1930—1961 was great (Table 2).

3. Climate investigations

3.1 Methods

The field work with climate measurements was started in the autumn 1974. Measurements were conducted during a three-year period at three places within the Ottfjället reindeer grazing area (Fig. 10). The investigations comprised measurements of air temperature, soil temperature, frost depth and snow depth, but during varying periods of time (see below and Table 3). The three sites all had a more or less southerly exposure which probably influenced the climatic conditions.

A south-exposed slope was selected within the area at about 810 m with a slope of 20° (station 1, Figs. 10 and 11). The vegetation was dominated by *Deschampsia caespitosa*. *D. flexuosa* occurred as scattered individuals and *Nardus stricta* was slightly more frequent.

Another measurement area was chosen in the upper part of a *Eriophorum angustifolium* fen (station 2), facing SSE, at about 800 m (Figs. 10 and 12).

The third station (station 3), which was fenced-in, had a slope of 4°. It was heterogeneous with an area of about 100 m². The height above sea-level was about 800 m (Figs. 10 and 13). Vegetation within the fence included a *Molinia caerulea* meadow with occasional *Scirpus caespitosus, Carex pauciflora, Andromeda polifolia*, and *Euphrasia frigida*. Another vegetation type was dominated by *Vaccinium* spp. and *Betula nana*. This gradually changed into a type with dominant *Empetrum hermaphroditum*, highly frequent *Carex bigelowii*, and *Lycopodium alpinum*, and just occasional specimens of *Nardus stricta, Vaccinium myrtillus, V. uliginosum*, and *B. nana*. To the south of the *Molinia caerulea* meadow the vegetation was more typical of a fen with *Scirpus caespitosus* as dominating species. This changed into an *Eriophorum angustifolium* fen. In the southwest corner of the

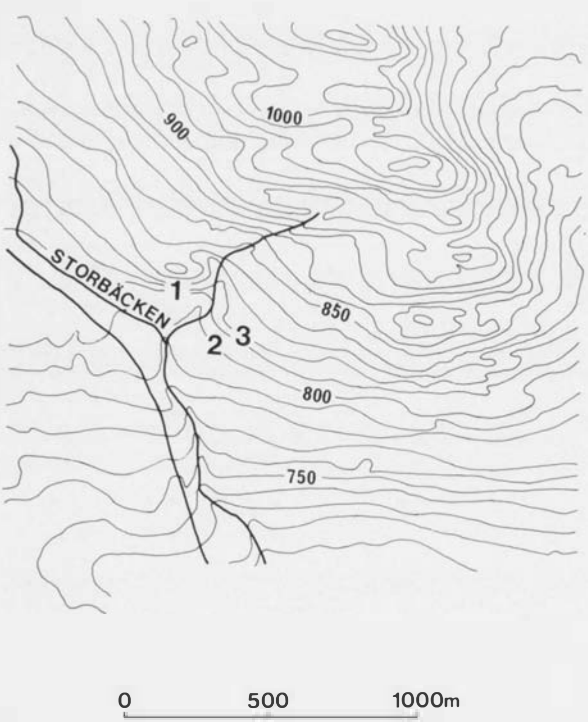


Fig. 10. Part of sub-area B (above tree limit) with the three measuring stations. 1. Station 1 (south slope), 2. Station 2 (the fen), 3. Station 3 (fenced-in area). A car track is seen to the left of the brook Storbäcken.

Table 3. Measurements made during 1974–1977. Ottfjället reindeer range.

	Station		
	1	2	3
Air temperature			
ca. once a week 1974–1977	x	x	
Continuous measurements			
1976–1977	–	–	x
Soil temperature			
ca. once a week 1974–1977	x	x	–
continuous measurement 1976–1977	–	–	x
Air humidity 1976–1977	–	–	x
Snow depth			
ca. once a week 1974–1977	x	x	–
ca. once a week 1976–1977	–	–	x
Frost depth in soil			
ca. once a week 1976–1977	–	x	x

Fig. 11. Station 1 (south slope). The area lies about 810 m a.s.l. The vegetation is dominated by *Deschampsia caespitosa* with occasional *D. flexuosa* and to a slightly greater extent *Nardus stricta.* A tussocky fen in front of the slope. Photo: Bengt Weilert, Aug. 1981.

Fig. 12. Station 2 (the fen). This measurement area was placed in the upper part of an *Eriophorum angustifolium* fen at the tree limit. These fens are common within the low alpine belt. The tree limit is occasionally broken by fens. The forest consists of pines, spruces and birches. Photo: Bengt Weilert, Aug. 1981.

fenced-in area the vegetation was richer with, for example, *Solidago virgaurea, Andromeda polifolia, Potentilla erecta, Empetrum hermaphroditum, Vaccinium* spp., and *Trientalis europaea.* Outside the fence the area to the north was a small *Molinia caerulea* meadow and towards the south and west there were fens. Small groves of spruce grew close to the fence (Fig. 13).

In 1974, when the field work started, the measurements of temperature in the soil and the air were started on the south-exposed slope (station 1) and in the *Eriophorum* fen (station 2). The soil temperature measurements were made with thermistors placed at different depths in the soil. Consideration was taken to the root depth of plants in determining the depths where the thermistors were placed. On the south slope twelve thermistors were buried vertically in the soil below each other at depths between 1 and 15 cm. The same number of thermistors were placed in the *Eriophorum*

Fig. 13. Station 3 (fenced-in area). This measurement area is heterogeneous. Outside the fence (on the northern side) is a small *Molinia caerulea* meadow, and to the south and east there are fens. Small groves growing close to the fence could have influenced the measurements. Groves above the tree limit mostly consist of spruce or birch. Photo: Bengt Weilert, Aug. 1981.

angustifolium fen. They were attached to strong plastic tubing which kept them in position. The first thermistor was placed at a depth of 5 cm and the deepest at 80 cm. The cables from the thermistors were drawn to the instrumentation box placed on a pole. Each cable terminated in a coupling device to which the instrumentation was attached during the measurements.

Originally it had been intended to make the measurements once a week but this was found difficult to achieve. The air temperatures were measured at the same time with a normal mercury thermometer. These measurements ended in September 1977.

Measurements could not be made during the period from late February to May 30, 1976, since the measuring apparatus could not be found in the deep snow. At Easter (early April) the snow depth was 5 m on the south slope (station 1) and 4 m on the fen (station 2). Attempts to localize the apparatus with military metal detectors and avalanche probes were unsuccessful, as also was digging.

In June 1976 the measurements were extended to comprise more continuous measurements of air and soil temperature and snow and frost depth. These measurements were made within the fenced-in area (station 3) where 16 thermistors were placed at different depths in the soil and in different plant communities. The soil temperature from each thermistor was registered hourly with a Grant temperature recorder.

The daily mean values were calculated from 24 recordings per day. Temperature values were even recorded at the same times as at stations 1 and 2.

A thermohygrograph (Lambrecht) was used to collect air data. The instrument was placed in an SMHI temperature cage. However, it was soon noticed that snow penetrated the cage and following the advice of Professor Liljequist, Uppsala, a fine-meshed steel netting was placed around the cage. Nevertheless, the snow was still able to penetrate and finally the cage was covered with parachute material which was found to be effective. The thermograms obtained gave daily maximum and minimum temperatures.

Within all three areas the snow depth was measured with permanent measuring sticks. The frost depth was investigated in the *Eriophorum angustifolium* fen and within the fenced-in area. The south slope had a soil layer that was too thin for a frost depth meter. The frost depth meter is of simple construction, consisting of a pipe graded in centimeters which is filled with a water solution of methylene blue which turns almost colourless on freezing. The tube is placed inside a wider tube buried in the soil.

The measurements of air temperature and relative humidity at station 3 ended on 15 June 1977.

Table 4. Monthly means, maximum and minimum means 1931-1960 at Storlien, and monthly maximum and minimum means for June 1976 - May 1977 at Storlien - Visjövalen and Ottfjället's station 3.

	J 6	J 7	A 8	S 9	O 10	N 11	D 12	J 1	F 2	M 3	A 4	M 5	X̄
Monthly mean temp.													
Storlien 1931-1960	8.6	12.0	10.7	6.6	1.5	-2.6	-5.6	-8.4	-8.0	-5.5	-1.2	3.9	1.0
Mean maximum temp.													
Storlien 1931-1960	13.3	16.6	15.1	10.3	4.5	0.1	-2.3	-4.7	-4.5	-1.6	2.2	8.1	4.8
Storlien-V. VI-76--V-77	12.8	15.5	15.9	7.1	3.8	0.1	-5.9	-7.8	-7.3	0.0	-0.7	6.8	3.4
Ottfjället VI-76--V-77	12.4	15.6	16.2	6.5	3.6	-0.1	-6.7	-7.0	-4.4	5.8	0.6	7.5	4.2
Mean minimum temp.													
Storlien 1931-1960	4.1	7.2	6.2	2.9	-1.6	-6.2	-9.2	-12.7	-12.4	-10.1	-5.1	-0.6	-3.2
Storlien-V. VI-76--V-77	4.3	7.2	6.7	0.3	-0.5	-4.7	-12.6	-14.0	-14.2	-5.6	-6.7	0.3	-3.3
Ottfjället VI-76--V-77	2.8	6.1	6.1	-1.2	-1.8	-5.4	-12.2	-14.0	-14.2	-6.3	-6.4	0.3	-3.9

The other measurements ended on 11 September 1977.

The local climatological values for air temperature obtained with the Lambrecht thermohygrograph at station 3 were compared with climate values from neighbouring meteorological stations that, according to SMHI, should be representative (Storlien-Visjövalen, about 50 km from Mt. Ottfjället, Ljusnedal in Härjedalen, and Östersund). Best agreement of the temperature data in the area of investigation was with the temperature values from Storlien-Visjövalen. Consequently, only values from that station have been included.

3.2 Air temperature

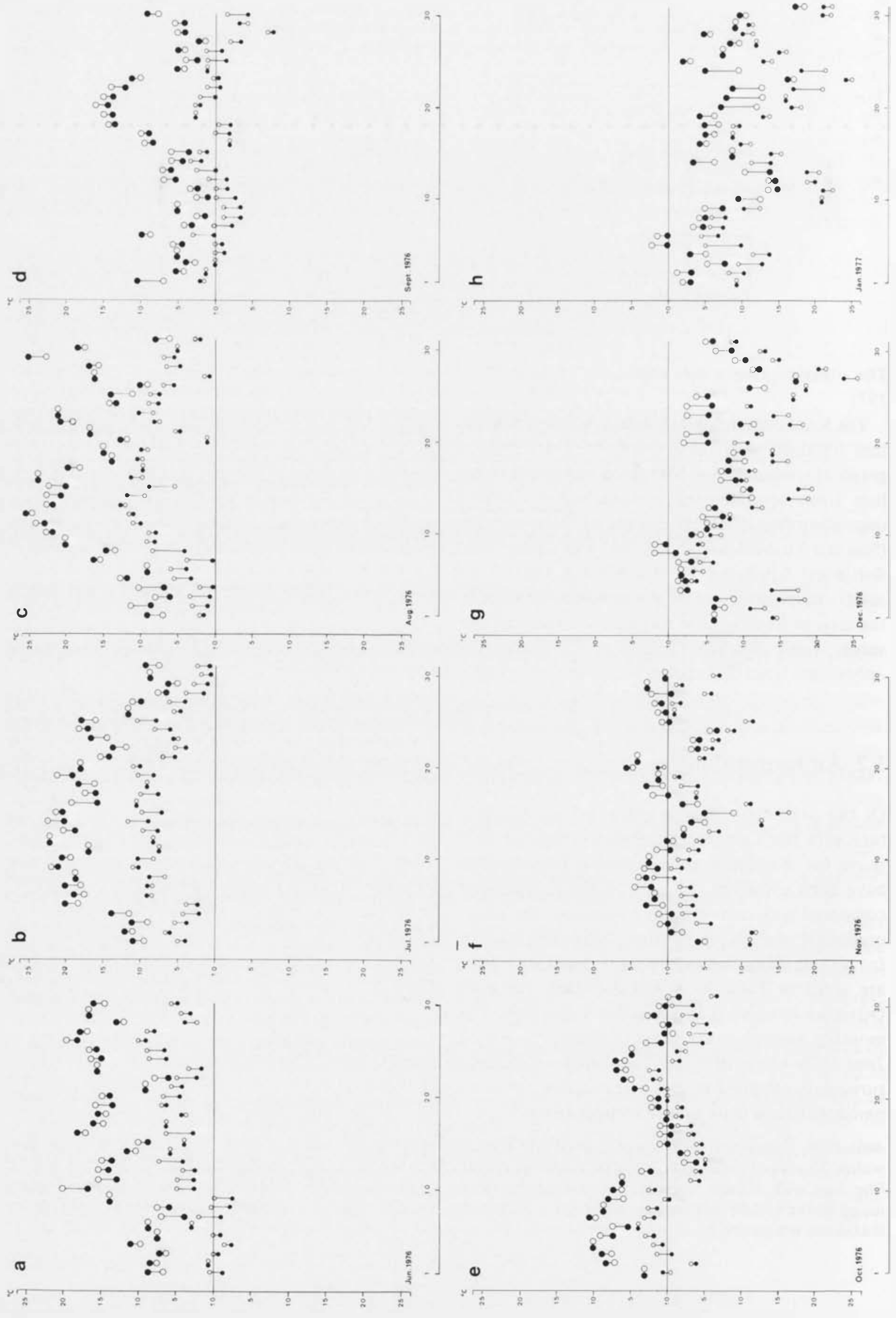
Of the continuous measurements of air temperature with the Lambrecht thermohygrograph only those for maximum and minimum temperatures have been extracted. In Fig. 14 these values are compared with corresponding values for the meteorological station at Storlien-Visjövalen. Apart from these daily values, the monthly mean values are given in Table 4 as well as values for both Ottfjället (station 3) and Storlien-Visjövalen. The monthly weather characteristics during the period June 1976—June 1977 are given below where measurements obtained in this investigation are compared with data from Storlien-Visjövalen.

June 1976. Temperature was lower (0.5°C) than normal within the area of investigation (SMHI monthly report). The days with highest temperatures at Ottfjället were noted in the middle and at the end of the month with maximum temperatures of +18°C (Fig. 14 a). The lowest daily maximum temperatures was +3°C. The minimum temperature at the start of the month was below 0°C for seven days. In comparison with Storlien-Visjövalen the minimum temperature in the area of investigation was lower (Table 4).

July 1976. Temperature deficiency of 0.5—1°C (SMHI monthly report). Within the area of investigation the maximum temperature varied between +14° and +23°C apart from the first three and the six last days in the month, when lower temperatures were measured (Fig. 14 b). Throughout the entire month the minimum daily temperature was above 0°C. The area of investigation and Storlien-Visjövalen had the same mean maximum temperature whereas the minimum temperature was lower at Ottfjället.

August 1976. Mean temperature during the month was slightly above normal (0.5°C) in western Jämtland (SMHI monthly report). Within the area of investigation the month started with maximum temperatures of only between +6°and +9°C (Fig. 14 c). Later the weather stabilized and maximum temperatures of more than +25°C were noted on August 12 and 29. On August 31 the maximum temperature had decreased to only +7.9°C. The minimum temperature was never below 0°C. The differences between the monthly mean temperatures at the area of investigation and Storlien-Visjövalen were small and fall within the margin of error.

September 1976. The coldest September of the century (SMHI monthly report). The divergence from the mean value in western Jämtland was 3°C. The estimated mean value for the Ottfjället area, based on SMHI data, is normally +7.1°C at 500 m above sea level and +4.5°C at 1000 m. The monthly mean value obtained with the Lambrecht thermohygrograph at 800 m was +6.5°C. The difference between the maximum and minimum temperature during the day was greatest between September 16 and September 23 (Fig. 14 d). This applied both within the area of investigation and at the meteorological station at Storlien-Visjövalen. The difference amounted to between +14° and +17°C. On no occasi-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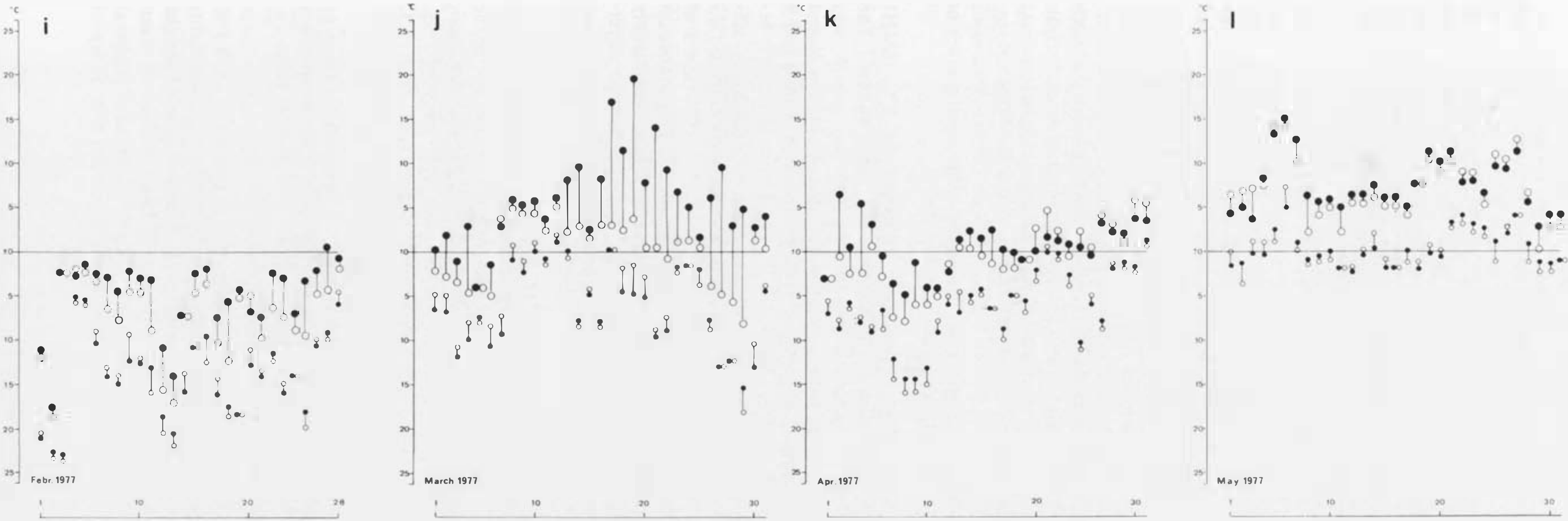


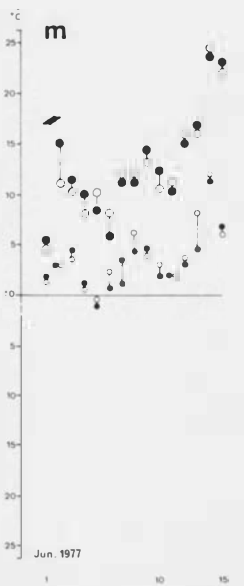


Fig. 14 a—m. The maximum and minimum temperatures at station 3, the Ottfjället reindeer range, during the investigation period 1976—1977. The air temperatures are compared with corresponding values for the meteorological station at Storlien-Visjövalen. Filled symbols give data from Ottjället and open symbols give data from Storlien-Visjövalen. Large symbols = maximum temperature, small symbols = minimum temperature. The construction of the figure is after an idea in Lundqvist (1968 cf. Fig. 18).

on did the maximum temperature fall below 0°C whereas the minimum temperature remained under 0°C except for some days at the start and in the middle of the month. The lowest minimum temperature of —7.8°C was measured on September 28. The mean value for the minimum temperatures was higher at Storlien-Visjövalen than within the area of investigation (Table 4).

October 1976. Temperature deficiency 0.5—1°C (SMHI monthly report). For most of the month the maximum temperatures were above 0°C (Fig. 14 e). The highest temperature during the month was +11.4°C and the lowest —4.4°C. The minimum temperature was above zero on ten occasions. The lowest minimum temperature was on October 31 with —6.5°C. The maximum temperature at the area of investigation agreed with the corresponding temperature at Storlien-Visjövalen whereas the minimum temperature was lower in the area of investigation during practically the whole month (Table 4).

November 1976. Mean temperature slightly below normal, 0.5°C (SMHI monthly report). The lowest maximum temperatures were —4, —5, and, —7°C (Fig. 14 f).Maximum temperatures were almost as often above as below zero, with a peak on November 20 (+5.1°C). Minimum temperatures remained below zero apart from on November 20. The mean value for the minimum temperatures was slightly lower at Ottfjället than at Storlien-Visjövalen (Table 4).

December 1976. Colder than normal, with a temperature deficiency of 4°C in the Ottfjället area (SMHI monthly report). The maximum temperature exceeded 0°C only on December 9 (+0.3°C), which was the highest value of the month (Fig. 14 g). The lowest maximum temperature, —17.4°C, and the lowest minimum temperature, —23°C, were on December 27. The difference between maximum and minimum temperatures has been as much as ca. 10°C on several occasions. In comparison with Storlien-Visjövalen there are differences particularly in the minimum temperature. On December 27 the minimum temperature was —23.6°C at Ottfjället. That was the lowest temperature during the years of investigation (cf. Storlien-Visjövalen —26°C, Östersund —28.5°C, Ljusnedal —33.5°C).

January 1977. Colder than normal with a deficiency of 4°C in the western mountain region (SMHI monthly report). Within the area of investigation the maximum temperatures varied between 0°C and —17°C (Fig. 14 h). The greatest difference between the maximum and minimum temperatures was ca. 13°C (on January 24). The maximum temperature diverged noticeably from that at Storlien-Visjövalen on January 20, 21, 22, and 24. The mean value for the maximum temperature was 0.7° higher at the measuring station in the Ottfjället area than at Storlien-Visjövalen whereas the minimum temperatures showed good agreement (Table 4).

February 1977. In this month western Jämtland had a temperature deficiency of 4°C (SMHI monthly report). Within the area of investigation the maximum temperature was considerably higher than at Storlien-Visjövalen on several days. The divergence in minimum temperature was less (Fig. 14 i and Table 4). The temperature remained below 0°C throughout the whole month apart from on February 27 when the maximum temperature was +0.7°C. The difference between maximum and minimum temperatures was large on some occasions (ca. 20°C).

March 1977. Temperature surplus of 2—3°C for western Jämtland (SMHI monthly report). The maximum temperature within the area of investigation was around 0°C with the exception of three days in the beginning of the month (Fig. 14 j). The minimum temperature remained below 0°C with some exceptions. The lowest value was —15.5°C. The difference between the maximum and minimum temperatures during the month was large. The largest difference occurred on March 19 with 24°C difference. In comparison with Storlien-Visjövalen the maximum temperature was considerably higher at Ottfjället. The divergence for the minimum temperature was not so large. The monthly mean value for March at station 3 was 5.8°C higher than at Storlien-Visjövalen whereas the minimum temperature was slightly lower in the area of investigation (Table 4).

April 1977. Temperature deficiency of 2°C (SMHI monthly report). On the whole the month was cold. The highest maximum temperature of the month was +6.9°C and the lowest —4.9°C (Fig. 14 k). The lowest minimum temperatures were recorded on April 8 and 9 with —14.3°, and —14.4°C. There were differences between the three measuring stations at Ottfjället. At stations 1 and 2 temperatures of —2°C were recorded on April 2 (between 12.30—12.40) and +1°C (noted at 12.00 on the thermogram, station 3). The maximum temperature was again on some occasions considerably higher than at Storlien-Visjövalen, although the difference was not as large as during March. The mean value was more than 1°C higher than at Storlien-Visjövalen (Table 4).

May 1977. Temperature deficiency of 0.5—1°C (SMHI monthly report). There were no warm periods during the month and no particular differences between the maximum and minimum temperatures were recorded (Fig. 14 l). The highest maximum temperature was +15°C and the lowest +3.1°C. During more than half the number of days the minimum temperature was below zero. The highest minimum temperature was +5°C. The area of investigation had slightly higher monthly mean values than at Storlien-Visjövalen but the minimum mean values were of similar magnitude (Table 4).

June 1977. A slight temperature deficiency of ca. 0.5°C (SMHI monthly report). The continuous measurements in the Ottfjället reindeer range ended on June 15 and the data only stretch as far as this date. The highest maximum temperature was +24.1°C. Minimum temperatures below 0°C occurred on only one day (Fig. 14 m).

The air temperature at station 3 at Ottfjället characterized in this way with only maximum and minimum temperatures shows no regular difference to values at the SMHI station at Storlien-Visjövalen. The most noticeable difference is in the March maximum temperature and to some extent that in February, which were considerably higher at station 3 (the Ottfjället area) than at Storlien-Visjövalen (see further comments in section 3.5).

3.3 Soil temperature

As described earlier, soil temperatures were measured at three stations. The results are presented in a series of figures where each profile represents a measuring occasion. All measurements made have not, however, been reported. In the present context the temperature data recorded before, during and immediately after the snow-melt are of particular interest. Particular attention has therefore been paid to this period.

3.3.1 Station 1

(1974) 1975. Measurements at station 1 (south slope) started on 3 November 1974. From this date the temperature remained relatively constant until 24 February 1975 (Fig. 15 a). The soil was slightly warmer at deeper depths than at the surface. On February 24 the difference was negligible. On this occasion the snow depth was 97 cm (Fig. 18 a). Then, no particularly important changes appeared until May 18, when the temperature closest to the soil surface was more than three degrees higher than on May 2. At the next measuring occasion, May 24, a decrease by almost three degrees was registered. On these occasions the snow depths were 25 and 17 cm respectively. There was a drastic decrease in snow depth between May 2 and May 18 (Fig. 18 a).

The ground was completely snow-free on 2 June 1975. Consequently, the temperature in the surface layer of the soil became progressively more variable with decreasing snow cover depth. During June temperatures increased throughout the entire measured profile.

The highest soil temperature in 1975 was measured on June 22 with a temperature of +21.5°C at depths of 1 and 3 cm. An interesting soil layer is at 5 cm below the surface. Temperature there was higher than at levels just above and below when the soil was snow-free (Fig. 15 a and b).

Early August was warm and soil temperatures remained above +15°C (Fig. 15 b). One week later the temperature was lower due to the influence of the air temperature (+24°C on August 10 but +8°C one week later).

Soil temperatures remained around +10°C during the first days of September and were relatively uniformly distributed from the surface down to a depth of 15 cm. On September 28 the highest temperature was at 15 cm with +6°C but at 1 cm +4°C (Fig. 15 c). On this occasion the air temperature was +2°C and snow was falling. The snow melted as October was warmer than normal with an air temperature surplus of 1.5°C for western Jämtland. The relatively high soil temperature (Fig. 15 c) during October continued until early November, a month that also had a temperature surplus, in this case 2°C. In late November the snow cover was complete but the depth was only 12 cm within the area of investigation.

On November 16 the temperature was lower than on November 1 but values were slightly higher deeper in the soil than at the surface. This stratification remained during the subsequent measurements.

The lowest temperatures in 1975 were measured on May 24 (Fig. 15 a) and December 6 (Fig. 15 c) with +0.3°C close to the soil surface and slightly higher at a depth of 15 cm. The temperature then remained relatively constant as long as the measuring apparatus could be localized (until 21 February 1976), when the snow depth was 243 cm.

1976. The measurements were again started on June 6 (Fig. 15 d). The snow cover at this time was still 122 cm. On June 13, with a snow depth of 100 cm, the soil temperature and the air temperature had increased slightly and despite the snow depth the soil temperature was slightly higher at the soil surface than at 15 cm.

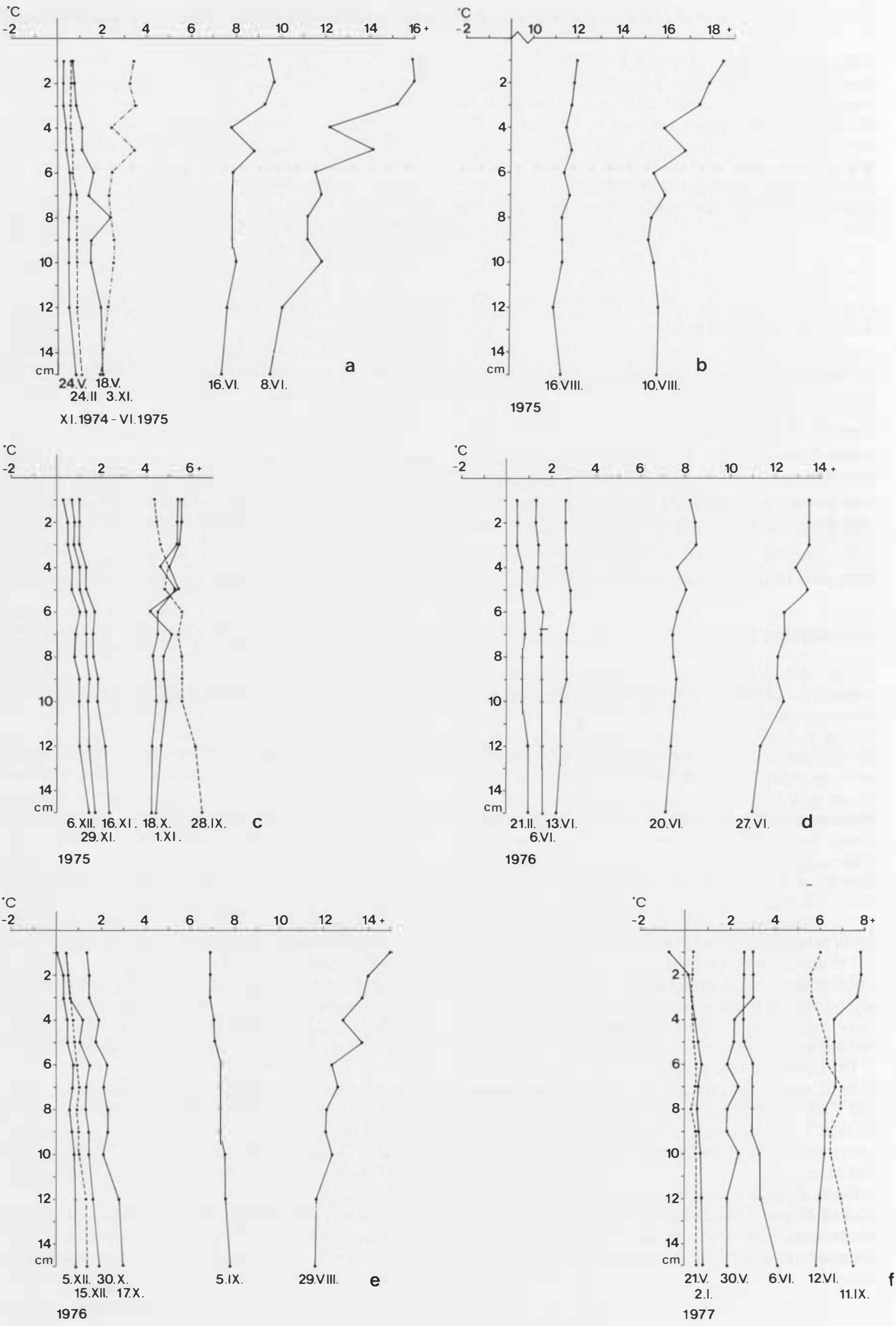
In comparison with 1975 the soil temperature was lower during June 1976 due to differences in the amount of snow, with 122 cm on 6 June 1976 and 0 cm on 8 June 1975 (see Fig. 15 a and d). The highest soil temperatures in 1976 were registered on July 12 with +21°C close to the soil surface and with +15°C at 15 cm. On this occasion the air temperature was +20°C.

August was slightly warmer than normal which is reflected in soil temperatures. On August 15 there were temperatures above +17°C down to 5 cm. Temperatures decreased down to +13.5°C at 15 cm. The air temperatures varied between +12 and +26°C.

According to the reports from SMHI, September was colder than normal with a temperature deficit of about 3°C. Within the area of investigation there were no particularly large differences between 1975 and 1976 as regards the soil temperature.

No snow fell in October. The soil temperature during the first two weeks of the month did not differ from the soil surface down to 15 cm being around +5°C. On October 17 temperatures were +1.3°C at 1 cm and +3°C at 15 cm, air temperature on this occasion being −2°C.

The lowest temperatures of the year were noted on two occasions in December with 0°C close to the soil surface and +0.9°C at 15 cm (Fig. 15 e). A complete snow cover of 20 cm depth was measured on this occasion.



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The soil temperature remained low throughout the whole month.

1977. January 1977 had a temperature deficit of 3°C in western Jämtland. The snow depth within the area of investigation was estimated to be 80 cm in early January and later to 100 cm. The soil temperature fell below 0°C. Thus, on January 2 it was —0.8°C at 1 cm (Fig. 15 f) when the snow cover was ca. 74 cm deep. Negative temperatures close to the soil surface were also measured on January 16. Soil temperatures below 0°C were only measured on these two occasions.

Also February was colder than normal. The soil temperature was close to 0°C throughout the entire month and the temperature difference with soil depth was minimal. The snow depth increased to 110 cm in early February which might have contributed to the soil temperature increasing to 0°C.

During March the temperature increased slightly more but did not exceed + 1°C. However, the air temperature was slightly higher than normal (Fig. 14 j).

There were no larger alterations during April and most of May. On May 21 the snow still had a depth of 45 cm. On this occasion the soil temperature was below + 1°C (Fig. 15 f). On May 30 the snow had melted above the thermistors and the temperature had increased a few degrees, most of the increase being at the soil surface (Fig. 15 f). On account of the disappearing snow and the increasing air temperature the soil temperature also increased.

During June 1977 the soil temperature was lower than in June 1975 and approximately the same as in early June 1976. The highest soil temperatures of the year were on July 10 with + 14.3°C at 1 cm and + 13.9°C at 15 cm. The measurements were ended in September 1977.

3.3.2 Station 2

(1974) 1975. Measurements at station 2 (the fen) started on November 3, giving a soil temperature of + 0.3°C at 5 cm (Fig. 16 a). It should be observed that the measuring profile was considerably deeper here than at station 1. Temperatures increased with increasing soil depth, giving + 1.1°C at 30 cm and + 3.9°C at 80 cm. Down to a depth of 10 cm the temperatures during the winter remained at + 0.3°C but varied slightly with increasing depth. A slight increase appeared at 15 cm in early January 1975. However, at greater depths the temperature decreased until late May. The lowest temperatures measured at 80 cm were on May 18 and 24 with + 1.8°, under a snow cover of ca. 20 cm. On this occasion the air temperature was + 5°C.

Changes of greater magnitude were not noted until early June (Fig. 16 b) when the snow melted (June 2) and the air temperature rose. The soil temperature close to the surface increased. On June 8 the air temperature was + 20°C.

The soil temperature at this station was lower during June 1975 than at station 1 on the same occasion (cf. Fig. 16 b and 15 a). The difference on June 8 is particularly interesting with temperatures between + 16 and + 9.5°C through the whole profile at station 1 but only about + 7°C in the upper part and + 2°C in the lower part at station 2. On June 22 the temperature was highest at 10 cm depth with + 19.8°C. It decreased rapidly to + 8.7°C at 15 cm and + 2.8°C at 80 cm depth.

During the summer, temperatures near the soil surface were higher than deeper in the profile. However, on August 16 temperatures were more uniformly distributed (Fig. 16 b). In late September there was a change giving + 3°C at 5 cm and + 6.9°C at 80 cm. The air temperature on this occasion was + 4°C.

On October 18 the temperature curve showed some irregularity (Fig. 16 c). Temperatures between 5 and 30 cm were at ca. + 2°C, then sharply increased to + 5.2°C at 35 cm, and continually decreased to + 3.9°C at 80 cm. On this measuring occasion the air temperature was —2°C at 16.00 h. Between October 15 and October 17 the snowfall was ca. 9 cm, which then melted. Penetration of the melt-water may be the reason for the irregularity in the temperature curve. On the measuring occasion (October 18) there was no snow in the area where the thermistors were placed. On November 1 temperature was + 4.5°C at 5 cm, and some degrees lower from 10 down to 40 cm, increasing to + 4.5°C at 80 cm. The area was still snow-free. On this occasion the air temperature was + 8°C at 13.45 h.

During November and December the temperature was slightly higher than during the same months in 1974. In early December the snow depth was 20 cm. Later in the month the amount of precipitation was 3—4 times higher than normal in western Jämtland.

1976. In early January 1976 the snow depth on the fen (station 2) was 165 cm. Soil temperatures showed no particular characteristics during the early months of the year. The last measurements were made on February 21 when the snow depth was 235 cm and packed hard. When the snow finally melted all the cables had been broken by the weight of the snow. Two cables were completely destroyed and prevented further registrations of temperature from 35 and 70 cm depths in the soil.

The measurements were again started on June 27 (Fig. 16 d). On this occasion, thus being less than fourteen days after the snow melt, the highest soil temperature of the summer was recorded, with + 13°C at 5 cm.

In August 1976 there were higher soil temperatures at the surface than in the same month in 1975, probably as a result of the high pressure over Scandinavia. On August 29, for example, the air temperature was + 25°C (= maximum temperature, cf. Fig. 14 c). At station 2 the air

◄ Fig. 15 a—f. Soil temperatures at station 1. The measurements at this station started in November 1974 and ended in September 1977.

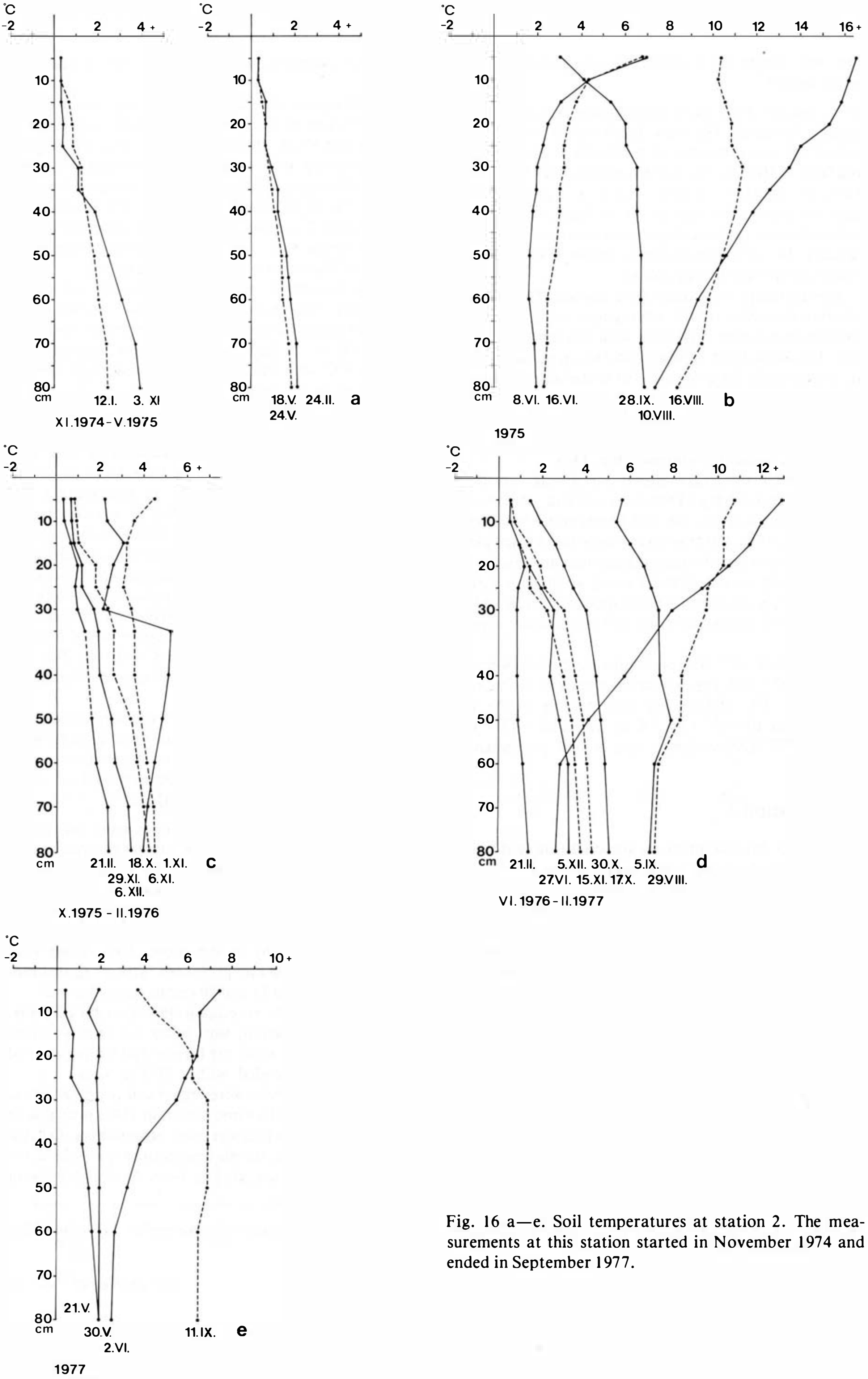


Fig. 16 a—e. Soil temperatures at station 2. The measurements at this station started in November 1974 and ended in September 1977.

temperature at 09.15 h was +22°C when measured with a normal mercury thermometer. The soil temperature at 5 cm was +10.7°C (Fig. 16 d). This temperature decreased with increasing depth down to +7.1°C at 80 cm.

In early September the temperature was highest at 50 cm, where +7.8°C was recorded. Later in the month the temperature profile levelled out and temperatures remained between +5 and +6°C throughout the whole profile.

In 1976 the months of October, November, and December were slightly warmer than the same months in 1975, with the lowest temperature near the soil surface and the highest at 80 cm.

1977. No exceptional changes in soil temperatures occurred during the first four months of 1977. In late May the temperature increased slightly in connection with snow-melt (Fig. 16 e).

The highest temperatures measured during 1977 were on June 27 with +12.3°C at 5 cm and +5.6°C at 80 cm. On this occasion the air temperature was +16°C at 11.45 h.

The measurements ended on September 11 when the profile had the appearance as illustrated in Fig. 16 e. The air temperature on this occasion (10.50 h) was +6°C.

3.3.3 Station 3

As described in section 3.1, the vegetation in the fenced-in area is of varying composition. Thermistors were placed in four plant communities at different soil depths. Four thermistors were placed in the southwestern corner of the area with the slightly richer vegetation, at depths of 2—8 cm. Two thermistors were placed at 10 and 20 cm depths in a small *Molinia caerulea* meadow in the northwestern part. Five thermistors were placed at depths between 12 and 26 cm in a fen area. The other five thermistors were placed in the heath part of the area at depths between 18 and 38 cm. In this plant community the snow remained slightly longer than in the other three communities. The thermistors were placed in the soil during the autumn 1975. No recordings were made during the winter. The intention was to start the measurements in late April 1976 in order to obtain information on soil temperature during the period of snow-melt. This could not be accomplished on account of the thick and compact snow cover which prevented access to the apparatus in the temperature cage.

Fig. 17 a illustrates the curves at three soil levels during the later part of the period of snow-melt and during the early part of the snow-free period in 1977. The snow melted completely between the observations on May 30 and June 6. The temperatures in the figure are mean values calculated from 24 registrations per day.

The soil temperatures had no particularly large fluctuations during the winter and remained between +1 and +3°C at these three levels. On May 28—29 the temperature increased at depths of 2 and 10 cm but remained unaltered at the 38 cm level. The soil temperature in-

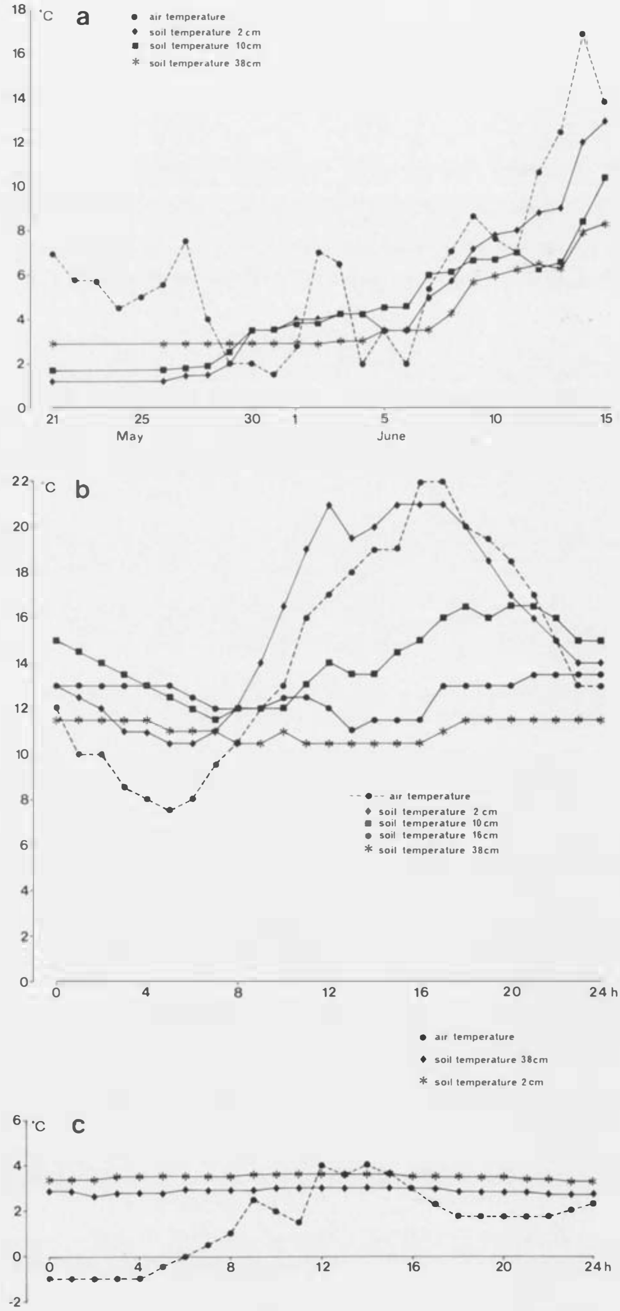


Fig. 17 (a). Soil temperature at different levels during the later part of the period of snow-melt and during the early part of the snow-free period in 1977. The temperatures in the figures are mean values calculated from 24 recordings per day. (b) Temperature below the soil surface varies during a 24-hour period. The figure illustrates the situation on 12 July 1976. It can be seen that the temperature varies during the day and decreases with depth in the soil. (c) Temperature below the soil surface during a 24-hour period, 30 May 1977. The area was covered with 45 cm snow. The daily variation was negligible and the difference between levels was small.

Table 5. Soil temperature °C in four plant communities at station 3. Daily means calculated from 24 recordings per day. The record comprises the end of snow-melt until 15 June 1977.

Plant	Soil	May				June											
community	depth cm	21-26	27-28	29	30-31	1-2	3-4	5-6	7	8	9	10	11	12	13	14	15
Species rich vegetation	2	1.2	1.5	2.0	3.5	4.0	4.2	3.5	5.0	5.7	7.2	7.8	8.0	8.8	9.0	12.0	12.9
	4	1.3	1.5	2.0	3.8	4.0	4.2	3.2	4.5	5.4	7.0	7.5	8.2	8.5	8.7	10.5	11.6
	6	1.4	1.5	2.0	3.6	3.9	4.2	3.2	4.5	5.6	6.9	7.1	8.2	8.5	8.6	9.9	10.9
	8	1.6	2.0	3.5	3.9	4.2	3.2	4.8	5.8	6.7	6.7	7.9	8.2	8.3	8.3	9.5	10.7
Molinia dominated vegetation	10	1.7	1.8	2.5	3.5	3.9	4.2	4.5	6.0	6.1	6.7	6.7	7.0	6.3	6.5	8.4	10.4
	20	2.0	2.0	2.5	3.5	3.9	4.5	4.8	6.0	6.0	6.0	6.0	6.0	5.8	5.7	6.3	7.3
Scirpus caespitosus fen	12	2.0	2.0	2.9	2.9	3.4	4.7	3.5	3.5	4.5	6.2	5.9	6.4	6.9	7.4	9.4	10.4
	15	2.0	2.0	2.5	2.7	3.2	4.3	3.1	3.0	3.9	6.1	5.6	6.0	6.3	6.4	7.6	9.0
	22	2.2	2.2	2.5	2.7	3.1	4.0	3.0	3.0	3.3	4.9	5.5	5.9	6.3	6.1	6.7	7.4
	24	2.2	2.2	2.5	3.0	3.1	4.0	3.0	3.0	3.4	5.1	5.3	5.5	6.3	6.1	6.2	7.3
	26	2.5	2.5	2.8	3.4	3.3	3.5	3.5	3.5	3.9	4.7	5.3	5.5	6.1	5.9	6.2	6.8
Vaccinium-Betula nana vegetation	16	2.3	2.3	2.5	3.2	3.5	4.2	4.5	4.5	5.0	6.1	6.7	6.9	7.0	7.1	7.4	8.2
	18	2.3	2.3	2.5	3.1	3.5	4.0	3.8	3.8	4.6	6.0	6.5	6.9	6.9	6.8	7.1	8.3
	30	2.5	2.9	2.9	2.9	2.9	3.0	3.8	3.8	4.6	5.9	6.0	6.3	6.5	6.6	7.0	8.3
	32	2.8	2.9	2.9	2.9	2.9	3.0	3.5	3.5	4.3	5.7	6.0	6.2	6.4	6.5	6.9	8.3
	38	2.9	2.9	2.9	2.9	2.9	3.0	3.5	3.5	4.3	5.7	6.0	6.2	6.5	6.3	6.9	8.3

crease was preceded by increases in air temperature (Fig. 14 l), when minimum temperatures were not lower than 0°C. During the last days of May the air temperature decreased but this did not particularly influence the soil temperature at the three levels. Only on one occasion, June 5, was the minimum air temperature below 0°C but this did not influence the soil temperature. Later, the soil temperature increased in pace with the air temperature. A small set-back was noted on June 12 at 10 cm and on June 13 at 38 cm following a brief decrease in air temperature a few days earlier.

Temperatures below the soil surface vary during a 24-hour period. Fig. 17 b illustrates the situation on July 12 in 1976. On this occasion the ground was snow-free. The figure illustrates that the temperature range variation during the day decreased with depth in the soil. Whereas the temperature at 2 cm varied between +10.5° and +21°C, at 38 cm it varied only between +10.5 and +11.5°C. The daily variation of maximum and minimum temperatures is also delayed with increasing depth. Hytteborn (1975) has also described this for Andersby ängsbackar, Uppland. The highest temperatures of the day at 2 cm were measured between 12.00—17.00, at 10 cm between 18.00—21.00, and at 16 cm between 21.00—24.00.

Nevertheless, below a snow cover the daily variation was negligible and the difference between levels was small (Fig. 17 c). The snow was ca. 45 cm deep. Only two levels are included as the difference was so small.

Table 5 is compiled from daily mean temperatures (24 registrations) between May 21 and June 15 in 1977 and illustrates temperature conditions below the different plant communities. The comparison is complicated since the measurements were not made at the same soil levels below the different plant communities.

During the winter months and until late May temperatures changed only slightly. On 21 May 1977 the snow depth at station 3 was ca. 70 cm, having been ca. 130 cm on May 1 (Fig. 18 c). During the same period the frost depth had decreased from 3 to 1.5 cm. The mean air temperature on May 21 was calculated to be +7°C with a minimum temperature just above 0°C. The soil temperatures were not lower than 0°C in any of the four plant communities. Temperature became slightly higher with increasing depth in all plant communities. The highest soil temperature was recorded in the heath vegetation at a soil depth of 38 cm, being the deepest measuring level in all communities.

On May 30 the snow still remained but was very loose. The frost had completely left the soil. The soil temperatures had risen one or two degrees since May 26. No particular difference between the various plant communities, or with depth, was measured.

The measuring area was completely snow-free on June 6 but patches without snow might have occurred earlier. The heath area was the last of the four plant communities to become snow-free. The soil temperature increased relatively slowly. Due to the variations in the air temperature, the increases in soil temperature were not uniform. Thus, e.g., the air temperature was lower between June 4—6 than between June 2—3. This is reflected in the soil temperatures at levels close to the surface in the area with richer vegetation which had a slightly lower temperature on June 5—6 than on the previous day. From ca. 10 cm downwards (in the *Molinia* meadow and in the heath vegetation) the temperature increase was more uniform. In the fen the soil temperature was lower on June 5—6 than on the previous day, even down to depths of 25 cm. In a fen the soil temperature is complicated by water movements in both vertical and horizontal directions.

On June 12, six days after the snow had melted, the soil temperature was highest in the vegetation-rich area and with little difference between the various levels. Lower temperatures were recorded in the *Molinia caerulea* meadow and in the heath vegetation. The thermistors were placed at lower levels in these two plant communities in comparison with the area with richer vegetation. Temperatures in the latter plant community were highest, which was to be expected as there they were measured closer to the soil surface. The lowest temperature was at the deepest level in the *Molinia* meadow, being deeper than at the corresponding level in the heath area.

3.4 Measurements of snow and frost depths

The measurements of snow depth were started simultaneously with those of soil temperature at stations 1 and 2, i.e., on 3 November 1974. The measurements were extended in 1976 with station 3. Formation of drifts occurred to some extent at station 1, slightly less at station 3 whereas station 2 is in a more exposed position.

3.4.1 Snow depth

In 1974 the area received a lasting snow cover in early November (Fig. 18 a). For most of the winter the snow depth was between 50 and 100 cm. The greatest depths were measured in April and May. The area with the measurement poles was snow-free on 2 June 1975.

During the measurements in 1975/76 there was a lasting but relatively thin snow cover during late November (Fig. 18 b). Snowfall was slight during December. In January 1976 western Jämtland had a large excess of snow. Thus, according to the SMHI monthly report, snow depth at Storlien-Visjövalen increased from 120 cm in late December to 205 cm in January. This is the largest snow depth ever reported from this meteorological station. Fig. 18 b shows that large quantities of snow fell within the Ottfjället area during January. The snow depth increased during February. March was very cold and no particular changes in snow depth were noted. More snow then fell, particularly during the first week of April. Within the area of investigation the snow depth was locally 4—5 m. Normally western Jämtland has a snow depth of, on average, 0.8 m in late April/early May, but several meteorological stations reported depths of about 2 m which showed good agreement with the snow depth in the Ottfjället area. The area of investigation was not free of snow until 20 June 1976.

Data from the winter of 1976/1977 are given in Fig. 18 c. The greatest snow depths were from late March until early May. The area of investigation was completely free of snow on June 6 in 1977.

Comparison between the three stations shows that in all years station 1 had the deepest snow cover on most measuring occasions whereas the least snow cover was at station 2, with one exception. The snow remained longer at station 3 than at the two other stations (until June 6), whereas stations 1 and 2 were snow-free on May 30. Despite the greater snow depth at station 1, both areas were snow-free at the same time, due to the southerly position of station 1.

Within the area where the reindeer calving took place during the year of investigation there were snow-free patches already in late April. Calving took place in May. This implied that the female reindeer at calving had access to *Carex bigelowii, Juncus trifidus*, and to some extent *Deschampsia caespitosa* and *D. flexuosa.* Even though the access to lichens within the area is not satisfactory they appear to give the females extra grazing during the period of snow-melt. Later during the snow-melt period there are buds on shrubs, and dwarf-shrubs available to the females (cf. Chapt. 8).

The area where the non-calving reindeer, including the males, are to be found during the spring is characterized by fens and forest. The fens around the Nulltjärn lakes and the fens in the neighbourhood of the soil subjected to frost-heaving (map in Warenberg 1977) have patches that became snow-free fairly early. Here the reindeer can find *Eriophorum* spp. and *Scirpus caespitosus.* If the snow is deep and can carry the animals, as in the spring of 1976, the reindeer can reach lichens on trees, mainly *Alectoria* spp. in the area of investigation.

3.4.2 Frost depth

Frost depth was measured only during the winter of 1976/1977. The first occasion when frozen soil was noted was on December 19. Thus, the soil did not become frozen before the first snow. The lowest soil temperatures during the early part of the winter of 1976 were at station 2 on November 21 with +0.4°C at a depth of 5 cm and at station 3 on November 30 and December 5 with +0.9°C at depths of 2 and 4 cm. On these occasions the soil was not frozen and the snow depth was ca. 30 cm. On December 19 there was only 0.3—0.5 cm of frost in the soil (Fig. 18 c). The soil temperature at station 2 on this occasion was +0.7°C at 5 cm depth and at station 3 it was +1.6°C at 4 cm depth.

On February 21 the soil was frozen down to 3 cm at station 2. This frost depth remained until May (no measurements were made during the period May 1—21). The soil temperatures were relatively low during this period and the lowest was +0.3°C. On May 21 the frost depth

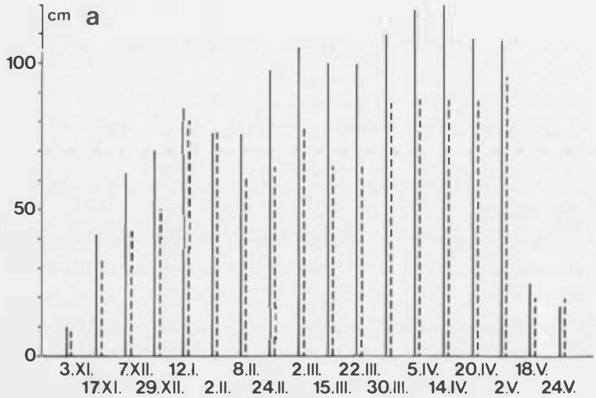
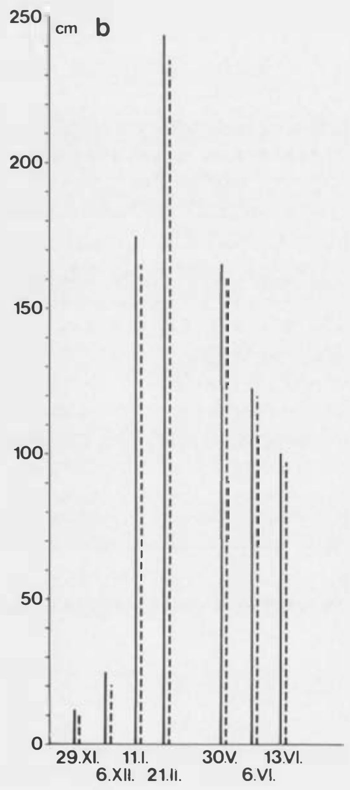
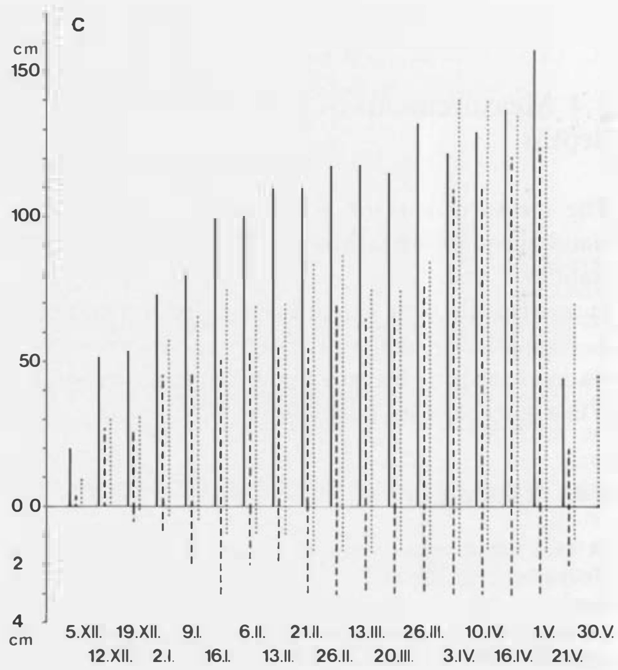


Fig. 18 (a). Snow depth at stations 1 (solid lines) and 2 (broken lines) during the winter 1974/1975. (b) Snow depth at stations 1 (solid lines) and 2 (broken lines) during the winter 1975/1976. Note the break in the time scale: (c) Snow depth at stations 1 (solid lines) and 2 (broken lines) and 3 (dotted lines) and frost depth at stations 2 (broken lines) and 3 (dotted lines) during the period 1976/1977. Observe the different scale of snow and frost depths.





had decreased by 1 cm but the soil temperature was still +0.3°C at a depth of 5 cm. The area was free of snow and frost in the soil on May 30 in 1977, the soil temperature having increased from +0.3°C on May 21 to +1.9°C on May 30 at a depth of 5 cm.

At station 3 the deepest frost depth was 1.5 cm. This remained constant from February 21 until May. At this station the soil temperature was higher than at station 2. The lowest temperature in levels close to the soil surface at station 3 was +1.0°C.

In wind-swept and exposed areas of heath, the depth of frozen soil was greater on the occasions during the winter and late winter or early spring when the shoot development of the plants was studied. The only places with shallow depths of frozen soil were naturally those with good snow cover. In fen areas with thin snow cover there was also considerable frost depth (found by digging). However, no measurements of frost depth were made at other places than stations 2 and 3.

3.5 Additional remarks and discussion

At a given time during the day the differences in air temperature between the three stations were relatively small. The largest difference was two degrees, apart from one occasion on 6 February 1977 at 13.00 h when the temperature was —4°C at station 1, —2°C at station 2 and —5°C at station 3. A mercury thermometer may be slightly unreliable and the lower value at station 2 might be a measuring error. Stations 2 and 3 are close to each other (see Fig. 10) but station 2 has a more exposed position.

Comparing the continuous measurements of air temperature at station 3 at Ottfjället during 1976/1977 with the corresponding period at the meteorological station at Storlien-Visjövalen, it can be seen (Fig. 14 a—m) that for several days in January and until early April the maximum temperatures were higher in the area of investigation. It is particularly interesting to note the high maximum temperatures at Ottfjället in March. The southerly exposure of the area of investigation and the northwest exposure of Storlien-Visjövalen may possibly explain some of the large difference between the maximum temperatures. The deep snow surrounding the temperature cage may also be a contributory reason as the maximum temperatures are highly dependent on local conditions.

Section 2.3 discusses the relatively large differences in the number of sunshine hours during March between Storlien-Visjövalen and Frösön. The Ottfjället area is situated between these two stations and possibly, as at Frösön, had a larger number of sunshine hours than Storlien-Visjövalen, which would to some extent explain the differences in maximum temperatures. In the other months the differences were not exceptional. The minimum temperatures did not show such large divergences.

Table 4 gives monthly mean maximum temperatures for Storlien during the period 1931—1960. In comparison with these values there are divergences in the mean maximum temperatures calculated from the Ottfjället thermograms for the year 1976/1977. The greatest difference was in March. Differences were also noted in December 1976 and January 1977. In comparison with Storlien-Visjövalen's mean maximum temperatures in 1976/1977 the difference between the temperature data from Ottfjället was not as large, with the exceptions of February and particularly March.

The mean minimum temperatures during 1976/1977 within the Ottfjället area were lower in all months than corresponding values from Storlien for the period 1931—1960. In comparison with Storlien-Visjövalen in 1976/1977 the difference was negligible.

In the case of soil temperatures the fluctuations between days are large in the layers close to the soil surface that are influenced by the air temperatures with in-coming and out-going radiation and by snow cover. An example of this occurred in May 1975 when the thermistors placed at station 1 became exposed on May 18 due to snow-melt. The rest of the slope had a snow cover of 25 cm. The measurements were made at 12.00 h when the air temperature was +16°C and the sky was cloudless. Since the measurements on May 2 the soil temperatures had increased throughout the whole profile, with increases of several degrees at the surface and at 5 cm. It is difficult to decide whether this increase occurred successively or suddenly as no measurements were made from May 2 until May 18 (Fig. 15 a). The next measurements were made on May 24 when the air temperature was +4°C. This probably influenced the soil temperature at station 1 throughout the entire profile but most at levels close to the soil surface. At station 2 the difference in soil temperature was negligible between May 2 and 18 and also between May 18 and 24. The area in which the thermistors were placed had a snow cover of 20 cm (Fig. 18 a). Consequently, the variations in air temperature only influenced the soil temperature at station 1 (being snow-free) and not at station 2 (with snow cover).

The strong influence of air temperature on the soil temperature can be exemplified by several soil temperature profiles. In the case of station 1, the whole profile was generally influenced whereas stations 2 and 3 were mainly influenced in layers close to the soil surface.

Only on two occasions were soil temperatures below 0°C at station 1, and on the following three occasions they were 0°C. These temperatures were recorded during December 1976 and January 1977. On no occasions were temperatures 0°C or lower at stations 2 and 3. The lowest soil temperatures were +0.3°C and +0.9°C at stations 2 and 3 respectively.

Due to its southerly position and shallow soil, station 1 had higher soil temperature on more occasions than station 2 which was permanently wet during the snow-free period. As discussed above, temperatures were often influenced throughout the entire profile at station 1 whereas changes at station 2 were greatest above 20 cm. This applied during the snow-free period. Extremely small changes occurred at both stations during periods of snow cover.

Small cavities often occur in a contact zone between snow cover and soil. These have been described by Coulianos & Johnels (1962) as subnival air spaces and are formed when, e.g., grass, shrubs or dwarf shrubs prevent the snow from reaching the soil. Coulianos & Johnels (op. cit.) measured these subnival air spaces to be as much as 3—5 cm, measured from the soil surface up to the bottom of the snow cover. On 5 March 1962 they measured a temperature at the soil surface of 0°C below a snow cover of 20 cm whereas the temperature at standard height was —18°C. They also observed quicker snow-melt above a subnival cavity than in other places. This particularly concerned open places and south-exposed slopes.

Station 1 which is exposed to drifting, still becomes snow-free at the same time as station 2. The vegetation at station 1 is dominated by *Deschampsia caespitosa* which would be capable of causing sub-nival cavities, although the great pressure of heavy snowdrift would diminish this possibility. Station 3 was slightly sheltered by trees in its western part which might have caused the slightly later snow-melt. In this area there are also some drifts caused by the fence erected around the station.

The calculations prepared by SMHI indicate that the area should have snow cover by late October. A definition of lasting snow cover is given in *Klimathandbok för försvarsstaben* (1975) which states that a lasting snow cover is considered to begin on the day during the winter when snow cover has occurred and has remained intact at least one day. During the years of the investigations, this area did not have lasting snow cover during October. During the winter of 1974/1975 there was no snow cover until early November (Fig. 18 a) and in 1975/1976 not until late November. In 1976/1977 the area was snow-free until early December. It should be noted that this applies only to the subareas of investigation.

Variations may occur from year to year within the same area as regards both snow cover and frost depth. During the three years of the present measurements the winter months of January—April 1976 had extreme snow depth. Within the area depths of more than 2 m were measured. In this year the snow-melt was unusually late. Leaf-burst on the birches was in late May—early June and formed an unusual contrast against the white snow. Station 2 had the thinnest snow cover during all the three years of investigation. This depended on the more exposed situation of this station.

The dependency of frost depth on snow conditions is well documented (Tanttu 1915; Sjörs 1948; Ångström 1958; Geiger 1966; Eurola 1968). These authors consider the snow to have a protective effect that prevents heat losses from the soil. Geiger (op. cit.) reports that soil water does not freeze at 0°C. When the air temperature decreases the first part to freeze is the mobile water in the large soil pores and the last to freeze, if ever, are the strongly adhering water films of the smallest pores. As an example, it may be noted that in fresh cement the pore water does not freeze until —3 or —4°C.

The measurements of frost depth were only made for one season. There was slightly deeper frost penetration at station 2 than at station 3 but it was not deep at any of the stations. It is difficult to explain the reason behind this shallow frost depth. There is a close relationship between shallow frost depth and soil temperatures that are seldom or never below 0°C. Greater frost depth and lower soil temperatures may be expected when the soil is snow-free and the air temperatures below 0°C, as during the early part of the winter in 1976.

4. Winter grazing

The reindeer, *Rangifer tarandus* L., often needs to seek for feed under very difficult conditions and particularly during the winter when snow cover and/or ice crust hinder grazing of the ground vegetation. The reindeer may then have difficulty in reaching the ground lichens which, according to the general opinion, they are dependent on. The lichens are rich in carbohydrates but deficient in protein. Nevertheless, the reindeer has the ability to store fat, minerals and also vitamins during summer grazing. According to Rydberg (1977), the reindeer can conserve energy and protein. Rydberg (op. cit.) also reports that reserves of both energy and protein have been more or less completely utilized by the time the spring arrives. Thus, if the reindeer is unable to improve its conditions during the snow-free period, it will have difficulties in surviving the winter.

The grazing habits of the reindeer differ considerably from those of other domestic animals. During a day's grazing the reindeer will cover wide areas instead of systematically grazing a smaller area. This is important during the winter, when feed is scarce. Calculations of the reindeer's energy requirement have been made where differentiation is made between the needs for maintenance and for production. The maintenance requirements imply the amount of energy needed for normal body functions without changes in body weight. This also includes the amount of energy needed in, e.g., grazing. The production requirement is the amount of energy needed by the reindeer for growth, reproduction, suckling, and fat deposition. The maintenance requirement increases under difficult conditions, when digging and seeking for feed requires energy. Summation of the maintenance and production requirements will give the total requirement (Table 6).

The figures in the table refer to an average reindeer where the live weight is assumed to be 70 kg for a female and 90 kg for a male. A female reindeer requires ca. 5 kg of lichens per day and a male ca. 6 kg per day in order to satisfy the maintenance requirement (S. Persson 1966). Eriksson (1979) uses the value 5.6 Mcal metabolisable energy per day and average reindeer for the winter period, and 8 Mcal for the summer period (females with live weight of ca. 70 kg). He probably is referring to the total requirement.

Jacobi (1931) reports that the rumen of an adult reindeer contains up to 10 litres of feed. The rumen volume of a three-year old male (live weight 75 kg), slaughtered during a post-graduate course at Hede, Härjedalen, on 20 February 1979, was 10 litres and its contents weighed 9.5 kg.

The reindeer willingly grazes other plants than lichens during the winter if the region is without snow cover or not covered by ice-crust, as illustrated by investigations made in the Soviet Union and Sweden. At Petjora higher plants comprise more than 30 % of the winter feed and on the Chukchi peninsula phanerogams make up 80—90 % of the reindeer's diet with, e.g., *Eriophorum vaginatum* (Andreev 1957, cit. by Ahti 1959).

In Sweden, rumen investigations in reindeer have been made to determine the consumption of grazing plants on the areas used for winter grazing and to elucidate what elements of ground vegetation are consumed by the reindeer (Eriksson 1977, 1981). The investigations comprised five areas, ranging from northern Lapland to Härjedalen. The analyses concerned reindeer that grazed during the winter on the bare mountain, in the subalpine birch belt and in pine forests. The results show that lichens are important but that dwarf-

Table 6. Nutrient requirement of reindeer for maintenance and production, Mcal per day (from Persson 1966).

	Summer grazing		Winter grazing	
	female	male	female	male
Maintenance requirement	3.5 4.2	4.6 5.6	4.6 5.6	5.6 6.7
Production requirement	2.8 3.5	4.2 4.9		
Total requirement	6.3–7.7	8.8–10.5	4.6 5.6	5.6 6.7

shrubs and shrubs, primarily *Empetrum* sp. and *Betula nana*, were included in the diet. Grassy species, e.g. *Juncus trifidus, Carex bigelowii*, and *E. vaginatum*, were important for the reindeer in Norrbotten and Västerbotten. However, lichens comprised a larger part of the diet in Härjedalen. Eriksson's investigation in Härjedalen was conducted in an area considered to have the richest representation of lichens in the country. Even pine needles have been found in rumen samples (Eriksson 1977, 1981). Eriksson interpreted this phenomenon to imply that pine needle litter could have been eaten during lichen grazing. They may have been so resistant that they remained in the rumen longer than other grazing plants and therefore are found in higher proportions in the analyses than they represent in the grazing.

According to information from Newfoundland, leathery evergreen leaves of *Chamaedaphne calyculata*, the evergreen heather plant *Gaultheria hispidula*, and *Betula papyrifera* comprise 10—18 % of the feed during the December to February period (Bergerud & Nolan 1970). *Gaultheria hispidula* is a small prostrate species which should provide little biomass. In Ontario it is reported that some evergreens and semi-evergreen species are important for grazing during the winter and early spring, e.g., *Arctostaphylos uva-ursi, Deschampsia flexuosa, Empetrum nigrum, Equisetum scirpoides, Linnaea borealis*, and also the non-evergreen *Vaccinium myrtilloides* (Ahti & Hepburn 1967).

As regards Scandinavia, *Deschampsia flexuosa* is considered to be one of the most important higher grazing plants during the snow period (Skuncke 1958, 1969, 1973; Steen 1965, 1966; Skjenneberg & Slagsvold 1968). *D. flexuosa* does not wither completely in the autumn but remains green even under the snow cover. The basal parts of the tuft often remain green throughout the winter. The content of crude protein in this green basal part is 7.1 % of the dry matter during the autumn (October) and 8.6 % during the Spring (Steen 1966 pp. 73—74). *Calluna vulgaris, Empetrum hermaphroditum*, and *Vaccinium vitis-idaea* are of importance during the winter when access to feed is poor. Grassy plants are more valuable than these species, especially during the spring (Skjenneberg & Slagsvold 1968). According to these authors, *Carex bigelowii* is the most important and richest in nutrients of the *Carex* species. *C. aquatilis, C. rostrata, Calamagrostis neglecta, Eriophorum* spp., and *Equisetum fluviatile* are also important. *Milium effusum* and *Vaccinium myrtillus* provide good grazing, and also do buds of birch and willow, even though the protein content decreases during the autumn (op. cit.). According to Rune (1960) *Equisetum fluviatile* and *Menyanthes trifoliata* are attractive to reindeer also during the winter when stems and shoots remain green until the lakes and water-courses freeze.

The species preferred by the reindeer during the snow period depend on plant communities common within their grazing area. Of great importance are also snow conditions such as snow depth and the hardness of the snow.

5. Shoot development of evergreens and semi-evergreen species

Among the semi-evergreen plants are species that develop green leaves and shoots early in the spring while the ground is still covered by snow.

5.1 Earlier investigations

Jónsson (1895) observed on Iceland that grass remained green for long periods during the autumn and that it became buried in the snow while still green. The actual species were not mentioned but were probably some of the species listed in the text. According to Jónsson the plants start to show signs of life during April. In late April *Betula nana* and *Salix lanata* started to open their leaf-buds. From May 12 the grass and *Carex* species, particularly the *Carex* species, thrived on the wet fens where the water protects the plants against the wind during the early weeks of the month. The other species which were more exposed to the wind and that had started their development were checked. He also observed that some montane species had 5—7 cm long shoots already below the snow cover and that these shoots rapidly became coloured red as soon as the snow cover disappeared. His conclusion was that these species start their development already below the snow cover as otherwise they would not have been so long when exposed. On March 26 in the same year he observed that *Alchemilla alpina* had green living shoots, protected by old leaves. Living leaves were also found on grass and *Carex* species among old withered leaves which, without doubt, have a protective role.

In studies of species adapted to a short and cold summer, Resvoll (1917) found that the majority were perennial, often dwarf and adjusted to a short growing period. Flowering generally occurs early during the growing period, depending primarily on the primordias having developed in the year before or even several years before the year of flowering. The first shoot, developed from a seed, needs time to establish roots, stems and leaves. This vegetative stage before the first flowering is named the initial strengthening stage (Sylvén 1906, cit. by Resvoll 1917) and generally lasts at least two years. The development of lateral shoots often takes three years with the following stages: the bud stage, development of the leaf rosette, and finally flowering in the third year. In some species the lateral shoots, particularly in monocotyledons, need a four-year development with a two-year leaf rosette stage. *Poa alpina* and *Carex lachenalii* (= *C. lagopina*) were studied in the mountains of Norway and, in addition, *Poa alpina* was studied on Spetsbergen north of lat. 79°. The lateral shoots develop from the folds of the scale leaves. In the first summer the lateral shoots are in a bud stage, in the following summer a number of low leaves develop and later one or two leaves. In the third summer the rest of the rosette leaves are formed and a flower bud. The final rosette leaves to be developed over-winter and retain their green colour. Flowering takes place during the fourth summer if the climate is, and has been, favourable. Often there were delays in the development, as for example with *Carex lachenalii* in 1916. The summer of 1915 was cold, colder than normal, and the warm weather came late. In the following year there were only last-year's stems and withered spikes of *C. lachenalii.* On August 15 the shoots were still in the rosette stage with small flower buds. The author was unfortunately unable to continue the observations but strongly doubted whether spikes with ripe seed could have developed during that season. The lateral shoots had secondary roots and could have contributed to vegetative reproduction.

Polygonum viviparum over-winters in the form of gemmas. The development from gemmas to flowering takes several years. The flower buds over-winter enveloped by leaf sheaths. *Sibbaldia procumbens* has over-wintering leaves and the flower buds are protected by large leaf sheaths. *Gnaphalium supinum* has no particular protection for the over-wintering shoots but the flower bud is protected by the densely hirsute leaf buds (Resvoll op. cit.).

In Diavolezzasee, Switzerland, the over-wintering of montane plants has been studied by Rübel (1925). He found that several species over-winter with green shoots enclosed in brown withered leaves. Other species over-winter with green shoot parts exposed. Among the species investigated were both herbs and grasses, e.g. *Hieracium pilosella, Antennaria dioica, Juncus trifidus, Luzula spicata, Poa alpina, Nardus stricta, Deschampsia caespitosa*, and *Sibbaldia procumbens.* Rübel (op. cit.) found under a 1.5 m thick snow cover in Berninahäuser (Jan., Febr. 1924) for example, specimens of *Deschampsia caespitosa* with 4—8 cm long green leaves among old, dry leaves and between them leaves with a length of 1 cm. During the rest of the winter they grew slowly at a temperature of 0 to +2°C. No details were given of whether this was the air temperature or the temperature at ground level. *Potentilla crantzii* over-wintered with green leaves even though they were not fully developed. *Sibbaldia procumbens* also over-wintered green. Individuals dug out during the middle of winter and late part of the winter had green leaves, slightly violet in hue. On both occasions the snow cover was 1.5—2 m.

Schroeter (1926) was of the same opinion as Rübel that *Sibbaldia procumbens* over-winters green, and also that it is dependent on snow cover. It has a strong root stock covered with leaf remnants. According to Schroeter (op. cit.), new leaves develop beneath the snow during the winter and the species flowers soon after snowmelt. *S. procumbens* has been classified as a species capable of assimilating beneath the snow (cf. Schroeter 1926 p. 971). Alpine shade plants (Schroeter op. cit.) are able to assimilate at low temperatures, on account of the high sugar contents of the cell sap which lowers the freezing point. The lowering of the freezing point in *S. procumbens* was measured to be 19°C. This increases the suction power. The high sugar content depends on the sugar formed through assimilation at low temperatures not having been converted to the osmotically inactive starch (Schroeter op. cit. p. 971).

Böcher (1974) investigated several species in the greenhouse in two climate chambers, under cold conditions with temperatures not exceeding 9°C during the day, and under warm conditions with a day temperature up to 16°C. Among the species that developed in the greenhouse, he found that *Potentilla crantzii* formed new shoots in late September. It was kept under natural conditions during the winter and over-wintered with green leaves.

During 1970—1974 the present author made observations of reindeer belonging to the Ottfjället reindeer range, which were present during the winter in mountain areas on the other side of Lake Ottsjön. They dug vigorously in the snow. By studying the hollows made in the snow it was realized that the reindeer were looking for fresh food, in this case *Deschampsia flexuosa*. This species had green leaves among their old withered leaves below a snow cover of ca. 30 cm. Investigations on the range showed that most species had green shoots or leaves already below the snow cover. The species investigated during the above-mentioned period were *Deschampsia caespitosa, D. flexuosa, Poa alpina, Festuca vivipara, Nardus stricta, Eriophorum angustifolium, E. vaginatum, Carex bigelowii, Scirpus caespitosus, Luzula wahlenbergii, Polygonum viviparum, Gnaphalium supinum, Potentilla erecta*, and *Sibbaldia procumbens*. All these speces were found to have green leaves or green over-wintering vegetative organs below the snow cover (Warenberg 1977).

5.2 Own investigations

The species discussed in the present work belong to the evergreen and semi-evergreen plants. In the present context the discussion is restricted to the Ottfjället reindeer range, being the area with which I am most familiar.

The previous chapter contains descriptions of earlier investigations and it is clear that the reindeer willingly graze other species than lichens if they get the opportunity. Consequently, it is important to make a closer investigation of the shoot development of some of the higher plants looked for by the reindeer during the late winter and spring in the area around the Handölsdalen Lapp community.

5.2.1 Methods

On May 1977 a number of plants were dug up on the Ottfjället reindeer range and planted in a cold greenhouse at Frösön. At this time there was still a snow cover on the range. The following species were taken to the greenhouse in a frozen condition with an adequate layer of soil surrounding them: *Andromeda polifolia, Betula nana, Deschampsia flexuosa, Juncus trifidus, Loiseleuria procumbens*, and *Rubus chamaemorus*. On May 22 additional species were taken to the same greenhouse: *Deschampsia flexuosa, Eriophorum angustifolium, Molinia caerulea, Nardus stricta*, and *Scirpus caespitosus*. Daily observations enabled me to form an opinion of the development of some of the species. However, there was no possibility to measure the temperature. Consequently, a greenhouse was erected in the author's own garden where four thermistors recorded the soil temperature and two thermistors recorded the air temperature in the greenhouse. The temperatures were registered with a Grant temperature recorder. The results are not published here.

In the autumn 1977 some of the above-mentioned species were transferred from the cold greenhouse to the greenhouse in the garden, together with additional plants from the Ottfjället area. The greenhouse in the garden was also a cold greenhouse. The plants were buried in the garden for over-wintering and were taken to the greenhouse in the spring 1978 before the frost had left the soil.

The following species were allowed to develop in the greenhouse and could be studied daily: *Anthoxanthum odoratum, Carex aquatilis, C. bigelowii, Deschampsia caespitosa, D. flexuosa, Eriophorum angustifolium, E. vaginatum, Juncus trifidus, Molinia caerulea, Nardus stricta, Potentilla* *erecta*, *Scirpus caespitosus*, and *Vaccinium myrtillus*. These species, thus, developed in an artificial environment and at temperatures that were too high.

In order to obtain a correct picture of the appearance of species used for reindeer grazing before and after snow-melt, as well as the continued development, the following species were investigated in the correct environment, particularly with regard to their preparation for winter conditions: *Anthoxanthum odoratum, Carex aquatilis, C. bigelowii, C. lasiocarpa, Comarum palustre, Deschampsia caespitosa, D. flexuosa, Eriophorum angustifolium, E. vaginatum, Festuca vivipara, Gnaphalium supinum, Juncus trifidus, Luzula pilosa, Menyanthes trifoliata, Nardus stricta, Potentilla erecta, Scirpus caespitosus, Sibbaldia procumbens*, and *Vaccinium myrtillus*.

These species were chosen because I was able to observe with binoculars that they were grazed during the spring and early summer. Hoofmarks and droppings of reindeer in the neighbourhood of grazed plants also helped to confirm the grazing.

Sketches were made of the species on different occasions during the spring, early summer and autumn. The period around snow-melt was particularly interesting. In addition, some of the species were photographed after they had been sketched. The sketches are reproduced in full size with some exceptions (Figs. 22, 27, 28, 31, and 43—45 in half scale, Fig. 32 in two-thirds). Old plant parts are shaded and green and yellow-green plant parts are not shaded.

To check whether the plants are able to develop in darkness, black 1x1 m screens were placed 1 dm above the ground surface at 4 places in the reindeer range. The experiment gave few results on account of mildew forming below the screens. They were probably placed too close to the soil. The screens placed above the tree limit were broken by heavy snow cover.

The experiment was repeated with black pieces of plastic in the spring 1978 but the material was torn apart by the spring storms.

5.2.2 Anthoxanthum odoratum

Anthoxanthum odoratum is a common plant in communities dominated by grasses and herbs. The species has a characteristic scent of coumarin. The reindeer use it for grazing but prefer other grasses. In large quantities coumarin is regarded to be toxic and hay consisting only of *A. odoratum* is refused by animals (Schroeter 1926 p. 409).

As with most grasses, *A. odoratum* over-winters partly evergreen. New leaves were found to be initiated already during the autumn. On average, these measured 1 cm (see Fig. 19). The leaves were protected under the snow. On no occasions were there indications that new stems developed during the autumn. On several occasions during May, however, there were indications of stems beneath a snow cover of 20—30 cm. The leaves were also longer than they had been in the autumn. Consequently, the leaves had grown under the snow and probably stem initiates had already developed during the autumn and grew beneath the snow.

At ca. 900 m the snow cover had generally melted by about June 20—25, with the exception of snow-beds, during the years of the investigations. *A. odoratum* started its development later at higher altitudes. As can be seen from Fig. 20, there is a fairly large difference between 890 and 990 m on June 24. The plants growing at 890 m had inflorescences and were, on average, 10 cm long. There were some traces of grazing but not to any great extent. Faster growth was observed soon after snowmelt.

Fig. 19. *Anthoxanthum odoratum* is common within the reindeer range. New leaves were initiated during the autumn. These leaves developed beneath the snow cover. Probably stems also initiated during the autumn. Unshaded parts represent green or yellow-green plant parts, whereas old parts are shaded. 29 Oct. 1978.

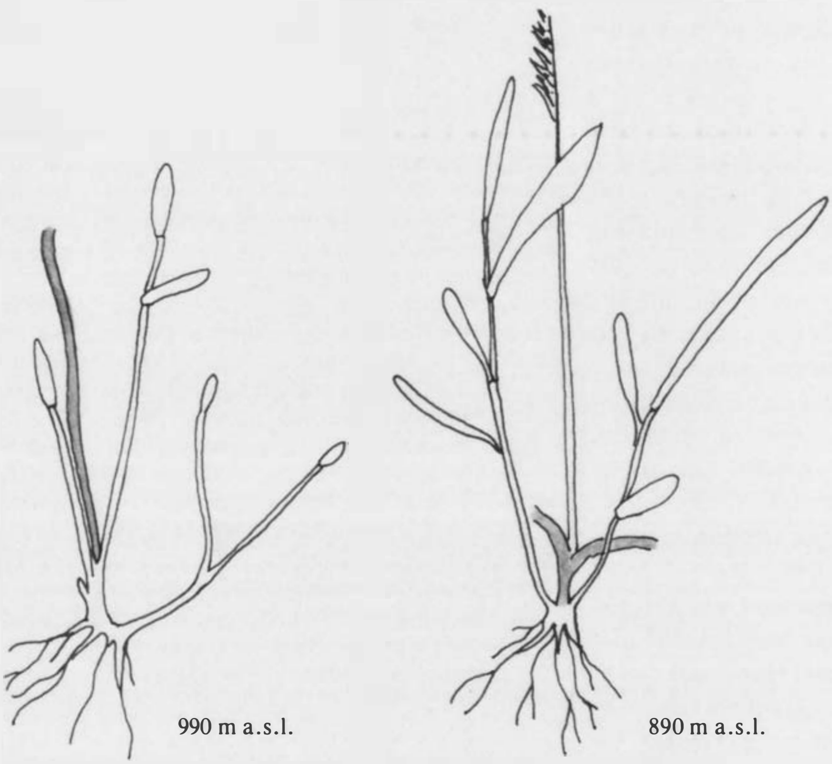


Fig. 20. At higher altitudes *Anthoxanthum odoratum* started its development later than at lower altitudes. On June 24 plants growing at 890 m a.s.l. were flowering when plants growing at 990 m a.s.l. had only leaves. 24 June 1978.

Plants that had been transferred to the greenhouse on 29 April 1978 then had leaf lengths varying from 1 to 3 cm. On June 2 all of them had panicles and the total length of the plants was, on average, 40 cm. They were very vigorous.

In September these plants were transferred to flowerpots and were allowed to develop indoors.

5.2.3 Carex aquatilis

Only few observations of *Carex aquatilis* were carried out. One observation was made during the winter (March). This tall plant is relatively rare within the area of investigation (A in Fig. 2). It occurs relatively sparsely in brooks in and around the Nulltjärn lakes.

According to Hylander (1953—1966), *C. aquatilis* has a strong rhizome, extending over long distances. Metsävainio (1931) observed root hairs that were most abundant on younger roots. Species lacking root hairs often have mycorrhiza. According to Miller & Laursen (1978), they are dependent on mycorrhiza. According to the same authors, species with mycorrhiza have a greater ability to take up nitrogen and phosphorus from nutrient-poor soils than those that lack mycorrhiza.

As with *Eriophorum angustifolium*, the stem base of *C. aquatilis* remained green for a long period during the autumn. This is important as the reindeer can thereby obtain feed far into the autumn. The well-developed root-stock of this species increases its value as a grazing plant for reindeer.

Like several other *Carex* species, new shoots are initiated already during the autumn (Fig. 21). Observations in March revealed no growth of these shoots. However, during the snow-melt they quickly developed. In late May in 1977 and 1978 there were ca. 9 cm long green leaves on *C. aquatilis.* In 1976, a climatically extreme year, the development did not start until around mid-June.

Within the area of investigation, flowers of *C. aquatilis* were initiated on 4 June 1978 and were fully developed on June 24.

A stand was transplanted in the greenhouse on 29 April 1978. The shoot base was then light green. On May 23 it had developed 18 cm long leaves that had grown to 31 cm on June 2. In the greenhouse the length of the leaves was, on average, 38 cm but the plant carried no spikes during the summer.

5.2.4 Carex bigelowii

Carex bigelowii is an important plant for reindeer grazing during the late winter and early spring (Warenberg 1977). It is fairly abundant within the Ottfjället area, as also in all low and middle alpine areas within the Handölsdalen Lapp community. The great importance of this species for reindeer was observed already in 1972.

Fig. 21. *Carex aquatilis* occurs in swampy places. New shoots were initiated during the autumn. No growth during the winter was observed but during the snow-melt period they developed quickly. 6 Oct. 1978.

That year it was grazed (small, fresh leaves) on May 1 when the animals scratched off the snow cover.

According to Callaghan (1976), *C. bigelowii* has perennial rosettes and disperses mainly vegetatively, initiated from a lateral meristem in the axil of a leaf belonging to the parent tiller. Each lateral produced, according to Callaghan (op. cit.), is capable of developing in a similar pattern. The maximum longevity for the above ground parts appears to be four years but the rhizomes could survive longer. Mortality of young shoots was high. The species forms clones, as illustrated by Fig. 22 (cf. also Callaghan 1976). The illustrated specimen also had living roots and rhizomes. A leaf far to the left in Fig. 22 was also alive.

On 27 June 1977 a south-exposed slope at ca. 980 m was investigated in a place where the snow had recently melted. Many plants of *C. bigelowii* had leaves preserved under the snow. They were still green with brown, slightly wrinkled tips. Among these leaves there were new, light-green leaves and under the soil there were rhizomes with yellow-white tips and bases of weak green. Further up the mountain, where the snow cover remained intact, ca. 5 cm thick but very loose, several shoots had small green-yellow leaves among old withered leaves. When the snow disappeared these new leaves developed very rapidly.

No new observations of the species were made until 1 May 1978. Occasional small snow-free patches were seen on the south-exposed slopes of the area of investigation (B in Fig. 2). Locally the snow cover was only 10 cm deep and relatively loose. On several plants new shoots had developed green tips. Some of these were only yellow-green in colour. Some of the old leaves were still green at the base, being protected by the snow.

At the following observation on June 14, the area was completely snow-free and the frost had left the soil. Several shoots had just started to form spikes and some plants had even developed spikes (Fig. 23). Ten days later the inflorescences were fully developed. The rhizomes formed during the previous year had developed leaves and the old withered leaves were no longer present on most of the plants investigated.

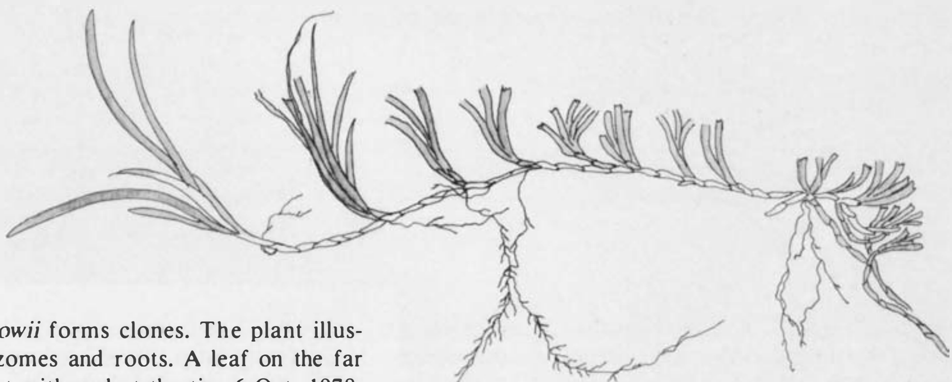


Fig. 22. *Carex bigelowii* forms clones. The plant illustrated had living rhizomes and roots. A leaf on the far left was also alive but withered at the tip. 6 Oct. 1978. Scale 1:2.

Fig. 23. *Carex bigelowii.* A shoot which started its development last year and will flower this year is seen on the left. To the right is a shoot which will be sterile this year. A new rhizome is in the centre. The snow has just melted, but despite this the plant had grown since the autumn observation. 14 June 1978.

To obtain evidence that *C. bigelowii* develops under snow, a number of 1x1 m plots were marked out in October 1979 within the area of investigation where it was hoped that the *Carex* individuals would develop without being disturbed. One specimen from each plot was investigated and sketched (Fig. 24). On 9 April 1980 new investigations were made. The rhizomes had not developed since October 1979 (Fig. 25). The snow cover was ca. 40 cm and packed hard. When the snow became looser later during the month some development had occurred. However, it was not until mid-May, when the snow cover had been reduced to ca. 20 cm and had a coarser structure, that the shoots started to develop more rapidly. In early June, when the snow had melted but the soil was still frozen, the shoots were as illustrated in Fig. 26.

The development described above was similar for most of the plants within the plots and for the species during the years of study. Thus, a positive growth occurred if the snow cover was not packed too hard and was not too deep.

On 29 April 1978 two stands of *C. bigelowii* from the Ottfjället reindeer range were planted in the greenhouse and had the following development: on May 7 the leaves were 1 cm long and 4 days later they had grown another 1 cm. On May 23 the average length of the plants was 4.5 cm with indications of spike formation. On June 2 the average length was 6 cm and one of the plants had spikes on stems that were 9 cm long. One week later this plant had finished its flowering.

Fig. 24. Rhizomes were developed by *Carex bigelowii* during the autumn. This also occurs in other sedges. October 1979.

Fig. 25. The plant illustrated in Fig. 24 was again examined on 9 April 1980. The rhizomes had not developed since October 1979. The snow cover was 40 cm and packed hard.

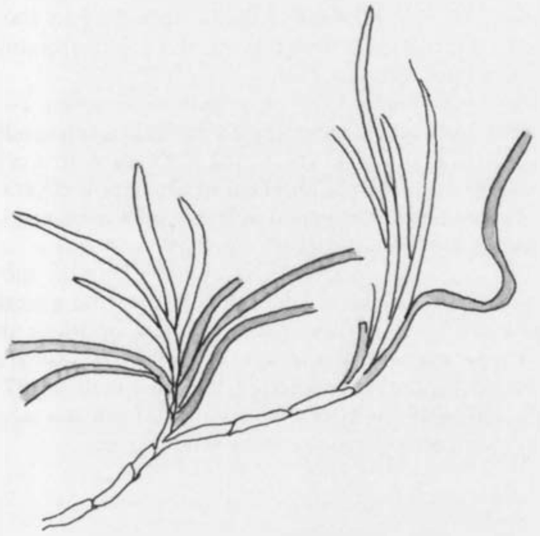


Fig. 26. *Carex bigelowii* with leaves at a more advanced stage of development. The individual was taken on 4 June 1980. It started to grow more rapidly below a coarse snow cover of ca. 20 cm in mid-May.

Fig. 27. *Carex lasiocarpa* is found in fens below the tree limit. It also grows in shallow water within the reindeer range. This species also initiated rhizomes during the autumn. The above-ground shoots grow vertically up from the rhizomes. It is difficult to decide whether growing occurs beneath a snow cover as only a few observations have been made of this species. 8 Nov. 1979. Scale 1:2.

In October one of the *C. bigelowii* plants was moved into the garden in order to over-winter in out-door conditions. At this time new rhizomes were found. In mid-April these rhizomes had grown, on average, 1 cm below the snow cover. The leaves grew rapidly when the snow melted.

The other plant was placed in a flower-pot and was allowed to develop in-doors. This plant also had newly formed rhizomes. One month later, ten new shoots had grown in the flower-pot with leaf-lengths of 8 cm, on average.

5.2.5 Carex lasiocarpa

Carex lasiocarpa is more common than *C. aquatilis* within the area of investigation. It grows in shallow water and in fens below the tree limit. It has stiff, grey-green stems. The stem sheaths are initiated fairly deeply in the soil. The rhizome is branched and extends over long distances from which the above-ground shoots grow vertically (Fig. 27). It is grazed throughout the entire snow-free period and the roots and rhizomes have been found to be particularly important during the period of snow-melt. In similarity with the two *Carex* species described earlier, rhizomes are initiated in the autumn.

Observations of the growth of this species have been made on a few occasions during November and in late May. In May the shoots that had measured 3 cm in November had now increased to 6 cm. At the observations in May there was no snow but the soil was frozen to a depth of some centimeters. Probably the *C. lasiocarpa* had grown under the snow but as no measurements had been made during the winter it is difficult to decide when the growth took place.

5.2.6 Deschampsia caespitosa

During the summer several species become too lignified for the reindeer to graze but are utilized during the spring and early part of the summer. *Deschampsia caespitosa* is one of these. It is a tall grass that grows in sturdy compact tufts. The leaves are coarse, which is certainly the reason why the reindeer avoid this species during the summer. Tufts with leaves about 20 cm long are already becoming too coarse for the fastidious reindeer. According to Skjenneberg & Slagsvold (1968), the species has higher protein content than most other grasses. The stems are sturdy and smooth. In contrast to *D. flexuosa, D. caespitosa* usually grows on moist ground.

Fig. 28. *Deschampsia caespitosa* is a variable grass especially in size, length and leaves. This species had positive growth during the winter. In April fresh green leaves were observed beneath a snow cover of ca. 50 cm. This phenomenon was observed also in January in plants growing beneath a snow cover of 30—50 cm. 5 Apr. 1980. Scale 1:2.

According to Davy (1980), several leaves remain green and photosynthetically active during the winter. Davy has observed that new leaves and shoots may be formed during the winter, although slowly. He also considers that low temperature during the spring will delay the development of its panicle.

My first observation that this species forms new leaves during the winter was made 1973. This was a unique occasion as in January of this year Ottfjället had a shallow and incomplete snow cover. On a south slope at ca. 850 m there were tufts of *D. caespitosa* with 1—2 cm long leaves under a snow cover of 30 cm. The surface structure of the snow was crumbly but had two layers of frozen snow further down.

On several occasions during the investigation I have observed newly initiated leaves and stems of *D. caespitosa* and also that new leaves were formed during the winter and grew under the snow.

In 1978 a lasting snow cover did not occur in the area of investigation until early November. Some tufts were investigated in late September and early November. Between these two occasions the leaves had grown ca. 2 cm. Snow had fallen occasionally during October but had melted.

In mid-May there are often snow-free patches at several places within the range. On these patches *D. caespitosa* tufts were observed to have several green leaves of different lengths. This was commonly observed despite the soil still being frozen. According to Davy (1980), this species is frost-tolerant but soil temperature can be critical for its survival.

During the years of the investigation there were 2—8 cm long green leaves on several *D. caespitosa* tufts under a snow cover of ca. 40 cm during November. In April, fresh green leaves were observed under a snow cover of ca. 50 cm. The leaves varied in length between 2 and 12 cm (Fig. 28).

On moist places above the tree limit where the snow remains until late June, the reindeer can find delicate leaves of *D. caespitosa* under the snow or where the snow has recently disappeared. Among old withered leaves found during the periods of snow-melt in 1977, 1978, and 1979 there were several new, fresh leaves, of which some were green and some yellow-green.

5.2.7 Deschampsia flexuosa

Deschampsia flexuosa, known to the Lapps as *sia*, is a very valuable grazing plant for reindeer. It is generally considered to be one of the most important ones. It can be grazed throughout the entire snow-free period and as long as it can be dug out from under the snow. *D. flexuosa* has a loose tuft and in shaded localities has numerous vegetative shoots and few stems, whereas in sunny localities it has fewer vegetative shoots but more stems. It produces new basal shoots throughout the entire summer and can preserve some shoots alive through the autumn and also during the winter. Kovakina (1958, cit. by Svoboda 1973) observed a positive growth of *D. flexuosa* during the winter on a lowland tundra.

D. flexuosa was present in several plant communities within the Ottfjället reindeer range. It occurs, for example, in *Carex bigelowii* heath, *Vaccinium myrtillus* - *Empetrum* heath, and also according to Fladval et al. (1971) in snow-bed vegetation. It is considerably more frequent in the forest area (Warenberg 1977). It also occurs on the frost-heaving soils at Nulltjärnsbacken where the reindeer are often found during the period of snow-melt and where I have observed pits dug by the reindeer and containing remnants of *D. flexuosa*.

The species forms new leaves long into the autumn according to observations by Skuncke (1958, 1969, 1973), Rune (1960), Steen (1965), and Skjenneberg & Slagsvold (1968). On 10 October 1979 *D. flexuosa* was studied both above (B in Fig. 2) and below (A in Fig. 2) the tree limit. In most of the tufts investigated there were green, fresh leaves of different lengths. Fresh leaves were also found in April 1980. These leaves comprised both newly initiated leaves and older leaves that had grown larger (Fig. 29).

Young light-green leaves can be found on *D. flexuosa* already during January. This was observed on 14 January 1973 in tufts covered by a 33 cm deep and relatively compact layer of snow. On average, the leaves were 20—

Fig. 29. *Deschampsia flexuosa* is a very important grazing plant for reindeer. In the reindeer range it is present in several plant communities. Young green leaves can be found on this species also during the winter. 6 Oct. 1979.

26 mm long. In January 1978 and 1979 the leaves had an average length of 24—30 mm.

Between 25—28 June 1977, *D. flexuosa* was studied at several places within the area of the Handölsdalen Lapp community above the tree limit. The ground was still covered by snow. All tufts investigated were found to have developed green shoots below the snow cover. At the same time, *D. flexuosa* was observed in places where the snow had recently melted. These tufts had longer leaves than those that grew under the snow. The leaves developed very quickly after the snow-melt and were grazed by the reindeer.

There are no problems in obtaining *D. flexuosa* to grow in the greenhouse. A tuft moved into the greenhouse on 2 May 1977 had small green fresh leaves among the old leaves at the time of the transfer. At the time when the plant was dug up there was a 20 cm snow cover with frozen soil. On May 25 the average length of the leaves was 4.5 cm and they were completely green. The fastest longitudinal growth was between June 9 and June 23. This specimen did not form panicles during the summer of 1977 but did so during 1978 following overwintering in the garden.

On 23 May 1977 other tufts of *D. flexuosa* were planted in the greenhouse. These tufts had grown in a pine plantation at Vålöjan (the height of the pines being ca. 1.5—2 m). When transferred to the greenhouse the tufts had 4 cm long leaves, which had grown to an average length of 8 cm on June 9 and had fully developed on June 29. These tufts were more vigorous than those that had grown on the mountain. New tufts from the mountain and the pine plantation were brought into the greenhouse 1978 and had the same development as in earlier years.

According to Skjenneberg & Slagsvold (1968), *D. flexuosa* reacts negatively to manure but does not appear to be injured by chemical fertilizers. A young tuft was taken directly from the mountain in mid-October 1978 and allowed to grow in-doors. On December 1 the leaves were, on average, 10 cm long. They had a slightly weaker green colour than normally seen on tufts that have developed under normal conditions. In late December the tuft had one fairly weak panicle.

5.2.8 **Eriophorum angustifolium** and **E. vaginatum**

The *Eriophorum* spp. are very valuable grazing species for reindeer. According to Skjenneberg & Slagsvold (1968), the *Eriophorum* spp. can survive severe cold and a large proportion of the leaf mass remains green during the winter. This particularly refers to *E. angustifolium* (Skuncke 1958; Temnojev 1939 cit. by Courtright 1959). The rhizomes of *E. angustifolium* are rich in nutrients and the reindeer dig for them as soon as they can smell them through the snow cover (Warenberg 1977). Miller & Laursen (1978) have found mycorrhiza on *Eriophorum* species at Barrow, Alaska. Metsävainio (1931) considers *E. angustifolium* and *E. vaginatum* to lack endomycorrhiza.

Eriophorum angustifolium and *E. vaginatum* are common throughout the Ottfjället area. *E. angustifolium* also occurs above the tree limit, often together with *E. scheuchzeri. E. vaginatum* occurs slightly more sparsely above the tree limit but dominates the fens in the S and SW parts of the range.

Shoots averaging 10 cm in length can be found on *Eriophorum* spp. below a snow cover of ca. 60 cm already in late April. *E. angustifolium* has horizontal, thick, underground rhizomes. These rhizomes curve up towards the soil surface and develop into above-ground shoots in the following year. Already in late September *E. angustifolium* has developed rhizomes and even initials of new spikes (Fig. 30). The rhizomes vary in length. The stem base of the investigated plant was still green and had sap. The stem base is often 11—12 cm beneath the peat and from it 4—5 rhizomes grow in different directions. The rhizomes generally grow horizontally but soon curve up towards the soil surface (Metsävainio 1931).

During the snow-melt, different stages of *E.*

Fig. 30. *Eriophorum angustifolium* is common in the fens throughout the Ottfjället reindeer range. This species occurs also above the tree limit. Thick, horizontal rhizomes are developed from the root-stock in the autumn and grow into above-ground shoots in the following year. Spikes were also initiated in the Autumn. 6 Oct. 1979.

Fig. 31 a—b. Different stages of *Eriophorum angustifolium* can be found during the snow-melt period. The plants illustrated in the figure grew in two separate fens at ca. 810 m (B in Fig. 2). In one fen the plants had only small light-green leaves and in the other the plants had already developed spikes at the same time. 3 June 1978. Scale 1:2.

angustifolium can be found depending on how far the snow-melt has proceeded. In early June, at a height of ca. 810 m, small light-green plants and specimens with developed spikes grew together in years when the snow-melt occurred normally. This was a common feature throughout the entire area of investigation, implying that the reindeer have simultaneous access to young plants and mature rhizomes (Fig. 31). In the forest region the individuals had, by now, generally developed further, with more developed rhizomes in more advanced stages of development.

The stem base of *Eriophorum vaginatum* is hidden by the peat. According to Chapin et al. (1980), the root system is strong and most of the biomass belongs to the underground parts. The actual root stock is short and, according to Hylander (1953—1966), it lacks horizontal shoots but branches into a strong tuft. Raunkiaer (1895—1899) considers that the tuft formation depends on the lateral shoots growing vertically. Metsävainio (1931) reported that the roots have root hairs.

New shoots developed during the autumn. These grow vertically from the base of the plant. The shoots initiated during the autumn over-winter. Spike initiates are also formed during the autumn (Fig. 32 a).

A number of special observations were made during the winter 1979—1980. On November 25, with ca. 30 cm snow cover, new shoots were noted on most *E. vaginatum* tufts within the Nulltjärn area (Fig. 32 b). Occasional green leaves were also observed. Some of the shoots were hidden whereas others had emerged slightly above the peat. Old withered leaves remained as protection. In December the shoots were, on average, slightly more developed and on some tufts even spikes had developed (Fig. 32 c). In mid-March 1980, under ca. 50 cm snow, 8—10 cm green shoots on several *E. vaginatum*

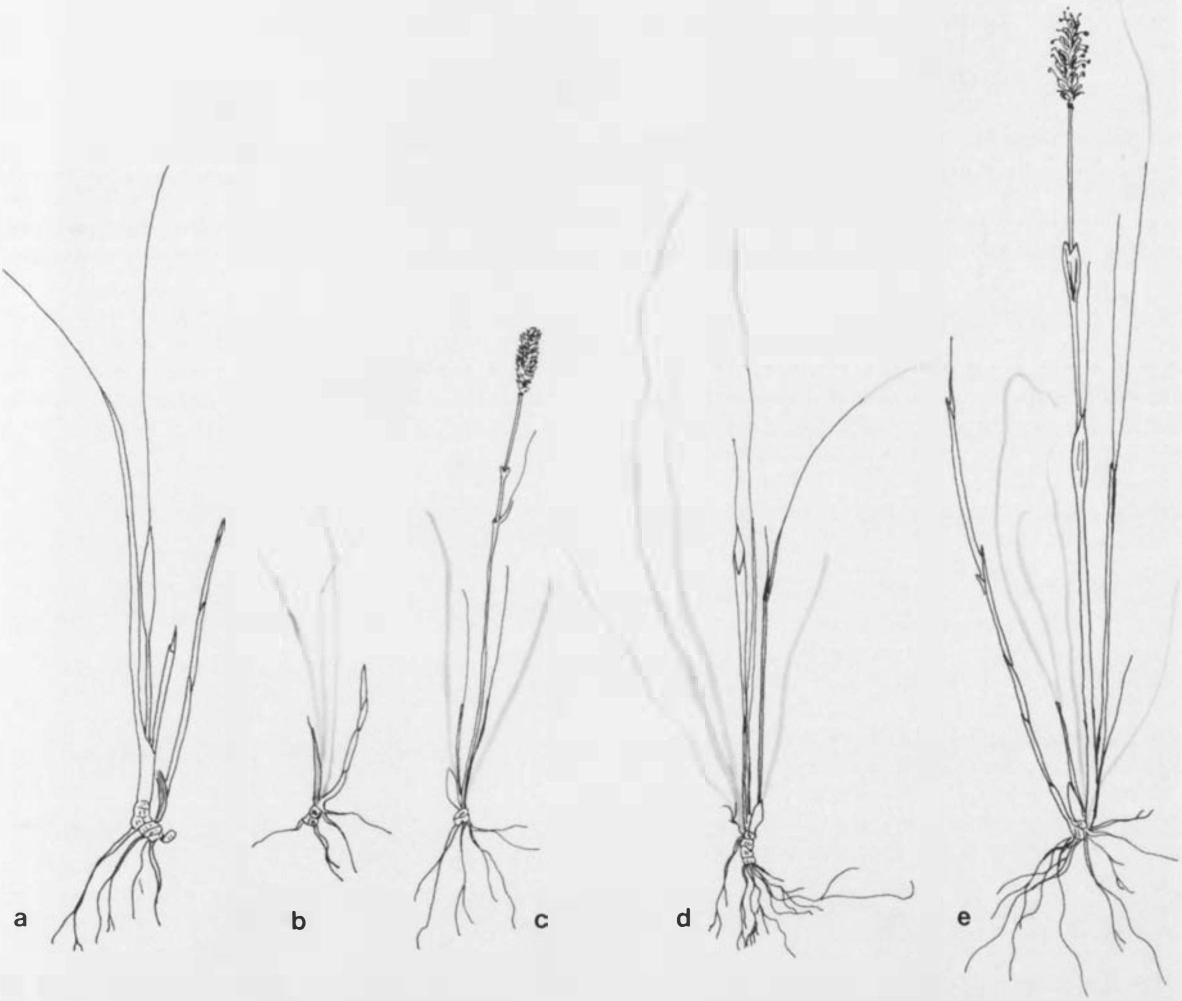


Fig. 32 a—e. Illustrations of growth of *Eriophorum vaginatum*. New shoots developed during the autumn. These shoots grew vertically from the plant base and over-wintered. Spikes were also initiated during the autumn. This species had positive growth during the winter. In the area of investigation the snow commonly melts early around *E. vaginatum* tufts, which makes it easier for the reindeer to find fresh feed early in the spring. a. 6 Oct. 1979, b. 25 Nov. 1979, c. 5 Dec. 1979, d. 15 March 1980, e. 2 May 1980. Scale 2:3.

tufts were observed and fresh shoots on several tufts had been grazed. A few reindeer had remained within the range and the droppings in the snow indicated that these plants had been grazed.

During April 1980 the snow cover within the Nulltjärn area (A in Fig. 2) was ca. 40 cm. No particular change in the development of *E. vaginatum* was noted since the observation in March (Fig. 32 d).

On 2 May 1980 the fens in the Nulltjärn area had snow-free patches. On these patches *E. vaginatum* had shoots with an average length of 10 cm. Several plants had developed spikes (Fig. 32 e).

The development was confirmed by observations in earlier years. On 14 May 1978 there were larger snow-free patches on the fens at Nulltjärn. The *E. vaginatum* plants were 18 cm tall. In these places *Scirpus caespitosus* also grew, with an average height of 1.5 cm. Several reindeer were present in the area and grazed the new plants.

E. vaginatum showed the same stage of development on the fens above the tree limit as on the fens in the Nulltjärn area. On the mountain, ca. 890 m, a number of *E. vaginatum* tufts were investigated on 9 April 1980 when the snow cover was 24 cm. Several of the tufts had green shoots.

E. vaginatum starts to grow early under the snow, perhaps earlier than *E. angustifolium*. When grown in the greenhouse, both *E. angustifolium* and *E. vaginatum* developed into strong tufts. On 29 April 1980 a tuft of *E. vaginatum* was removed from Smällhögarna and transferred to the greenhouse. At this time the stems were, on average, 7 cm long. On May 7 they had increased to 10 cm and on May 11 the tuft had developed spikes. On May 23 the leaves on the plant in the greenhouse had an average length of 6 cm and on June 12 they were 19 cm long.

5.2.9 Festuca vivipara

Festuca vivipara commonly occurs above the tree limit within the Ottfjället reindeer range. It prefers moderately moist soil but also occurs in drier localities. It is a hardy grass. The leaves are thin and soft and the reindeer can graze the species throughout the snow-free period and also dig out fresh leaves from beneath the snow.

During October *F. vivipara* tufts have fresh green leaves among the old withered ones (Fig. 33).

In March 1980 several tufts of *F. vivipara* had green leaves. The snow cover was ca. 15 cm on observation sites where they were studied. Similarly, in early May 1972 it was observed in the area of investigation (B in Fig. 2) that several tufts of *F. vivipara* had green leaves with an average length of between 3 and 7 cm (Warenberg 1977). The snow-depth on this occasion was 15 cm. The same observation concerning the average length of the leaves was made in May during the years of investigation. On the occasion when the observations were made the snow-depth was between 15—25 cm, with the exception of May 1976 (cf. section 3.4.1). Traces of grazing have also been observed.

In mid-June the species was found to be well-developed practically throughout the entire reindeer range. The spikelets developed later.

On 6 October 1978 a tuft was transferred to a flower pot and was allowed to develop at room temperature. Many new green or light-green leaves developed rapidly. However, no viviparous spikelets developed.

Fig. 33. *Festuca vivipara* commonly occurs above the tree limit. This grass develops green leaves during the winter, but the leaves are thin and give little biomass. This species had low contents of protein, sugar and minerals. 6 Oct. 1978.

5.2.10 Festuca ovina

Festuca ovina often grows together with *F. vivipara*. It develops new leaves at about the same time as *F. vivipara*. *F. ovina* is fairly common and occurs in most plant communities except in the fens within the reindeer range. According to Gelting (1934), *F. ovina* can grow also on wind-exposed areas but probably generally over-winters under the snow. The literature does not indicate whether this species is particularly favoured by trampling and/or manuring. As opposed to *F. vivipara*, only parts of the plant are grazed, namely the fresh shoots and tips of the leaves. According to Raunkiaer (1895—1899), it is the earliest of all *Festuca* species to form panicles. Some of its leaves remain fresh and green throughout the winter.

As with *F. vivipara*, I have observed green leaves during winter on *F. ovina* and also observed growth under the snow, although the growth was not particularly large.

5.2.11 Juncus trifidus

Juncus trifidus is the characteristic plant of the dry mountain heath and occurs fairly abundantly on Ottfjället. It is xerophilous and thrives extremely well on windswept areas which early become snow-free. According to Schroeter (1926 p. 460), it has two subspecies—the boreal-arctic and the central European-Asian ones. The boreal-arctic subspecies is considered by Schroeter (op. cit.) to be the true *J. trifidus* and is called *J. trifidus* ssp.

trifidus. He considers that it does not tolerate compact and long-lasting snow cover. The lower, faded part of the stem has a sweet taste and high content of crude protein during spring and early summer (Skjenneberg & Slagsvold 1968).

J. trifidus initiates green shoot bases already during the autumn and over-winters partly evergreen. On 6 October 1978 and 1979 *J. trifidus* tufts had new green shoots. In late November 1979 the stems had grown slightly (Fig. 34 a) and in early April 1980 they had further increased in length (Fig. 34 b). Observations made in earlier years gave similar results. Hugo Sjörs, Uppsala, observed green shoot bases in this species in the sub-alpine region of Ustaoset, Norway, during September 1968 (pers. comm.).

The current-year shoots often remain during the snow-period. During the first week of May 1977 and 1978 several wind-swept areas with *J. trifidus* growing in relatively dense tufts were investigated. The over-wintering shoots were found to have survived the winter well. After a month the plants were fully developed. At higher altitudes on the mountain, ca. 1000 m, the development was slower. Individuals that grew in the neighbourhood of snow did not develop spikes until late June.

The plants that developed in the greenhouse (transferred on May 2) had grown 3 cm after three weeks. They developed spikes after a further three weeks. The development of the individuals in the greenhouse was approximately the same in 1977 and 1978, with a slightly later growth in the 1978 specimens.

5.2.12 Luzula pilosa

Luzula pilosa occurs fairly commonly within the *Vaccinium myrtillus - Picea abies* forest in the area of investigation. The species forms tufts. The shoots have a curved, upward directed stolon part that, according to Raunkiaer (1895—1899), makes the tufts fairly loose and the tufts divide into several independent individuals in pace with the death of the rhizomes.

The species is grazed early in the spring, as soon as the reindeer can find it under the snow cover. However, it is not grazed to the same extent as, e.g., *Carex* spp., *Deschampsia* spp., and *Eriophorum* spp. According to Ericson (1977), the species is valuable as grazing for forest lemmings and declines in number during lemming years. It is clearly susceptible to grazing.

Occasional observations of the development of this species have been made. *L. pilosa* belongs to the evergreen plants. The stolons, that are green and hairy, develop during the autumn (Fig. 35). In the first year they develop leaf rosettes that over-winter. In the following season the stem develops with its inflorescence.

In May 1980 several tufts were observed. The previous year's non-flowering shoots had inflorescences. Some of the stolons initiated in the previous year also had visible panicles (Fig. 36).

When placed in the greenhouse *L. pilosa* developed into sturdy plants. One plant, transferred on 29 April 1978, had developed panicles on May 23 and had finished flowering on June 2.

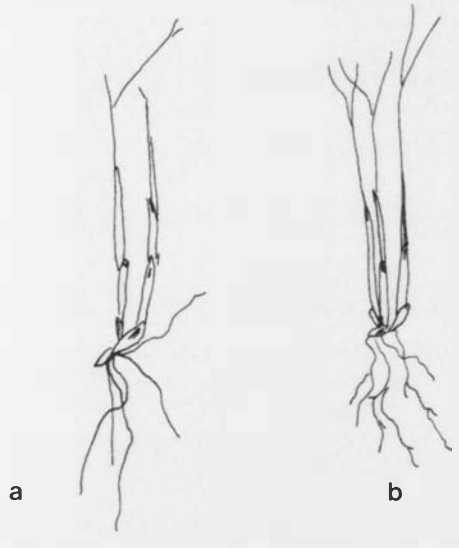


Fig. 34 a—b. *Juncus trifidus* initiated green shoot bases during the autumn. These shoot bases over-winter. Observations indicated that these had grown between October and November and developed further until early April. a. 6 Oct. 1978, b. 9 Apr. 1980.

Fig. 35. *Luzula pilosa* belongs to the evergreens. The green and hairy stolons were initiated during the autumn. 14 Oct. 1979.

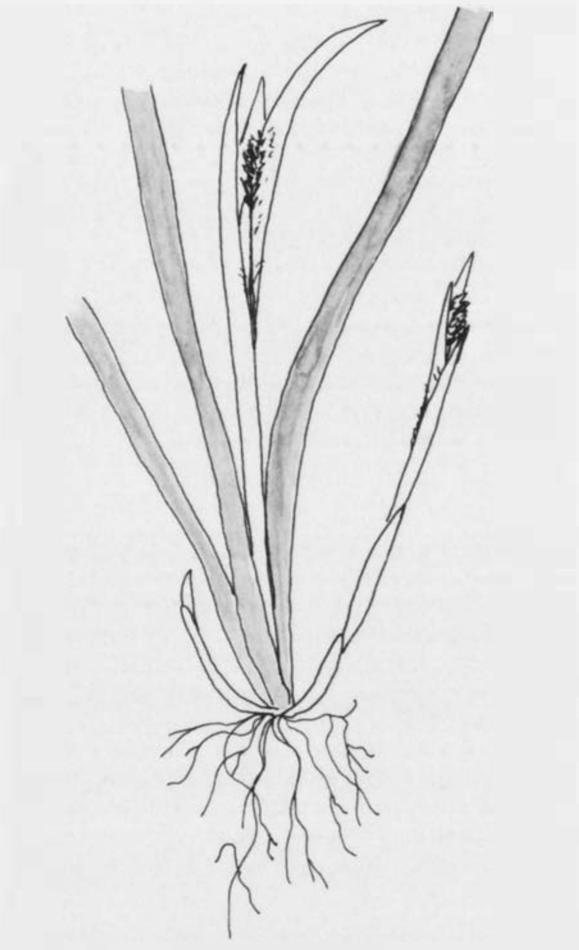


Fig. 36. Plants of *Luzula pilosa* occasionally observed in May showed that the previous year's non-flowering shoots had visible panicles. Also stolons initiated in the previous year had visible panicles. 18 May 1980.

5.2.13 Molinia caerulea

Molinia caerulea has a joint just above a bulbous stem base. On sterile shoots the current-year leaves fall off the plant at the joint and the remaining part remains green for a long period (Fig. 37). The stem base over-winters in or just above the soil surface and can provide the reindeer with nutrients during the late part of the winter and spring. Alongside the old stem bases are formed new bulbous stem bases that over-winter in the protection of scale leaves (Fig. 37). The cell walls in the new stem bases store hemicellulose (polysaccharide) as a reserve nutrient. This is dissolved when the stem starts to grow (Schroeter 1926 p. 412). The root system is strong and the root threads form a net-work (Fig. 38). The strong and twisted roots cause the plant to take the form of a tuft, according to Raunkiaer (1895—1899). The species requires moist soil and thrives in sloping fens and wet meadows.

In late September it was observed that *M. caerulea* had new stem bases extending from the short stock. Small green leaves emerged from its bulbous stem bases (Fig. 39).

Observations in late May showed that *M. caerulea* had young green shoots. In two weeks these developed into 10 cm long leaves. The plants did not produce panicles until early July.

On 14 June 1978 green-yellow leaves of *M. caerulea* were found to develop under a ca. 20 cm cover of fairly hard snow. When the snow melted they grew fairly rapidly (Fig. 40).

Further up the mountain the snow remained longer. On June 27 it had just melted and the plants were already green. Some of them had been grazed. The reindeer can, thus, find it as a young plant even in July where the snow melts late.

In the greenhouse *M. caerulea* developed faster than on the mountain. Plants transplanted on April 29 were fully developed on June 12, and plants transplanted on May 22 were fully developed with panicles exactly one month later.

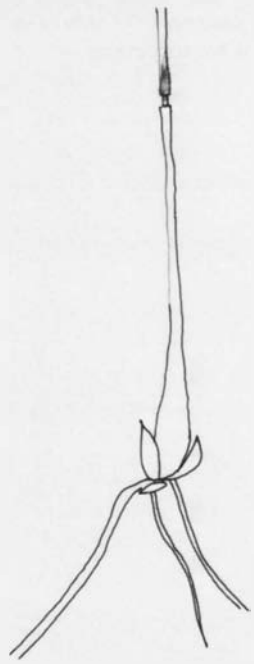


Fig. 37. On sterile shoots of *Molinia caerulea* the current-year leaves fall off the plant in the autumn or in the winter at the joint, and the remaining bulbous basal part remains green during the winter. New bulbous parts are formed alongside the old bases, and these new parts over-winter. Oct. 1978.

Fig. 38. The root system of *Molinia caerulea* is strong and forms a net-work. The root is eaten by the reindeer. The Ottfjället reindeer range, Aug. 1979.

Fig. 39. In late September I have observed new small green leaves that have emerged from the new bulbous stem bases of *Molinia caerulea.* The Ottfjället reindeer range, 29 Sept. 1979.

Fig. 40 a—b. In mid-June 1978 green-yellow leaves of *Molinia caerulea* were observed below ca. 20 cm snow cover, which was fairly hard. As soon as the snow melted the leaves grew rapidly. a. 14 June 1978. b. 24 June 1978.

5.2.14 Nardus stricta

During the period of snow-melt *Nardus stricta* is a valuable grazing plant for reindeer. Later it becomes too coarse and is avoided by most of the animals. It causes colic in, e.g., horses (Skjenneberg & Slagsvold 1968). *N. stricta* grows in large, dense tufts. According to Fossati (1980) it grows in places with short snow cover. This does not agree with the Swedish conditions. In Sweden it grows along the lower edges of sheltered mountainsides or in snow beds. The underground main stem creeps in a zig-zag manner where each internode forms a new above-ground shoot. Tightly-rolled fungal hyphae are present within the small lateral roots. Lateral roots with endotrophic mycorrhiza have few root hairs and apparently the fungi have taken over the tasks of the root hairs (Schroeter 1926 p. 404 ff.). The species prefers dry habitats, but also occurs in moist ones.

Investigations within the Ottfjället area show that this species over-winters partly evergreen. The old leaves remain on the plant for a long time and among them are found new small green leaves (Fig. 41).

Around May 1 several small green leaves were found among the remaining old withered ones. The latter may be green at the base and brown at the tip. The new green leaves started their development in the previous autumn (see above) and it is relatively common that reindeer dig down to the tufts of *N. stricta* and graze the small leaves during May, and further up the mountain during June, before the leaves become too coarse.

In the greenhouse, plants of *N. stricta* developed from small green leaf-shoots to fully developed plants within four weeks.

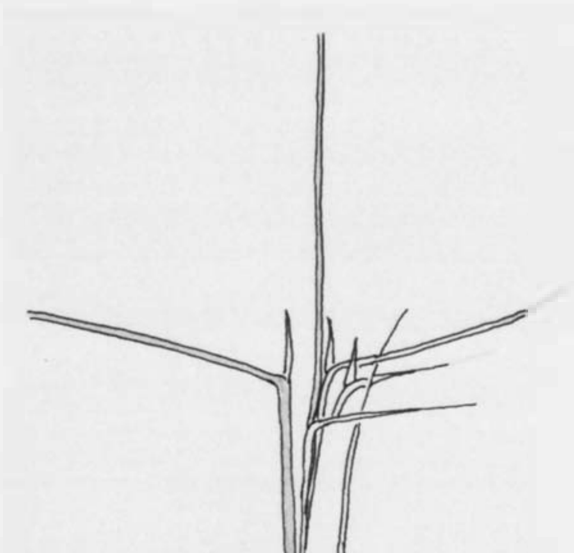


Fig. 41. *Nardus stricta* tufts may consist either of old dry leaves, leaves that are green only basally, or of totally green leaves. New green leaves grow in the autumn from the sheaths of the old leaves. 6 Oct. 1978.

5.2.15 Scirpus caespitosus

Scirpus caespitosus is of the great importance to reindeer during the spring. It grows in dense tufts and lacks creeping rhizomes. The stems are yellowish and surrounded at the base by leaf sheaths. The upper part of the sheath has a rudimentary leaf and rapidly develops green stems that the reindeer graze willingly before they become too coarse. Despite the soft stem base within the leaf sheath, even when the plants are more developed, the reindeer do not graze it very much during the summer. The stem grows also after flowering and may perhaps have reached twice its original length when fruiting. In Scotland it is grazed by red deer and also by sheep (Hugo Sjörs, pers. comm.). It is a valuable grazing species for reindeer in the Cairngorms, Scotland (Warenberg 1976). In earlier times it was used for hay in Norway, as also were *Carex rostrata, C. lasiocarpa, Molinia caerulea,* and *Eriophorum angustifolium* (Moen 1970). Mowing on fens also occurred in Sweden. Among the species collected as hay were *Eriophorum angustifolium* and *Scirpus caespitosus* (Elveland 1975). Booberg (1930) reports a strong invasion of *S. caespitosus* on the Gisselås fens in Jämtland as a result of grazing in connection with mowing.

The green stems are initiated in the autumn and thus the species over-winters partly as an evergreen (Fig. 42

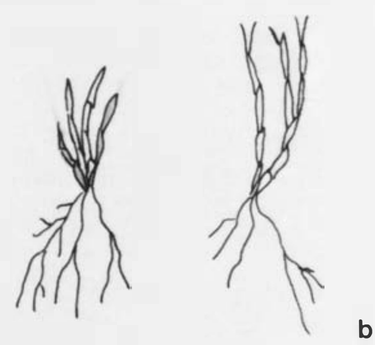


Fig. 42 a—b. *Scirpus caespitosus* is of importance to the reindeer during the spring. The green stems were initiated in the autumn. The species over-winters partly as an evergreen. It had its largest development during the snow-melt, especially in places that early become snow-free. a. 6 Oct. 1978, b. 14 June 1979.

a). There is little if any growth during the winter. However, during the snow-melt it has a rapid development in places that early become snow-free (Fig. 42 b). Several tufts of *S. caespitosus* were allowed to develop in the greenhouse. On 2 May 1977 a tuft with a height of 3.2 cm was transplanted. On May 11 the average length of the stems was 11 cm.

5.2.16 Comarum palustre

Comarum palustre is very palatable to reindeer. It has sparsely branched rhizomes about 1 m long. Above-ground shoots are partly sterile and partly flower-bearing. The sterile shoots have dry skin-like and red-brown stipules that are fused with the stem. The leaf-stipules of the flower-bearing shoots are green, foliated and pinnate. According to Skuncke (1958), *C. palustre* has developed green shoots on the stem in the autumn. The shoots retain their freshness throughout the winter. Observations made within the reindeer range indicate that these shoots are initiated during the autumn and in the following year grow out into leaves. October 1978 was unusually warm and the snow seldom remained for very long. During this month, *C. palustre* developed new leaves (Fig. 43). The same observation was made in earlier and later years. The further development of these leaves during the following cold period could not be investigated. If they were not protected by a snow cover they probably froze.

The rhizome is fairly strongly lignified but the reindeer graze it as fast as they can gain access to it beneath the snow. According to Metsävainio (1931), it has endomycorrhiza, which are common on fen species with roots lacking root hairs. The above-ground stem is soft. It frequently develops under the water surface or may be covered by litter.

Within the Ottfjället reindeer range *C. palustre* is common in fens even above the tree limit. When the reindeer first enter the range in the late part of the winter or early spring (late April) they often visit fen areas where traces can be found of grazed *Menyanthes trifoliata* and *C. palustre* that have been dug up by the animals, and particularly the rhizomes of *M. trifoliata* and the above-ground stems of *C. palustre*. My own observations indicate that the above-ground stem of *C. palustre* is more attractive to the reindeer than the underground parts.

The over-wintering light-green shoots (see above) had a reddish hue when they emerged from the snow cover during the spring periods they were studied within the range. After a week they developed into leaves. The leaves clearly had a rapid development.

The observations indicate that the species forms new leaves for a long period during the early summer. If the weather is favourable, it also has the ability to form new leaves during the autumn. This is greatly to the advantage of the reindeer which thus can obtain new leaves as fresh food during a longer period.

5.2.17 Menyanthes trifoliata

One of the plants sought by the reindeer early in the year is *Menyanthes trifoliata*. It is fairly common within the Ottfjället reindeer range. The stem can be more than 1 cm thick and grows on the surface in fens and around small mountain lakes. the articulate rhizome is covered with fibrous scale leaves (Fig. 44). It is succulent and soft

Fig. 43. *Comarum palustre* has small green shoots on stems that are initiated in the autumn and over-winter. In the spring these shoots grow out into leaves. If the autumn is warm and snow-free, leaves can develop. 6 Oct. 1978. Scale 1:2.

Fig. 44. As a grazing plant *Menyanthes trifoliata* is superior from the nutrient aspect among the grazing species analysed from the Ottfjället reindeer range. The rhizomes are important in autumn and spring for the reindeer. 10 June 1978. Scale 1:2.

but has a bitter taste. However, it is clearly palatable to the reindeer. The rhizome of *M. trifoliata* is grazed during the snow-melt. In areas which become snow-free already during May this species develops shoots with long stems which give the reindeer valuable grazing. I have not observed any growth of the species during the winter.

Mainly the leaves are grazed during the summer. According to Skuncke (1969), only the rhizome is of importance as winter grazing, whereas the succulent parts are available only for six weeks during the summer.

5.2.18 Vaccinium myrtillus

Vaccinium myrtillus is evergreen. The leaves fall off in the autumn but the shrub remains green throughout the winter if covered by snow. Otherwise it will freeze. The top parts of the shoots die regularly and the growth occurs through the topmost lateral bud. The overwintering lateral parts are small and flattened (Fig. 45). *Vaccinium myrtillus* has long creeping rhizomes through which it reproduces vegetatively. According to Flower-Ellis (1971), the shrub population is regarded as a clonal hierarchy, where a few old bushes together with younger bushes form a stand of widely differing ages.

In 1971 grazing was observed on shoot parts of *Vaccinium myrtillus* already during February and also during May. The adult animals ate the small branches of *V. myrtillus* during May while the newly-born calves ate the small lateral shoots. These are well protected under the snow and grow considerably before leaf-burst. If the snow is not too compact the reindeer can easily dig down to the *Vaccinium* plants. Under a fairly compact snow cover of ca. 25 cm, lateral shoots were found on *V. myrtillus* on the mountain heath. An extremely small growth of *V. myrtillus* was noted during the winter. However, the growth in the forest area started earlier than above the tree limit.

Vaccinium myrtillus is of great importance to the reindeer throughout the winter and, if the snow cover is not too compact, also during snow-melt. Later during the early summer and summer the leaves are valuable and are willingly eaten by the reindeer.

There were no difficulties in getting *V. myrtillus* to develop in the greenhouse. On one specimen, transplanted on 29 April 1978, the lateral shoots had developed into small branches on May 5. It flowered on May 22 and in late July the berries were ripe. However, they were not as juicy as berries that matured in a natural environment.

Fig. 45. The evergreen species *Vaccinium myrtillus* initiated lateral buds on the stems in the autumn. Only a small growth of *V. myrtillus* was noted during the winter. 6 Oct. 1978. Scale 1:2

5.2.19 Other species investigated

The other species that over-winter with green plant parts and that are of some importance as grazing for reindeer during the late part of the winter and the spring are *Potentilla erecta, Sibbaldia procumbens, Alchemilla alpina*, and *Gnaphalium supinum*.

Within the Ottfjället range *Potentilla erecta* is common and occurs on Ottfjället even above 1 000 m. The stock is thick and woody but I have never observed it to be grazed (Fig. 46). The leaves are, however, attractive to the reindeer. *P. erecta* has green over-wintering vegetative organs. This species has a weak positive growth during the winter. *P. erecta* developed well in the greenhouse and plants transplanted on 29 April 1978 flowered on June 2.

Sibbaldia procumbens occurs commonly throughout the area above the tree limit and also along streams in the forest area. The leaves have long petioles. New parts are initiated in the leaf axils. In the following year these parts grow out into flower-bearing shoots. The shoots are initiated in the previous autumn, which was the case on all specimens investigated on 29 September 1978 (Fig. 47 a). *S. procumbens* has its widest distribution on moist meadows and in snow-beds. Here the reindeer can find it as fresh feed far into the summer (Fig. 47 b).

Alchemilla alpina occurs fairly commonly within the Ottfjället area. It has a woody, strongly branched root, from which the leaves grow in rosettes. It is a valuable plant for reindeer grazing and is grazed during late spring and summer and as long as it remains green during the autumn. It does not belong to those species that earliest become available as grazing during the spring.

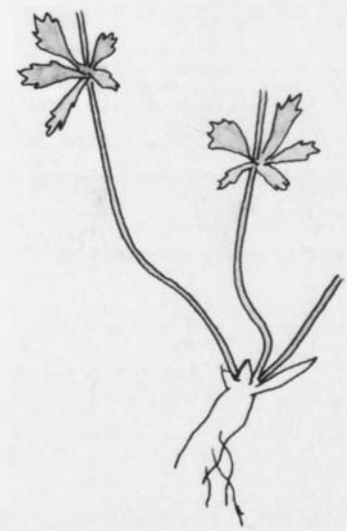


Fig. 46. *Potentilla erecta* is common on Mt. Ottfjället. This species had a weak positive growth during the winter. On top of the stock there are some green overwintering parts. 29 Oct. 1978.

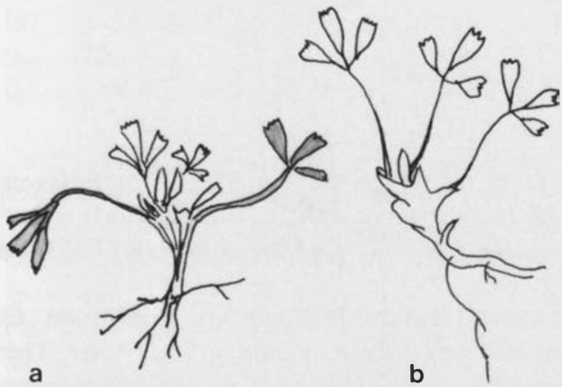


Fig. 47 a—b. New shoots of *Sibbaldia procumbens* were initiated in the autumn. As this species occurs also in snow-beds, the reindeer can find it as fresh feed late in the summer. a. 29 Sept. 1979, b. 14 June 1978.

As also in *Sibbaldia procumbens*, new shoots are initiated on *A. alpina* in the autumn (Fig. 48). This species requires the protection of snow. Jónsson (1895 p. 288) found green living shoots on *A. alpina* on 26 March 1894 on Iceland. These shoots, which he judged to be leaf shoots, were protected by the old withered leaves.

Gnaphalium supinum is fairly common within the area of investigation and primarily occurs in snow-beds but also on newly exposed soil. Newly initiated overwintering shoots lack special protection in the form of

Fig. 48. *Alchemilla alpina* initiated new shoots in the autumn. I have observed a weak positive growth during the winter. Green leaves occasionally over-winter. 29 Sept. 1978.

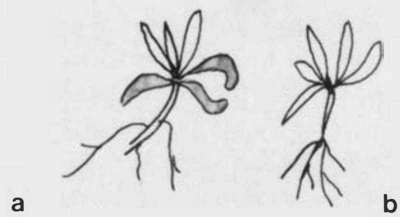


Fig. 49 a—b. *Gnaphalium supinum* primarily occurs in snow-beds. This species had green leaves in the autumn. During the winter new leaves had developed beneath a snow cover. a. 20 Sept. 1977, b. 14 June 1978.

bud scales. In late September 1977 several individuals of *G. supinum* had green leaves. In the following year several leaves had developed beneath a snow cover that was ca. 20 cm at the time of the investigation (Fig. 49). As this species grows primarily in snow-beds it does not become available as reindeer grazing until fairly late and also probably provides fairly little biomass.

5.3 Summing-up of results

My studies of single specimens repeated on different occasions have provided knowledge on the ability of different species to grow under snow cover.

Deschampsia flexuosa forms new leaves throughout the entire vegetation period. Some leaves remain green throughout the winter, covered by snow. During January new leaves can be found on *D. flexuosa* under a snow cover (cf.

5.2.7). This also applies to *Deschampsia caespitosa, Festuca ovina,* and *F. vivipara.* The over-wintering parts of these species may be considered as evergreen. *Nardus stricta* also belongs to this group, as it was observed to have small green leaves among the old remaining ones below a snow cover of ca. 70 cm (Warenberg 1977). These small leaves grow while the snow still covers them and develop fairly rapidly during the period of snow-melt.

Anthoxanthum odoratum belongs to the same group of species with regard to its over-wintering parts. In the autumn before the snow, it has newly initiated leaves with an average length of 1 cm, which are protected under the snow. These leaves grow slowly beneath the snow cover but develop very rapidly during the snow-melt. Panicles are developed around June 20.

Juncus trifidus over-winters with green newly initiated shoot-bases among the old stems. These shoot-bases are already initiated in late September. Investigations have shown that these shoot-bases grow to twice the size from October to May.

Scirpus caespitosus initiates green stems during the autumn. These stems grow rapidly during the spring in places which early become snow-free. They are, however, fairly short when flowering, which occurs early.

Of the species studied on the Ottfjället reindeer range, *Luzula pilosa* and *Vaccinium myrtillus* belong to the evergreen plants, the latter only because of its green stems. *L. pilosa* initiates stolons during the autumn. It has a rapid development, as demonstrated in individuals kept in the greenhouse (cf. 5.2.12).

Carex aquatilis, C. bigelowii, C. lasiocarpa, and *Eriophorum angustifolium* belong to the species group with rhizomes initiated in the previous year. These grow below a relatively thick snow cover and, like most of the investigated species within the area, develop rapidly during and following snow-melt.

Eriophorum vaginatum lacks horizontal rhizomes but has developed new shoots and also spike-initiates before the snow cover becomes lasting.

Molinia caerulea over-winters with bulbous stem bases. These are initiated during the autumn alongside the old stem bases (Fig. 37, 5.2.13). In favourable years the new stem bases grow slowly in comparison with other graminaceous plants investigated.

Table 7. Survey of mode of over-wintering of the green parts of the plants studied. The survey is an attempt to group the species into categories.

1) Most of the current-year production is evergreen.
2) A small part of the current-year production is evergreen. 2a) Lack rhizomes, both older and late initiated leaves and stipules over-winter. 2b) Rhizomes, these develop during the autumn. They form green parts, the older parts are only green at the base. 2c) Lack rhizomes. The over-wintering green parts consist only of organs initiated late, protected by old leaf remnants and/or scale leaves.

	1	2		
Species		a	b	c
Alchemilla alpina	-	-	-	+
Anthoxanthum odoratum	-	+	-	-
Carex aquatilis	-	-	+	-
C. bigelowii	-	-	+	-
C. lasiocarpa	-	-	+	-
Comarum palustre	-	-	-	+
Deschampsia caespitosa	-	+	-	-
D. flexuosa	-	+	-	-
Eriophorum angustifolium	-	-	+	-
E. vaginatum	-	+	-	-
Festuca ovina	-	+	-	-
F. vivipara	-	+	-	-
Gnaphalium supinum	-	-	-	+
Juncus trifidus	-	+	-	-
Luzula pilosa	+	-	-	-
Molinia caerulea	-	+	-	-
Nardus stricta	-	+	-	-
Potentilla erecta	-	-	-	+
Scirpus caespitosus	-	+	-	-
Sibbaldia procumbens	-	-	-	+
Vaccinium myrtillus	+	-	-	-

Green vegetative shoots are present on *Comarum palustre* during autumn and winter. There are small light-green buds on the above-ground parts. If the weather is favourable during the autumn some of them can form leaves, which generally freeze when temperatures fall below 0°C. The over-wintering buds have a fairly rapid growth during the spring. In late May, when most of the snow around Lakes Nulltjärnarna has disappeared, they are already a few cm long and have fully developed leaves after two weeks.

Potentilla erecta, Sibbaldia procumbens, Alchemilla alpina, and *Gnaphalium supinum* also over-winter with green organs.

A list of the probable over-wintering conditions of the species investigated is given in Table 7.

6. Biomass of some semi-evergreen species

It is of interest to know what food was available to the reindeer on the Ottfjället reindeer range early during the year and also to the reindeer that were planned to be taken to the range in the spring of 1982. Quantitative investigations were made on the available biomass before and during snow-melt as regards some of the plants grazed by the reindeer during the spring. The investigations were conducted in 1979. In the present context the term biomass refers to above-ground, living, plant material. The investigation concerned *Carex bigelowii, Eriophorum vaginatum, Deschampsia flexuosa*, and *Juncus trifidus*, being some of the species found to be of importance for reindeer grazing on the range (Warenberg 1977). During the spring of 1979 only about 10 reindeer were present on the range. Consequently the investigations were not influenced by the grazing pressure.

6.1 Methods

Carex bigelowii was investigated within the reindeers' calving areas on *Carex bigelowii* heath (B in Fig. 2 and map in Warenberg 1977) but the biomass values are probably also representative for areas of *C. bigelowii* heath within, for example, *Vaccinium myrtillus - Empetrum* heaths. *Juncus trifidus* was investigated on wind-swept patches and in other heath areas. *Eriophorum vaginatum* was studied in fens in the forest area and *Deschampsia flexuosa* in areas of *Vaccinium myrtillus - Picea abies* forest. The two former species are important for the females during calving whereas the two latter are important for non-calving reindeer, including the males. During calving the females remained above the tree limit in the eastern part of the mountain (within sub-area B in Fig. 2). Non-calving reindeer mainly stayed in sub-area A (Fig. 2) during the spring.

The density (number per unit of area) and weight per individual of each represented species or other counting unit (see below) were used in determining the biomass. This method probably gives greater accuracy with the same work input than the surface harvest method and has been used in deciduous forest investigations (Kubiček & Brechtl 1970) and in fen investigations (Flower-Ellis 1975). The density of each species was determined separately. In the case of *Carex bigelowii, Eriophorum vaginatum*, and *Deschampsia flexuosa* the investigation was conducted along line profiles. Sampling areas of 1 x 1 m were marked at intervals of 50 m. *Juncus trifidus* was investigated in 10 x 10 m sampling areas. This species prefers sites exposed to the wind, e.g., wind-swept patches, where it grows sparsely, and line profiles were found to be unsuitable. Density determinations must be done within a given area and as it was easier to measure 10 x 10 m plots than the area of wind-swept patches the former methods was used. Within the area of investigation the patches are relatively small and therefore only one 10 x 10 m plot was used per windswept patch. In larger areas of heath 2—4 plots were used.

Counts were made within each plot. For *C. bigelowii*, counts were made of each individual shoot. For the other three species counts were made of the number of tufts. These were divided into large (> 100 stems or leaves per tuft) and small tufts. For each fifth plot analysed the number of stems or leaves per tuft were counted for a tuft with a previously determined location.

The stems or leaves were cut off the counted tufts and weighed fresh in groups of 50 (*D. flexuosa*), 10 (*J. trifidus*), or 5 (*E. vaginatum*). As regards *C. bigelowii*, ten entire shoots with previously determined locations were cut from each sampling area. Only the living material was used. This had either been produced during the previous autumn and survived, or had grown beneath the snow during the winter, or had grown during the snow-melt. The samples were dried for three days at 80°C and were weighed dry.

The biomass per unit of area was calculated by multiplying the number of shoots per unit of area by the weight per shoot (or corresponding counting unit). In order to calculate the amount of biomass of each investigated species that was available to the reindeer, the total area of the investigated plant communities must also be determined within the above-mentioned grazing areas (see Fig. 2, 2.1). This was done by cutting out each individual plant community from the vegetation map in Warenberg (1977) and weighing pieces representing each community. A known area was cut and weighed in a corresponding manner.

The biomass investigations were continued throughout all the periods of snow-melt, in the investigated areas being approximately May 20—June 6 in 1979 and also a 1—3 week period with no snow cover. In the case of *C. bigelowii* the investigation period was longer, April 11—June 20.

In the determinations, 1 kg dry matter has been assumed to equal 2.15 megacalories (Mcal) (Steen 1966; Eriksson 1979) in order to convert the biomass from kg ha^{-1} to metabolizable energy value Mcal ha^{-1} (1 Mcal = 10^6 calories). For conversion to joules the result multiplies by 4.18.

6.2 Results

The *Carex bigelowii* material was divided into two parts. The period of investigation April 11—May 30 comprised areas at the same altitude and with the same rate of snow-melt. During April the shoots had to be dug out. The last period of investigation, June 1—20, comprised areas situated higher on the mountain with later snow-melt and with shoots that started to develop later. These areas became more or less snow-free around June 11.

The density within the first area investigated was, on average, 47.1 shoots m^{-2} (Fig. 50). In the higher area the number of shoots per sampling area was greater, 62.1 shoots m^{-2}, but the difference probably did not depend on a higher density of *C. bigelowii* with altitude but was probably

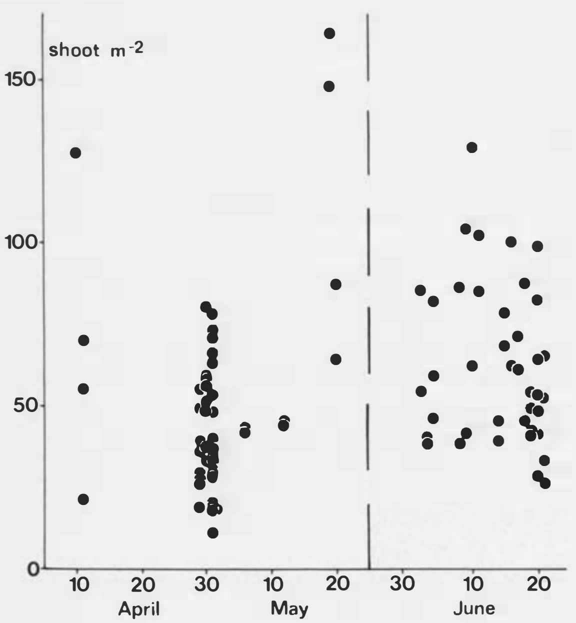


Fig. 50. Number of shoots m^{-2} of *Carex bigelowii*. The Ottfjället reindeer range, 1979. The investigation was performed in two areas at different times. Snow melted earlier in the area investigated first. A weak indication of an increase in the density with time in the area investigated first can be seen but no clear indication of an increase in the other area.

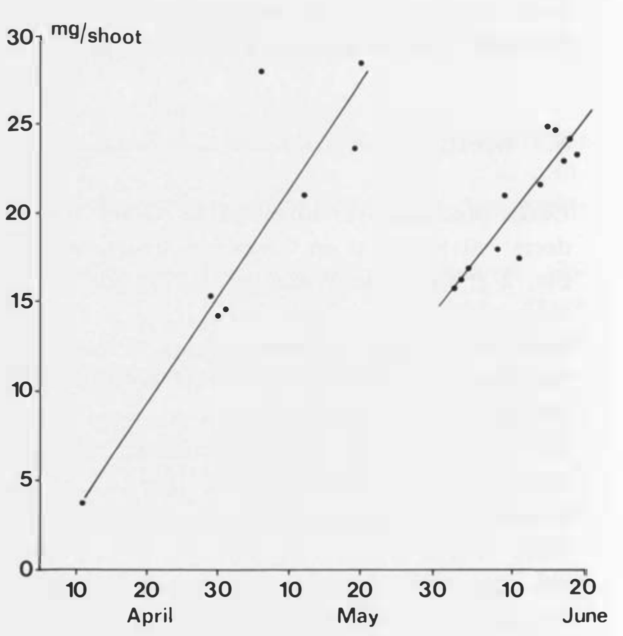


Fig. 51. Weight per shoot of *Carex bigelowii*. The Ottfjället reindeer range, 1979. The investigation was performed in two areas. Each point is a mean value of 10 shoots. The equation for the area investigated first is $y = 0.59x + 4.14$, and for the other area $y = 0.60x + 12.06$.

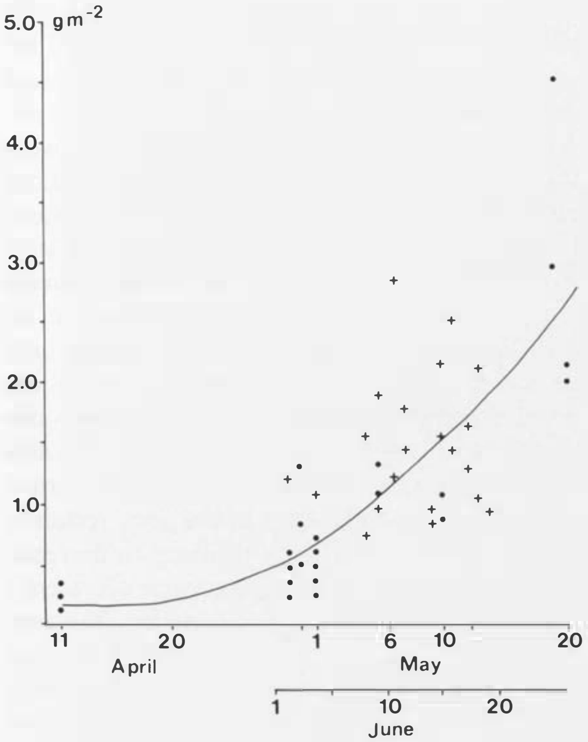


Fig. 52. Increase in biomass of *Carex bigelowii*. The Ottfjället reindeer range, 1979. Dots = a lower part of the investigation area, plus signs = a part about 200 m higher. The increases in both areas were not significantly different and are thus illustrated with the same curve, with a delay of 34 days for the higher area (with a later snow-melt).

more of a coincidence. A weak indication of an increase in density with time in the first area investigated can be seen in Fig. 50. No clear indication of increase could be found in the area investigated later. In both areas the variation in density was large.

The weight of *C. bigelowii* shoots increased during the period of investigation (Fig. 51) in both areas. In the lower area the average weight on the first day of investigation, April 11, was 3.9 mg per shoot. At the end of the month the average weight had increased to 15 g per shoot. The snow started to melt in mid-May and on about May 20 the shoot weight was about 29 mg per shoot. The growth increase of *C. bigelowii* in the higher area was about one month later, which approximately corresponds to the later snow-melt. The mean weight per shoot in early June was slightly more than 16 mg and in the middle of the month it was ca. 24 mg. The variation between the samples in the area investigated later was lower than in the area investigated earlier.

When calculated as the weight increase per shoot and day, the growth rates did not differ between the two areas and amounted to between 0.5 and 0.6 mg per shoot and day.

The biomass per shoot and day is given in Fig. 52. In the figure the values for the higher altitude area have been shifted and indicate a delay of 34 days in this area. At the start of the period the biomass was low. It increased during April from 0.3 g m^{-2} to 0.6 g m^{-2}. Within the area investigated first, the biomass increased until May 20 up to, on average, 3.0 g m^{-2} (65 Mcal ha^{-1}). In the higher alti-

Table 8. Number of tufts m^{-2}, number of stems or leaves per tuft, growth in mg per stem or leaf and per day, and production mg m^{-2} and day of Juncus trifidus, Deschampsia flexuosa and Eriophorum vaginatum. J. trifidus is determined on wind-swept areas and on areas of mountain heath. D. flexuosa in the forest and E. vaginatum in fens in forest areas. Ottfjället reindeer range, spring 1979.

	Juncus trifidus		Deschampsia flexuosa		Eriophorum vaginatum	
	small tuft	large tuft	small tuft	large tuft	small tuft	large tuft
No. of tufts, m^{-2}	6.6	3.5	10.0	4.2	12.0	4.6
SE	0.4	0.2	0.5	0.2	0.5	0.3
No. of stems (leaves) per tuft	59.0	150.0	68.0	204.0	64.0	168.0
SE	2.8	5.7	4.1	8.7	3.9	3.7
Growth per stem (leaf) and day, mg	0.15		0.03		0.34	
SE	0.03		0.01		0.03	
Production m^{-2} and per day, mg	136.0[a)]		42.0		523.0	
SE	18.4		11.2		43.8	

a) refers to May 27 – June 15.

tude area the biomass in early June was, on average, 0.9 g m^{-2} (19 Mcal ha^{-1}) and in the middle of the month it was 1.8 m^{-2} (39 Mcal ha^{-1}).

The shift of the time scale for the higher altitude area (Fig. 52) shows that the growth of biomass in the two areas is similar. The growth process can be described as a second degree equation. The faster growth is determined by the time of snow-melt and the following development in growth did not differ despite the differences in altitude.

In the heath area *Juncus trifidus* was investigated between May 25 and June 22. The investigated area amounted totally to 664 ha and comprised the same area as that where the *Carex bigelowii* investigations were made.

Table 8 shows that the number of small tufts m^{-2} was higher than the number of large tufts. Totally, the small tufts numbered, on average, 6.6 m^{-2} and the large tufts 3.5 m^{-2}. The number of stems per small tuft was, on average, 59 whereas on the large tufts there were 150. I have not observed that new stems were formed during the early summer. No increase in the number of stems per tuft can be seen from Fig. 53.

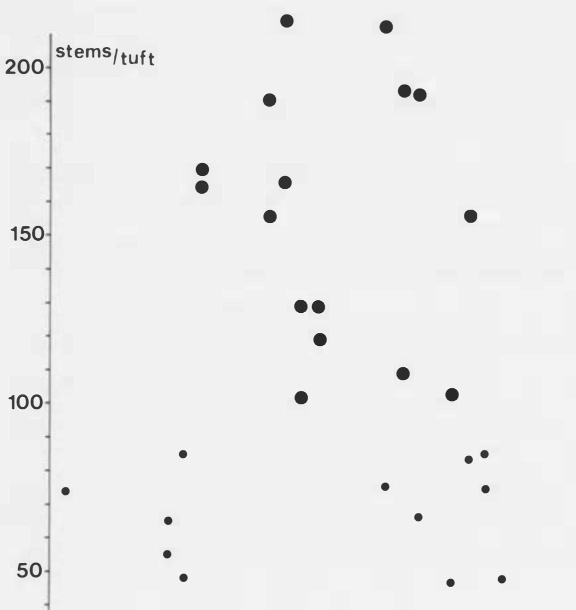


Fig. 53. Number of stems per tuft of *Juncus trifidus*. The Ottfjället reindeer range, 1979. Small dot = small tuft, large dot = large tuft (more than 100 stems).

The first weight calculations were made between May 6 and May 19. According to these calculations the weight per stem at that time was, on average, 3.9 mg. On May 27 the average weight per stem was 4.3 mg, thus showing a small weight increase (Fig. 54). The weight per stem then showed an almost linear increase but with a wide scatter until June 15. Between June 16 and 22 the investigations were concentrated on the eastern parts of sub-area B, the size of which amounted to 240 ha. This area became snow-free somewhat later than the former area. The weight per stem in the area remained constant or showed a weak tendency to decrease, probably since the sampling was done on recently exposed plants during this six-day period. The average weight of a plant that had recently emerged from the snow was larger in the higher area than in the lower area where the snow melted earlier. This is probably related with the longer period of insolation during the later period of investigation.

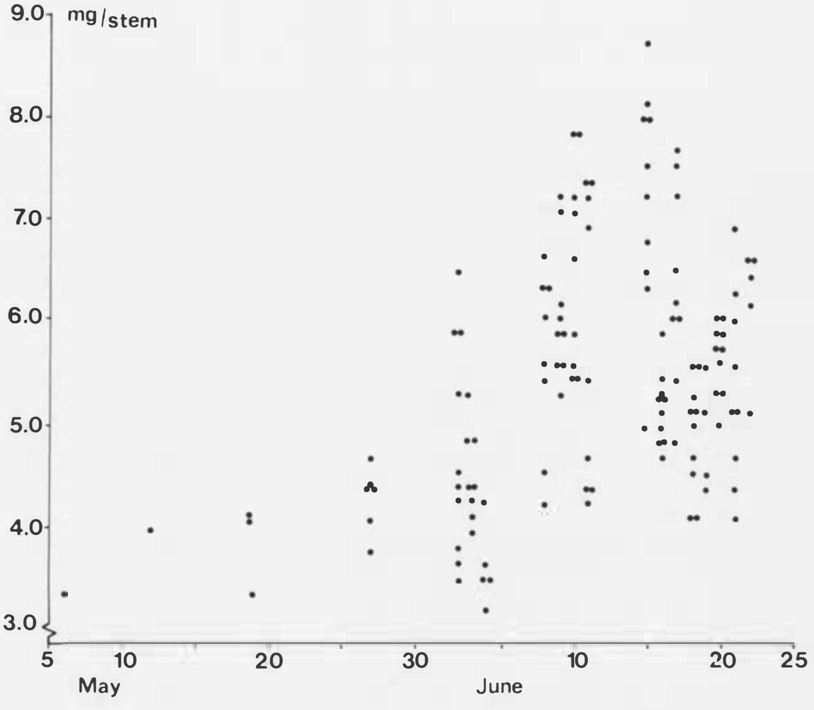
Calculations of the average growth per stem and day, and per m^2 and day were made. The calculation was based on measurements between May 22 and June 15. The growth per stem and day according to these calculations amounted to 0.15 mg, and per m^2 and day to 136 mg (Table 8).

On the first day of the investigation, May 27, the biomass within the area that was earlier snow-free amounted to 3.3 g m^{-2} (71.6 Mcal ha^{-1}). The biomass then increased and on June 15 was calculated to be 5.9 g m^{-2} (127 Mcal ha^{-1}) (Fig. 55). In the eastern part of the area with a slightly later snowmelt, the biomass at the end of the period of investigation amounted to 6.0 g m^{-2} (129 Mcal ha^{-1}).

In the forest and fens of the Nulltjärn area, with a size of ca. 1084 ha, investigations were made on *Deschampsia flexuosa* and *Eriophorum vaginatum* during the period May 25—June 24 for the former and from June 1—June 24 for the latter. In the middle of the period, some snow still remained in the forest but it was of a loose type.

Also in the case of *D. flexuosa* the small tufts were more numerous than large ones (Table 8). On average within the investigated forest area (760 ha)

Fig. 54. Weight per stem of *Juncus trifidus* during the spring. The Ottfjället reindeer range, 1979. Each point represents a mean value of ten stems.



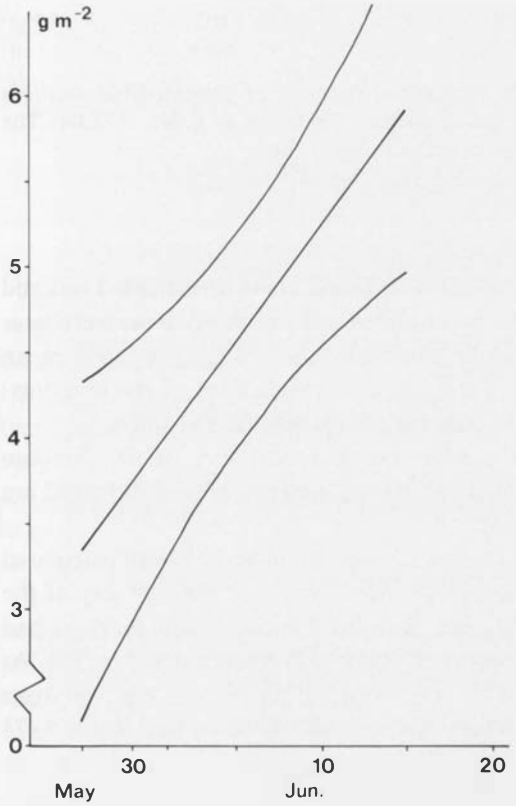


Fig. 55. Increase in biomass of *Juncus trifidus* and 95 % confidence limits. $y = 0.14x + 3.20$. The Ottfjället reindeer range, 1979.

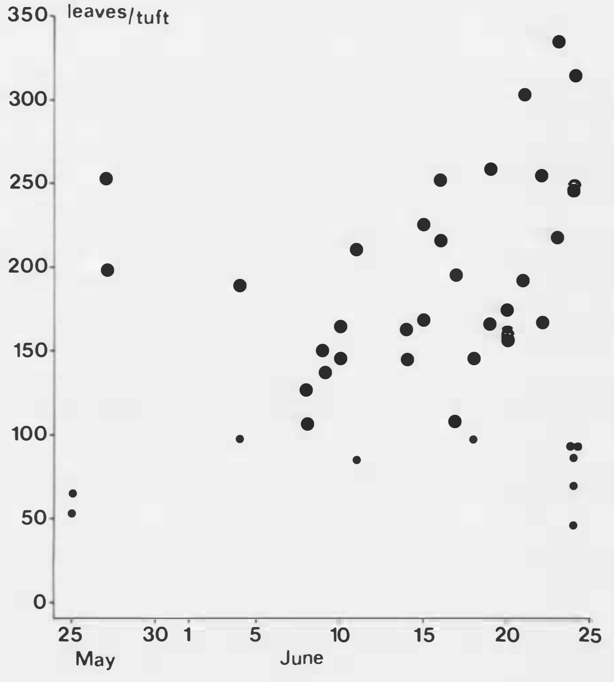


Fig. 56. Number of leaves per tuft of *Deschampsia flexuosa*. The Ottfjället reindeer range, 1979. The number of leaves per small tuft did not increase during the period of investigation whereas the number of leaves per large tuft increased after June 8 but with a large spread. Each point is a mean value of several tufts. Small dot = small tuft, large dot = large tuft (more than 100 leaves).

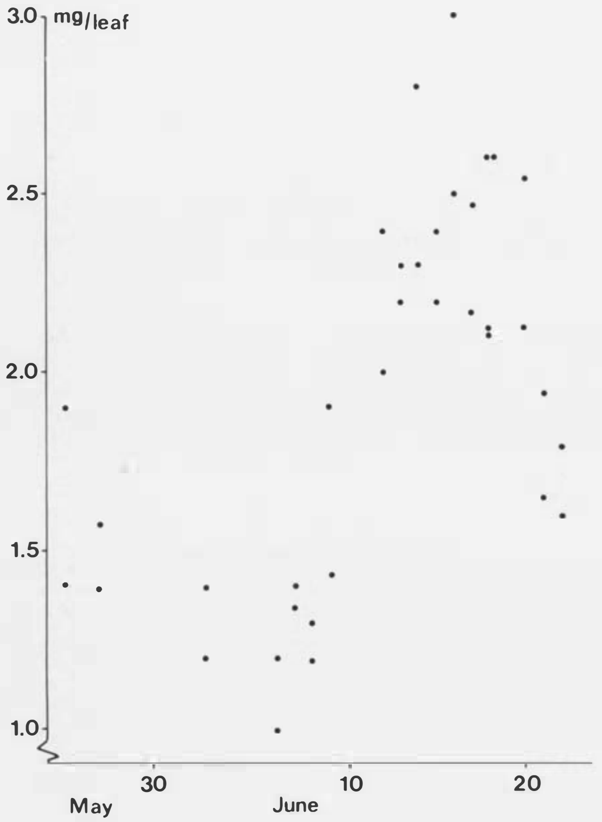


Fig. 57. *Deschampsia flexuosa*, weight per leaf. The Ottfjället reindeer range, 1979. Each point is a mean value of 50 leaves.

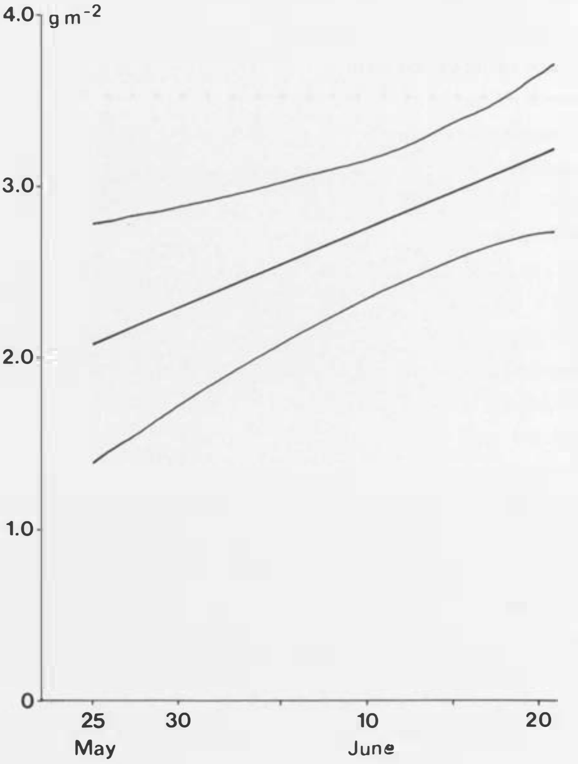


Fig. 58. Increase in biomass of *Deschampsia flexuosa* with 95 % confidence limits. $y = 0.04x + 2.04$. The Ottfjället reindeer range, 1979.

there were 10 small and 4.2 large tufts m^{-2}. On the small tufts the number of leaves per tuft was, on average, 68, whereas on the large tufts there were 204 leaves per tuft. The number of leaves per large tuft increased with time following June 8 but with a large spread. The number of leaves per small tuft did not increase during the period of investigation (Fig. 56).

The weight per leaf at the start of the investigation period was very low. An increase was not noticed until about June 15 (Fig. 57). The lower weight per average leaf for the last days of the investigation (June 21—25) may possibly depend on new leaves having grown out (cf. Fig. 56). As earlier mentioned, *D. flexuosa* produced new leaves throughout the entire growing period. As the weighed leaves were randomly chosen it is possible that also newly initiated leaves were selected for weighing. Nevertheless, it is also possible that the snow melted later in the areas investigated last and that the investigated tufts in these areas were later in their development, thus causing a lower mean weight per stem. On the last days of the investigation the area was completely free of snow.

The growth per leaf and day of *D. flexuosa* amounted to 0.03 mg, and per m^2 and day to 42 mg (Table 8).

For *D. flexuosa* the biomass has been calculated to 2.1 g m^{-2} (45 Mcal ha^{-1}) for the first day of the investigation, May 25. On June 8 the biomass had increased to 2.7 g m^{-2} (58 Mcal ha^{-1}) (Fig. 58). At the end of the investigation period, e.g., on June 24, the biomass was calculated to be 3.4 g m^{-2} (73 Mcal ha^{-1}) (Fig. 58).

The fen area in which the investigation of *Eriophorum vaginatum* took place was estimated to cover 324 ha.

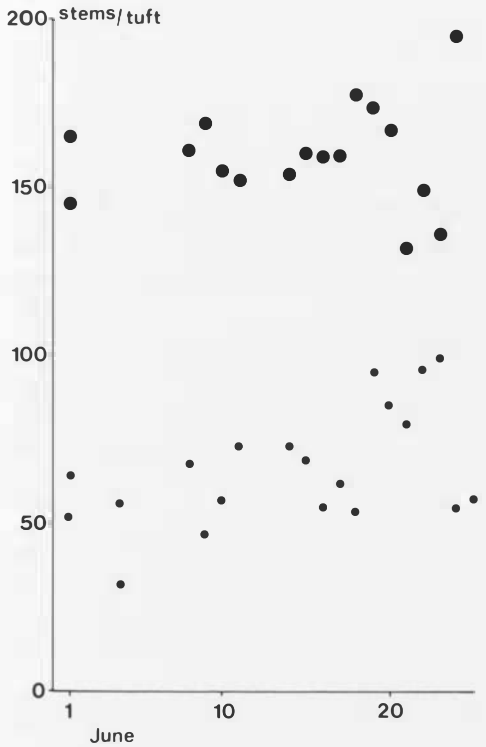


Fig. 59. Number of stems of *Eriophorum vaginatum*. The Ottfjället reindeer range, 1979. Each point is a mean value of several tufts. Small dot = small tuft, large dot = large tuft (more than 100 stems).

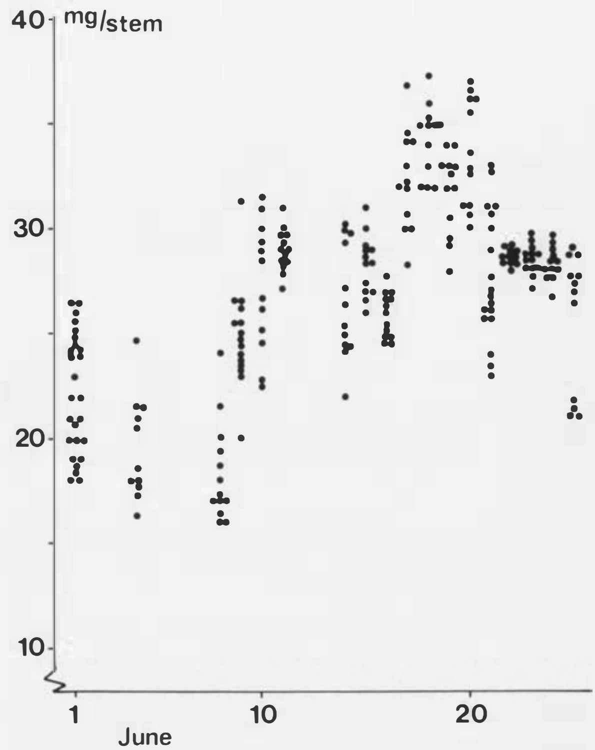


Fig. 60. Weight per stem of *Eriophorum vaginatum*. The Ottfjället reindeer range, 1979. Each point represents a mean value of 5 stems.

As with the two previous species there were more small tufts than large (Table 8). On average within the area of investigation, there were 12 small and 4.6 large tufts m^{-2}. The number of stems was, on average, 64 per small tuft and 168 per large tuft. Only a very weak increase in the number of stems per small tuft can be seen in Fig. 59. As regards large tufts, no tendency was observed during the period of investigation.

In the randomly chosen material, the weight per stem was slightly higher on the first day of investigation than on the two subsequent days (see Fig. 60). This was probably because the fens that were investigated on June 4 and June 8 became snow-free later, and that *E. vaginatum* had not developed so far. The weight of the stems then had a relatively linear increase until June 21. The investigations up to this date concerned fens that were in open localities. The last days of the investigation concerned smaller fens with more sheltered localities and where the snow melted slightly later. This explains the lower weights of samples from these days.

The growth per stem and per day for *Eriophorum vaginatum* was calculated to 0.34 mg and per m^2 and day to 523 mg (Table 8).

On the first day of the investigation, June 1, the biomass was estimated to 39 g m^{-2} (839 Mcal ha^{-1}) and on June 5 and June 8 to 35 g m^{-2} (753 Mcal ha^{-1}). On June 12 the biomass amounted to 40 g m^{-2} (860 Mcal ha^{-1}) and at the end of the period of investigation to 46 g m^{-2} (989 Mcal ha^{-1}) (Fig. 61).

6.3 Comparison with other investigations

Studies of biomass have been conducted within different alpine and arctic areas. Attempts to directly compare the results from the Ottfjället area with these investigations encounter certain difficulties on account of the different species investigated and also the different periods of investigation.

Bliss (1962) states that shoot production is slightly larger in arctic areas compared with alpine ecosystems. In this respect he is probably referring to alpine ecosystems south of the arctic circle, but this is not specifically stated. According to Bliss (op. cit.) the reason for larger shoot production in arctic areas probably depends on the long, light, days which result in a long photoperiod during the short growing period in these areas.

Most arctic plants have greater quantities of underground biomass than plant biomass above-ground (Dennis & Johnson 1970; Wielgolaski 1975). This also applies to many species outside the arctic area. It should be observed that the underground biomass represents the production of several years (Bliss 1962). The underground biomass is important as a source of grazing as the reindeer dig for it during the spring and autumn (Skuncke 1958; Warenberg 1977; Eriksson 1979). No calculations have been made of underground biomass in the Ottfjället reindeer range.

The biomass varies between different plant communities and also from year to year. The variation between different plant communities has been established in investigations conducted on the Hardangervidda, Norway (Kjelvik & Kärenlampi 1975; Wielgolaski 1975) and at Kevo, northern Finland (Kallio 1975; Kjelvik & Kärenlampi op. cit.). The investigations were conducted on lichen heath and dry meadows, in birch forest and in willow thickets and at Kevo also in wet birch forest. The values given in Table 9 are mean values from two or three growing periods.

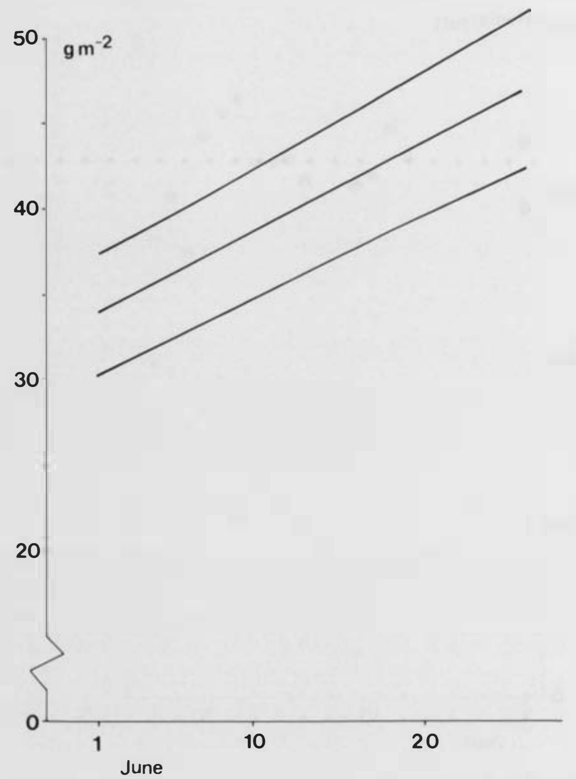


Fig. 61. Increase in biomass of *Eriophorum vaginatum* with 95 % confidence limits. $y = 0.52\ x + 33.29$. The Ottfjället reindeer range, 1979.

Table 9. Survey of information in the literature on above-ground biomass of Carex bigelowii and Deschampsia flexuosa g m^{-2} dry weight. Hardangervidda (H), Norway, and Kevo (K), Finland, 1969–1971. Materials from (H) were collected regularly from snow-melt to winter during three or two (willow thicket) vegetation periods. Mean values for all these collections were given. Materials from (K) are from August.

	$\bar{X}$	95 KI	Reference
Carex bigelowii			
Lichen heath (H)	1.0	± 0.2	Kjelvik & Kärenlampi (1975)
Dry meadow (H)	2.6	± 0.3	Wielgolaski (1975)
Deschampsia flexuosa			
Dry meadow (H)	6.2	± 1.3	Wielgolaski (1975)
Birch forest (H)	7.2	± 1.4	Kjelvik & Kärenlampi (1975)
Willow thicket (H)	4.7	± 0.8	Kjelvik & Kärenlampi (1975)
Birch forest (K)[a)]	0.1		Kallio (1975)
Wet birch forest (K)	2.6	± 1.6	Kjelvik & Kärenlampi (1975)

a) The species has a low degree of cover

As illustrated by Table 9, *D. flexuosa* has its largest biomass g m^{-2} in birch forest on Hardangervidda and smallest biomass in two Finnish plant communities. Kjelvik & Kärenlampi (1975) considered that this probably depended on better methods being used in the Norwegian investigation and that the area has a wetter climate and better soil.

The biomass in birch forest at Kevo was low, 0.1 g m^{-2}, since *D. flexuosa* had a low degree of cover. In the moist birch forest the biomass amounted to 2.6 g m^{-2}. The material was collected during August.

The values from the coniferous forest in the Ottfjället area, 3.4 g m^{-2}, did not diverge markedly from the cited values. This biomass was attained on June 24. Observations made suggested that growth was largest during June in my area of investigation.

The arctic tundra at Barrow, Alaska, has low summer temperatures, on average, 0.6°C during June, 3.7°C during July and 3.1°C during August. During the rest of the year the temperature is below 0°C (Tiezen 1978). The tundra is characterized by a short growing period, ca. 70—75 days, according to Weller & Cubley (1972) or ca. 87 days according to Bunnel et al. (1975). In addition, it has a long period of snow cover combined with permafrost. The latter factor hinders water and mineral uptake of the plants (Tiezen 1972; Dennis et al. 1978). This area becomes snow-free around June 15, about 7—10 days later than the normal for the Ottfjället area.

According to Tiezen (1972) there was more than 10 g m^{-2} living biomass that largely consisted of grass in the Barrow area in 1970, as that year was more or less snow-free around June 15. Of this amount *Carex aquatilis* had 5.4 g m^{-2} and *Eriophorum angustifolium* 2.7 g m^{-2}. According to Dennis et al. (1978), the biomass in the Barrow area at the corresponding time in 1971 was ca. 7 g m^{-2} at 1 or 2 days after snow-melt. Thus, from June 15 until the maximum production on August 5, under the condition that all the biomass was produced during the year, the daily increase of above-ground biomass was 1.85 g m^{-2} during 1970 and 1.46 g m^{-2} during 1971 (Dennis et al. 1978). In comparison with species investigated in the Ottfjället reindeer range, the above-mentioned species have, in all probability, a higher weight and consequently more biomass.

Eriophorum vaginatum has been subjected to biomass investigations at Eagle Summit in central Alaska (Andersson 1972). In this area the growing period in 1972 started on May 21. No details of biomass on this date are given. The first calculation was made on June 11 and then *E. vaginatum* had a living biomass of 3.81 g m^{-2}. On June 30 the biomass was lower, 2.58 g m^{-2}. *Carex* spp. and unspecified grasses were also included in the investigation on the same date. For *Carex* spp. the biomass on June 11 was 24.49 g m^{-2} and for grasses 1.63 g m^{-2}. These also had a lower biomass on the latter date. Andersson (op. cit.) had difficulty in explaining the reason and suggests the possibility that the cold weather in late June could have caused a reversal of production.

I have been unable to find material for comparison with *Juncus trifidus*. For *Carex bigelowii* there are data from Hardangervidda, Norway (Table 9). Fladvad et al. (1971) give a mean value of 613 g m^{-2} for the *Empetrum-Betula nana* heath in the Ottfjället reindeer range where graminaceous species only made up 23.6 g m^{-2}. The largest part of the biomass consisted of shrubs. For the *Carex bigelowii* heath the biomass was 384.4 g m^{-2}, of which 11.6 g m^{-2} consisted of grass. Among the seven graminids included in the investigation, *C. bigelowii* and *J. trifidus* were the most common, followed by *Deschampsia flexuosa*. The investigation by Fladvad et al. (1971) concerned biomass during July.

Observations in April 1979 indicated low mean weights per shoot and low biomass g m^{-2} for *C. bigelowii* within the Ottfjället area (Figs. 51 and 52).

Among the investigated species, *Eriphorum vaginatum* had the largest weight per stem and the largest biomass g m^{-2} (Figs. 60 and 61). In comparison with Eagle Summit in Alaska, the reindeer grazing on Ottfjället had more biomass g m^{-2} of *E. vaginatum* during and immediately after the snow-melt.

D. flexuosa had considerably lower weight per stem and less biomass g m^{-2} during the period May 21—June 22 than the above-mentioned species (cf. Figs. 57 and 58). However, it is regarded as one of the most important reindeer grazing species as it remains green for a long period, even under the snow. According to H. Persson (1980), it was found in early October 1973 in the pine forest at Jädraås with a biomass of 6.0 g m^{-2}.

7. Nutrient contents of some reindeer grazing plants

7.1 Method and material

The animals were kept on the Ottfjället reindeer range from early spring to autumn. During the 1970's the reindeer were driven on to the range in mid-April and allowed to graze there until mid-October. Consequently, it is important to know the nutrient contents of some of the grazing plants in the spring and in the autumn. The most important factors are the contents of protein, calcium and phosphorus in plants used for spring grazing. Calcium is important for animal growth and milk production of the females, and phosphorus is important for pregnancy (Steen 1966).

A number of species were collected for chemical analysis. The analyses were made upon one sample per species. Some of the species were collected both in the spring and in the autumn from the same plant communities.

Carex aquatilis was collected from a bay of Lake Stora Nulltjärn, and *Comarum palustre* from poor fens in the Lake Nulltjärn area. Samples of *Eriophorum vaginatum* and *Scirpus caespitosus* were taken from the same fens. *Menyanthes trifoliata* was collected along and in the small lake near the frost-heaving soils at Nulltjärnsbacken. This small lake is surrounded by fens. *Deschampsia caespitosa, D. flexuosa*, and *Vaccinium myrtillus* were collected in a forest area at Nulltjärnsbacken. The above-mentioned species were collected within sub-area A (see Fig. 2). *Carex bigelowii, Festuca vivipara*, and *Juncus trifidus* were collected within sub-area B (Fig. 2) on the mountain. This area did not contain species that had more specific demands on their habitat. *Carex bigelowii* was mainly collected from *C. bigelowii* heath, *Juncus trifidus* mainly from wind-swept patches and heath areas, and *Festuca vivipara* from south-exposed slopes of *C. bigelowii* heath and *Vaccinium myrtillus - Empetrum* heath. The *Molinia caerulea* material was collected from a small *Molinia caerulea* meadow to the north of station 3. *Selaginella selaginoides* grew in a small fen nearby.

According to Strömberg (1961), the area in which the samples were collected belongs to the Särvskållan sandstone region which is deficient in Ca, P, Mg, and Fe but which contain some K. The Särvskållan sandstone consists of quartzites, arkoses and mica schists, all being rocks rich in quartz but poor in lime and easily weathered material. Särvskållan contains seams of Ottfjäll-dolerite that are poor in K but rich in Ca.

The analysis of the spring material concerned green and yellow-green shoots or leaves. The material was collected between May 14—June 14, 1978. The autumn material was collected on 6 October 1978 and was of a slightly different character. In the case of *Carex bigelowii* the sample consisted of newly initiated yellow-green rhizomes and small green shoots that formed during the autumn (cf. Fig. 24, 3.2.4). The sample of *Comarum palustre* contained the entire plant but old withered parts were removed. Thus, part of the root system was also included. According to the Lapps, these roots are an important feed for reindeer and moose during the autumn. The sample of *Deschampsia flexuosa* consisted of green leaves. As regards *Eriophorum vaginatum*, new green-yellow shoots that emerge during the autumn were collected (Fig. 32a, 5.2.8). The sample of *Festuca vivipara* largely contained green leaves but also some withered grey-brown leaves that were difficult to separate from the rest. The sample of *Juncus trifidus* consisted of green shoot bases, which are initiated during the autumn (Fig. 34, 5.2.11). The *Molinia caerulea* material consisted of lower inter-nodes and small light-green leaves (Fig. 39, 5.2.13).

The plant analysis were conducted at the National Laboratory for Agricultural Chemistry at Ultuna, Uppsala, as regards sugar, and at Grimsö research station as regards crude protein, P, Ca, Mg, K, Na.

An atom-absorbtion spectrophotometer (Perkin-Elmer) was used for the analyses of magnesium, calcium, potassium, and sodium. Nitrogen and phosphorus were analysed in an automatic analyser: phosphorus with ammonium molybdate and ascorbic acid, nitrogen as ammonia according to the indophenol method. Two replicates of each plant sample were analysed at the Grimsö research station. Tables 10 and 11 give mean values of these analyses. The agreement between the replicates was very good. The sugar content in the collected material was determined in single analyses and provided orientating data.

Nitrogen is given as crude protein (= 6.95 x N-content) and contains, according to Courtright (1959), different amino acids and other nitrogen-containing substances. The crude protein content is given in the section on Results as the protein content of the dry weight (DM).

7.2 Results and comparison with other investigations

The value of comparisons between the analysis of the different species is decreased slightly since the samples were not collected on the same date. To do so was found to be impossible since, for example, the *Carex bigelowii* material took five hours for two people to collect. Nevertheless, values obtained should reflect the species differences fairly well.

The results from the spring and the autumn material are given in Tables 10 and 11, respectively. The samples are compared with Kellgren & Nilsson (cit. by Frödin 1952), Sjörs (in Malmer & Sjörs 1955), Russian data (cit. by Courtright 1959), data

Table 10. Chemical composition of a number of plant species in spring-grazed vegetation, only young, living shoots have been sampled. Samples from the area of investigation, May - June 1978. Places of collection: 1. below tree limit (A in Fig. 2); 2. above tree limit (B in Fig. 2).

			Contents in % of dry weight							
Species	Places of collection	Date of collection	Crude protein	Sugar	P	Ca	Mg	K	Na	Metals
Carex aquatilis	1	05-28	8.35	8.97	0.23	0.19	0.14	1.31	0.07	1.71
C. bigelowii	2	05-14	8.12	2.35	0.18	0.46	0.10	1.34	0.08	1.98
Comarum palustre	1	06-04	10.38	9.20	0.19	0.41	0.15	1.14	0.09	1.79
Deschampsia caespitosa	1	06-10	13.39	13.60	0.20	0.31	0.16	1.21	0.08	1.76
D. flexuosa	1	06-10	10.68	13.50	0.20	0.22	0.09	1.68	0.06	2.05
Eriophorum vaginatum	1	06-10	8.72	9.30	0.15	0.18	0.11	1.21	0.07	1.57
Festuca vivipara	2	06-14	5.24	5.60	0.11	0.26	0.05	0.66	0.06	1.03
Juncus trifidus	2	06-12	12.36	8.99	0.18	0.24	0.12	1.37	0.07	1.80
Menyanthes trifoliata	1	06-11	18.21	15.60	0.37	0.59	0.20	1.25	0.10	2.14
Molinia caerulea	2	06-11	9.28	5.70	0.17	0.19	0.11	1.07	0.06	1.43
Scirpus caespitosus	1	05-14	6.00	8.30	0.11	0.31	0.08	0.72	0.08	1.19
Vaccinium myrtillus	1	05-27	6.56	5.40	0.15	0.60	0.08	0.39	0.06	1.13

Table 11. Chemical composition of a number of plant species in autumn-grazed vegetation. Samples from the area of investigation, 6 October 1978. Places of collection: 1. below tree limit (A in Fig. 2); 2. above tree limit (B in Fig. 2). a) newly initiated shoots, b) above-ground plant parts, c) shoot base. d) entire plant.

		Contents in % of dry weight							
Species	Places of collection	Crude protein	Sugar	P	Ca	Mg	K	Na	Metals
Carex bigelowii a)	1	8.72	10.00	0.18	0.31	0.15	1.42	0.07	1.95
Comarum palustre d)	2	6.28	8.82	0.14	0.65	0.19	0.45	0.08	1.37
Deschampsia flexuosa b)	1	9.40	21.40	0.13	0.23	0.08	1.13	0.02	1.46
Eriophorum vaginatum a)	1	5.24	12.15	0.18	0.36	0.14	1.46	0.13	2.09
Festuca vivipara b)	2	4.41	3.56	0.09	0.42	0.06	0.23	0.08	0.79
Juncus trifidus b)	2	4.60	6.44	0.12	0.63	0.13	0.61	0.08	1.45
Molinia caerulea c)	2	6.00	2.92	0.11	0.18	0.07	0.64	0.06	0.95

Table 12. Literature data on protein contents of some species in the early green grazing and in summer grazing (at the time of the quantitative maximum). Percent of dry matter. a) in spring-grazed vegetation, b) in summer-grazed vegetation, c) date not given, d) in September. Values in Sjörs and Skogland are converted from nitrogen contents, using 6.25 as conversion factor, see also text.

Species	Kellgren-Nilsson (from Frödin 1952)	Sjörs (from Malmer & Sjörs 1952)	Courtright, 1959 (from Russian literature)	Rydberg (1960 from literature)	Persson (1963)	Steen (1966)	Skjenneberg-Slagsvold (1968 from Karev)	Skogland (1970-1973)	Flower-Ellis (1971)
Carex aquatilis	16.06[c]		10.54[c] 11.62[c] 9.50[c]						
C. bigelowii								7.3[a] 10.9[a]	
Deschampsia caespitosa	8.20[c]					5.9[a]			
D. flexuosa	8.46[c]		10.15[c]	10.16[c] 13.3[c]		8.6[a] 9.4[b]			
Eriophorum vaginatum							17.0[c]		
Juncus trifidus								8.1[a]	
Menyanthes trifoliata	15.14[c]	11.25[b] 13.75[b] 15.60[b]	13.4[b] 15.7[c] 9.9[c] 13.7[c] 13.1[c]	17.9[b] 6.3[b]	25.0[a] 13.3[b] 10.5[b]	17.1[b]	15.0[c]		
Molinia caerulea	15.30[c]				17.4[a] 8.4[b]				
Scirpus caespitosus	16.70[c]	8.75[b] 7.51[b] 9.38[b] 7.50[b] 10.00[b] 8.75[b]				5.3[a]			
Vaccinium myrtillus									5.44[d] 6.88[d] 6.63[d] 7.31[d]

cited in Rydberg (1960), S. Persson (1963), Steen (1966), Karev (cit. by Skjenneberg & Slagsvold 1968 with no year of publication of Karev's paper), Flower-Ellis (1971), and Skogland (1970—1973). The literature data on protein contents of various species are given in Table 12. Values given in the Russian investigations are unreliable in the comparison as in most cases no information is given on either date of collection or the part of the plant analysed. This also applies to values of Kellgren & Nilsson (1893 cit. by Frödin 1952). The material was probably collected during the summer. A review of values obtained from papers mentioned above is given below but often without repetition of years of publication already given (see also Table 12).

Carex aquatilis. As data are generally not given in the above-mentioned references it is difficult to directly compare their values calculated from spring samples taken from the Ottfjället reindeer range. The Ottfjället samples contain 8.35 % crude protein of DM. Frödin (1952), based on the investigations of Kellgren & Nilsson (cit. by Frödin 1952), considered that *C. aquatilis* was the most valuable graminaceous species with protein contents as high as 16.06 % of DM. Karev found that the species contained 6.4 % protein of DM during the winter. Unfortunately, there is no information on which part of the plant was analysed. Other Russian sources mention 10.54, 11.62, and 9.50 % of DM, but information on date, part of plant analysed and plant community are not stated. The latter data probably originate from summer material. Temnoev (1939, cit. by Courtright 1959) found that a large part of the leaf mass of *C. aquatilis* remained green during the winter. Florovskaya (1939, cit. by Courtright 1959) analysed brown withered leaves as well as green leaves of *C. aquatilis* collected during the winter. These analyses showed that green winter leaves contained more than withered winter leaves. In comparison with green summer plants, the protein content was lower in the green winter leaves. Figures on the protein content were not reported.

Carex bigelowii. The protein content of the spring sample was 8.12 % of DM. The exceptionally low sugar content (2.35 %) is difficult to explain and there is not material for comparison. The content of the mineral elements together amounted to 1.98 % of DM. Potassium and calcium made up the largest proportions. According to Skjenneberg & Slagsvold (1968) this species is one of the most nutrient-rich of the *Carex* genus. Skogland reports higher protein contents if the species is collected under snow cover than if taken from an area without snow. His analyses concerned samples taken during May. Relatively high protein values were found in the following species from Ottfjället: *Comarum palustre, Deschampsia caespitosa, D. flexuosa*, and *Juncus trifidus*. In all four species the protein content exceeds 10 % of DM and the mineral content is also relatively high (see Table 10). Material for comparison is available for *C. palustre*. S. Persson (1963) reports 17.1 % protein in spring samples, 8.2 % in summer samples and 7.1 % in autumn samples. All samples were collected within the Serri Lapp community. For *D. caespitosa* one value is from Kellgren & Nilsson (cit. by Frödin 1952) and is probably from a summer sample. Steen (1966) reports 5.9 % of DM for spring samples (Table 12).

Deschampsia flexuosa. The spring values from Ottfjället amounted to 10.68 % protein of DM. Russian investigations report 10.15 % protein of DM for *D. flexuosa*. Karev has a value of 6.8 % of DM for *Deschampsia*, but without stating which *Deschampsia* species was sampled. The protein content in material collected by Kellgren & Nilsson (cit. Frödin 1952) was 8.46 % for *D. flexuosa*. Terentiev (cit. by Rydberg 1960) gives 10.16 and 13.30 % of DM for the same species. Steen (1966) reports lower protein content in his spring samples which contain a mixture of green living leaves and withered leaves.

Material collected in the spring from the Serri Lapp community, Jokkmokk, contained 10.2 % protein of DM. Material collected during the summer had varying values, namely: 14.1 (1959), 6.7 and 9.0 % (1960). The protein content of autumn samples in 1960 amounted to 7.7 % and 1962 to 6.7 % of DM. The samples were collected from scattered places within the forest area belonging to the Lapp community (S. Persson 1963).

The calcium and phosphorus contents of *D. flexuosa* largely concur with summer material analysed by Steen (1966), whereas his spring material had higher levels of calcium and lower levels of phosphorus than material from Ottfjället. The highest potassium content of all analysed species from the reindeer grazing area on Ottfjället was in *D. flexuosa*.

Eriophorum vaginatum. In the spring sample the protein content was 8.72 % of DM and the sugar was 9.30 %. The content of minerals was lower than in *D. flexuosa*. *E. vaginatum* had the lowest calcium content of the analysed species from Ottfjället. Chapin et al. (1980) report low but uniform content of calcium in the species (June 21 = 0.017 mg/kg DM, August 24 = 0.015 mg/kg DM). Karev reported a protein content as high as 17.0 % of DM, but without stating the date of collection. In samples collected during the winter the corresponding value was 7.9 %.

Festuca vivipara. Table 10 shows that this species had the lowest contents of protein and magnesium in comparison with the other spring samples. Contents of the other elements were also low.

Juncus trifidus. This species had a high protein value, 12.36 % of DM. The mineral content was slightly lower in *J. trifidus* than in *C. bigelowii* but considerably higher than in *F. vivipara*. According to Skjenneberg & Slagsvold (1968), *J. trifidus* has a high content of protein but no level is stated. Skogland (1970—1973) reports 8.1 % of DM for material collected from beneath the snow in May.

Menyanthes trifoliata. This species had the highest protein content. The spring sample had 18.21 % of DM. This is higher than the 17.10 % of DM at the time of quantitative maximum reported by Steen (1966). Kellgren & Nilsson (cit. Frödin 1952) reported 15.14 % of DM for *M. trifoliata* but the date of collection is not given. According to Sjörs (Malmer & Sjörs 1955), the nutrient content varies depending on the plant community in which the species is collected (Table 12). Rydberg (1960) reports 6.3 to 17.9 % of DM despite both samples being collected on the same date, July 1, in Tuolpakka, Vittangi Lapp community. It is not stated whether the samples were collected from different places within the area of the community. Russian investigations also mention varying but relatively high percent values: 9.9—15.7, with unspecified dates of collection and plant community, and on August 12, 13.4 % of DM.

In other respects this species has higher values for minerals and sugar than most of the species analysed from the Ottfjället reindeer range. In this sample the calcium content, 0.59 % of DM, was the same as stated by Steen (1966) for a summer sample, whereas the phosphorus content was higher in the analysed sample from Ottfjället. The highest calcium content was found in material collected by Sjörs (op. cit.), with variations in the range 0.30—1.30 % of DM.

S. Persson (1963) analysed material of *M. trifoliata* from the spring 1960 and the summer of 1959 and 1960, both on above-ground and underground parts. In the case of the underground parts analyses were made of autumn-collected samples (autumn 1962). The protein value was considerably higher, 25 % of DM, during the spring (collected during June 1—22). The protein content decreased during the summer (collected during August 1—20) to between 13.3 and 10.5 % of DM. These values concerned above-ground parts. For the rhizomes a change occurred in the opposite direction, from 6.4 % during the spring, slightly less during the summer and 9.4 % during the autumn (September 17—October 20). No material from above-ground parts was analysed during the autumn.

Molinia caerulea. The material collected in the spring contained 9.28 % protein of DM. Contents of sugar and minerals were relatively low in comparison with the other species analysed (Table 10). According to Kellgren & Nilsson (cit. Frödin 1952) this species has a protein level of 15.30 % DM. The analysis probably concerned leaves collected at the time of quantitative maximum. According to S. Persson (1963) material collected during the spring from Serri Lapp community contained 17.4 % protein of DM, whereas material collected in the summer had 8.4 % and material collected in the autumn 2.8 %.

Scirpus caespitosus. A slight difference in protein content of this species can be seen in comparisons between material from Ottfjället and material from Mittådalen and Tännäs Lapp community collected by Steen in 1962. The material from Ottfjället contained 6.0 % protein of DM whereas the material from the two above-mentioned Lapp communities (collected during May) had 5.3 % protein of DM. Steen (1966) mentions even lower contents of calcium and phosphorus.

Material collected by Sjörs (Malmer & Sjörs 1955) from a calcareous extremely rich fen in Jämtland, contained 8.75 % protein of DM and a slightly higher value (10.0%) was found in material from an intermediate fen in Dalarna. The material from Jämtland was collected on July 13 and from Dalarna on 6—11 August 1953. Kellgren & Nilsson (cit. Frödin 1952) present the highest level, 16.7 % of DM for this species but without specifying the date of collection.

The sugar content in the spring sample from Ottfjället contained 8.3 % of DM and the mineral content was relatively low.

Vaccinium myrtillus. Green shoots on which leaves had not yet developed were analysed. The protein content was not particularly high, 6.56 % of DM. The sugar content was the lowest found in the analyses with the exception of the particularly low content in *Carex bigelowii*, mentioned above. The content of minerals varied widely, the highest content being of calcium and the lowest of sodium (and magnesium).

According to Flower-Ellis (1971) the nutrient content of current-year shoots of *V. myrtillus* varies depending on the position of the shoot in the stand. Shoots formed during the growing period and collected in September at Hamra, to the south of Stockholm, showed the following tendency from the periphery in towards the centre of a stand: 5.44, 6.88, 6.63, 7.31 % protein of DM. The same increase inwards was also found for phosphorus and calcium.

Since a number of species were also collected during autumn from the Ottfjället grazing area, a comparison can be made between analytical results from spring and autumn samples. The following observations were made (cf. Tables 10 and 11).

Carex bigelowii. The protein content of 8.12 % of DM in the spring sample had increased in the autumn sample. The remarkably low sugar content had increased considerably. The level of phosphorus was unchanged but the content of calcium decreased and those of magnesium and potassium increased.

Carex aquatilis. No plant analysis was made of autumn material. Steen's analyses of autumn-collected rhizome material gave contents of 5.2 % protein, 0.26 % calcium and 0.11 % phosphorus of DM.

Comarum palustre. The spring and autumn samples were collected from the edge of the same fen. The protein content had decreased considerably by the autumn. Calcium and magnesium were higher in the autumn sample, phosphorus and potassium were lower, and sodium almost unchanged.

Deschampsia flexuosa. The protein content decreased from 10.68 % to 9.4 % of DM, whereas the sugar content increased considerably. Among the minerals, only calcium increased slightly although the increase was negligible. The contents of the other minerals were lower in the autumn sample.

Steen reports that green basal parts collected during the autumn from Gällivare Lapp community had the following contents: protein 7.1 % of DM, calcium 0.24 % and phosphorus 0.13 % of DM. Withered stem parts, collected on the same occasion and in the same area, had contents of only 3.7 % protein, 0.09 % calcium and 0.09 % phosphorus of DM.

Eriophorum vaginatum. Both sugar and minerals had higher levels in the autumn material whereas the content of protein was lower.

Festuca vivipara. As also in the analyses of the spring sample, the autumn sample showed that this species is a poor grazing plant with regard to nutrients. The autumn material had the lowest protein value of the species analysed. The material collected on October 6 had higher content of calcium and a slightly higher content of magnesium and sodium than the spring material, which was collected on June 12 in the same year. However, potassium had decreased from 0.66 to 0.23 % of DM. The phosphorus content was also slightly lower in the autumn sample.

Juncus trifidus. The protein value was considerably lower during the autumn. This also applied to sugar, although the reduction was not as large as for protein. Among the minerals the increase of calcium was most marked. Magnesium and sodium showed a tendency to increase whereas phosphorus and potassium had lower contents in the autumn material.

Molinia caerulea. During the autumn the shoot bases (cf. 5.2.13) had low content of sugars and minerals. Comparison between autumn and spring material largely lacks relevance as the latter material contained both shoot bases as well as completely green shoots and leaves that had developed up to the time of sampling on June 11, whereas the autumn material had a negligible number of leaves.

7.3 Discussion and summing-up of results

In the analyses from the Ottfjället area it was important to know the nutrient contents of the plants, particularly the plants used in the spring grazing. The spring is the time of year when the reindeer may be in poor condition following a severe winter. The supply of forage during the late part of the winter may be too little for the needs of the reindeer. There may be several reasons for this, e.g., ice formation, snow cover or poor availability of grazing material. If this occurs the reindeer start to utilize their reserves, initially starch in muscular tissue and later reserve body fat. In situations of general lack of feed, proteins are also used and will be primarily taken from muscular tissue (S. Persson 1966).

It is generally considered that reindeer exist during the winter mainly on lichens, which are reported by S. Persson (1963) to have low but constant contents of protein. *Cladonia* spp. have protein content less than 3 % of DM whereas *Stereocaulon paschale* has slightly more than double that content. *Cladonia* spp. are also poor in minerals and vitamins are almost completely lacking (Karev 1956, Kursanov & D'yachkov 1945 cit. by Courtright 1959). The most important aspect of the lichens is their content of relatively easily-soluble carbohydrates, and also that the protein content remains constant throughout the year (S. Persson 1963).

The summer grazing seldom causes any particular problems but naturally it is important that the grazing plants are of good quality as proteins, minerals and fat are stored during the snow-free period, or as long as the reindeer can find green forage.

In conventional chemical plant analyses, values are generally obtained for protein, crude fibre, N-free extract, calcium and phosphorus. The material from the reindeer grazing range at Ottfjället had not been analysed for fat, and of the carbohydrates the analyses have only concerned sugar (inredos). Unfortunately there are few details in the literature that can be used in comparisons of sugar content. A high sugar content should increase the value of a plant as a species for grazing as to some extent the sugar should give the reindeer extra energy. According to Warren Wilson (1957), arctic species have high sugar contents.

Tables 10 and 11 contain information on contents of protein, sugar and various minerals in a number of plants used by the reindeer for grazing. These contents have been compared with data in the literature.

A disadvantage of comparisons between analytical values and which detracts from their reliability is that often there are no details of the phenological development of the plant at the time when the plant parts are collected for chemical analyses. The nutrient content of plants will vary depending on the time of collection and from which plant community the species originates (Sjörs in Malmer & Sjörs 1955; Wielgolaski & Kjelvik 1973). Sjörs (op. cit.) found that the protein content of *Menyanthes trifoliata* increased from 11.25 % of DM in material from a poor fen to 13.75 % in material from an intermediate fen, and 15.60 % in material from calcareous extremely rich fen.

Among the grazing species analysed from Ottfjället, *Menyanthes trifoliata* is superior as a grazing plant from the nutrient aspect. The area where the material was collected is surrounded by poor fens. The Ottfjället material has lower protein contents than material from Serri (S. Persson 1963), where the spring material contained 25 % of DM. As no information is available about the condition of the growth site, it is difficult to compare the two analytical results. The species has high values for all nutrients analysed, with the exception of calcium and potassium.

According to Bunnel et al. (1975), the protein content of monocotyledons is highest about 10 days following the start of the growing period. It decreases as autumn approaches. This also applies to the contents of phosphorus and potassium, whereas the calcium content increases fairly continuously from spring to autumn without a peak. Chapin et al. (1980) report the same for *Eriophorum vaginatum*.

The relatively high content of protein in *Juncus trifidus* (12.36 % of DM) collected on 12 June 1978, might indicate that growth has started and that the protein content has reached its highest value. The only material for comparison is from Skogland (1970—1973) who reports 8.1 % of DM for material collected during May from beneath snow cover.

Comarum palustre, Deschampsia caespitosa, D. flexuosa, and *Juncus trifidus* also belong to the most valuable plants for spring grazing with relatively high protein contents.

The protein content decreased towards the autumn in all species collected within the Ottfjället area except for *Carex bigelowii.*

In three of the analysed species from Ottfjället, *Carex bigelowii, Deschampsia flexuosa*, and *Eriophorum vaginatum*, the sugar content was higher in the autumn material. *D. flexuosa* had the largest increase. Its high content of sugar may be an advantage as the reindeer change their diet during the autumn months. According to Åhman (1977), a relatively high sugar content in grazing plants may be favourable for the adjustment of rumen microorganisms to a new grazing plant. Nevertheless, if the sugar content is too high it will cause disturbances to the fluid balance. This is an important factor to bear in mind when manufacturing supplemental feeds for reindeer (Ekelund 1966; Åhman 1977). McCrown (1978) reports that the daily fluctuations in sugar are not large and that the sugar content is lowest at the time of the quantitative maximum and highest at the start of the vegetation period. Selsjord (1968) reports 18.4 % sugar (saccarose) for *Deschampsia flexuosa* that had grown in a shaded locality, and 25.3 % in material collected from a sunny locality in late August (cf. section 5.2.7).

In most of the plants the contents of phosphorus and potassium were lower in the autumn than in the spring samples. However, calcium content was higher in the autumn sample, with the exception of *Carex bigelowii* and *Molinia caerulea.* The magnesium content was also higher in the autumn samples for most of the species. The sodium sample generally remained unaltered.

Festuca vivipara is without doubt the poorest of the analysed grazing plants with low contents of protein, sugar and minerals.

Festuca ovina is not as common in the Ottfjället area as *F. vivipara.* However, Steen (1966) reports that it has a considerably higher nutrient value than *F. vivipara*. During the autumn the following contents have been reported: protein 7.6 % of DM, calcium 0.65 % of DM and phosphorus 0.15 % of DM.

As mentioned earlier, the nutrient content of plants varies depending on the time of year when the material is collected as well as on the type of plant community. The ability of the plants to take up minerals from rock and soil is also important, as well as the soil's content of minerals. The rapid increase of mineral concentration in the soil following snow-melt may to some extent depend on the rapid increase of minerals in the melt-water (Rueslåtten & Jørgensen 1978). The ability of the plant to store nutrients in roots or over-wintering plant parts is also important.

8. Discussion of environmental factors, early growth, production, and grazing

Germination and growth of plants depend (besides on internal factors) on several external factors such as light, temperature, water, and nutrients. Under natural conditions the abiotic factors are frequently interconnected, and there are consequently difficulties in separating their influences on the plant. In addition, there is interaction between different species, or individuals of the same species, or between parts of an individual, ramets (Harper 1977). In habitats where snow persists far into the spring, the duration and depth of the snow are important. A snow cover has many effects. It influences the length of the growing season, it supplies the area with melt-water, and partly protects the vegetation from the influence of animals (Holway & Ward 1963). It also influences the light and the temperature conditions.

8.1 Influence of snow on light conditions

Light penetration of the snow cover influences the plant growth. Richardson & Salisbury (1977) investigated this penetration with special instruments. The ability of light of different wave-lengths to penetrate the snow was found to be different. Consistency and density of the snow influenced this ability. In ideal conditions such as high insolation, low albedo, etc., the light penetrated the snow down to a depth of two metres. The experiment demonstrated that green light (250 nm) had the least difficulty in penetrating the snow. The authors made the interesting observation that some young growing plants had a reddish hue when they emerged. I have made the same observation for *Comarum palustre* and *Polygonum viviparum*.

No light measurements were made in the present investigation. The above-mentioned experiments of Richardson & Salisbury (1977) provide evidence that light actually has the ability to penetrate snow and to influence the development of plants.

8.2 Influence of snow on temperature conditions

The soil temperature at the surface during the winters when the investigations were made remained above 0°C, apart from a few occasions. Temperatures between 1° and 3°C were found in the rhizosphere of the plants. Salisbury et al. (1973) found that if there is no snow cover until late autumn the soil temperature in layers near the surface decreases a few degrees below 0°C while deeper soil layers remain warmer. Later, when a snow cover has formed, warmth is spread upwards from the lower soil layers and influences the temperature positively. The lower snow layers and the upper soil layers keep temperatures of ±0°C throughout the winter until the snow starts to melt in the spring.

A snow cover thus influences the soil temperature, obviously of importance for the growth of plants. In extreme years with little snow the soil temperature should be low (if air temperatures are low), and the soil will freeze to a deeper level.

Wind-swept patches are often almost free from protecting snow cover during the winter. The soil temperature is low and the soil is frozen. No measurements of frost depth in such areas have been carried out, but in places where holes have been dug it was possible to observe a considerable layer of frozen soil.

Harris (1974), working at Okstindan, Norway, observed that the soil freezes faster and the frost penetrates deeper on snow-free soil than on soil with a snow cover. On the other hand, he found that the soil temperature in May at a depth of 5 cm rose above 0°C earlier on snow-free soil. At low air temperatures, however, the soil froze repeatedly down to 5 cm. During the summer the wind-swept patches are dry as the melt-water flows away.

Earlier it was mentioned that the air temperature below the snow in so-called sub-nival air spaces is 0°C (Coulianos & Johnels 1962).

8.3 Influence of environmental conditions on the early growth

Miller et al. (1976) list four critical environmental factors that influence photosynthesis, namely, insolation, air and soil temperatures, and vapour density. The temperature optimum for alpine shade plants is between +8° and +15°C (cf. Schroeter 1926 p. 971).

Alpine shade-plants (and lichens) have a particularly low threshold temperature value as regards photosynthesis (cf. Schroeter op. cit.). For vascular plants this temperature is —15°C and for lichens —20°C. They can even assimilate with ice formation in the cells (cf. Schroeter op. cit. p. 971). This depends on the high sugar content of the cell sap, which lowers the freezing point. The high amounts of sugar established by photosynthesis at low temperatures are not converted to osmotically inactive starch. The sugar has a depressing effect on the freezing point and as a result this increases the absorption of soil water (cf. Schroeter op. cit. p. 971).

According to Sørensen (1941), arctic plants begin their development when the temperature of the soil surface is around or slightly above 0°C. The temperature amplitude may be large at the soil surface during the spring, but Sørensen (op. cit.) considers that night frosts do not prevent the plants from utilizing the positive day temperatures. He considers that germination and growth of a plant are influenced more by soil temperature than by air temperature.

Several vascular plants in Sweden are active also when the soil is frozen and the soil temperature is around 0°C. Sjörs (1971) reports that *Eriophorum vaginatum* regularly flowers under such conditions. I have also observed this on several occasions within the area of investigation. Species on the Siberian tundra can even absorb water from partly frozen soil (Dadykin 1950, cit. by Larcher 1973).

As measurements of frost depths were only made during one year it is difficult to present any reliable conclusions on the importance of frost depth for the development of the investigated species. The frost depth was negligible in the plant communities where the measurements were made. In other types of plant communities such as those on wind-swept patches, in exposed areas of heath, and in fens in the forest which early loose their snow cover, frozen soil was found on those occasions during the early spring when the shoot development of the plants was studied.

Species which grow on wind-swept patches can probably photosynthesize early, provided that the sun shines and the air temperatures increase during the day. *Juncus trifidus* is such a species. It could be expected that the green shoot bases observed during the autumn would not survive the winter cold and the varying spring conditions. However, my investigations in 1979—80 and observations in earlier years proved their survival and that they even had a positive growth during the winter. Westergren (1902) observed that *J. trifidus* in the Sarek mountains was fully developed already during the snow-melt.

According to Webber (1978), the growth of arctic species is related to the disappearance of the snow cover and the frost leaving the soil. Tiezen (1972, 1974) observed little if any growth in arctic species under the snow when the soil temperature was below 0°C. Growth first started when the melt-water percolated through the snow mass. In connection with this, the soil temperature increased sharply. Both Webber's and Tiezen's investigations were, however, conducted on arctic tundra with permafrost.

According to my own observations, growth increases as soon as snow-melt starts. The growth rate then increases as the snow-melt continues. During the spring period, the greatest growth of the studied species occurred immediately after the snow-melt.

During the years of the investigation within the Ottfjället reindeer range the area became snow-covered fairly late and the depth of the snow was fairly normal. An exception was early 1976 with extremely deep snow. With a snow cover between 4 and 5 m, it was impossible to investigate the development of the plants and their reaction to the extreme pressure of such a thick snow cover. In this area a Grant temperature recorder, located on a south-exposed slope, was destroyed by the heavy and compact snow. However, the plants growing on the slope were not damaged although they developed late. They did not grow from the time of the observation in mid-November until mid-June. The last occasion possible to make an observation was in late December, a cold month with a temperature deficit of 4°C. Despite this, soil temperatures remained at ±0°C beneath a ca. 20 cm snow cover. No growth took place during this month. Around June 18 the leaves of *Deschampsia caespitosa* and the small shoots of *Vaccinium myrtillus*, for example, were completely intact when the snow cover melted. These species occurred on the abovementioned south-exposed slope. However, they grew insignificantly during the actual period of snow-melt.

8.4 Production conditions and grazing

Both qualitative and quantitative production within a plant community are important to the reindeer.

Of the four species included in the biomass investigations, *E. vaginatum* had the largest biomass m^{-2}. Within the sub-area of investigation denoted A (Fig. 2) there were numerous *E. vaginatum* fens and wet parts of these became early snow-free in the years of investigation. There were also other grazing plants such as *Eriophorum angustifolium, Rubus chamaemorus*, and *Scirpus caespitosus.* Along edges of fens were found *Comarum palustre* and *Menyanthes trifoliata*, the latter with a high protein value, 18.21 % of DM (Table 10). The *E. vaginatum* fens are important particularly during the period of snow-melt and during the first part of the snow-free period for non-calving reindeer. Fens within sub-area A and in the frost-heaving soils at Nulltjärnsbacken (map in Warenberg 1977) were visited by reindeer during the late winter on those occasions when the reindeer were still on the range. As regards quality, *E. vaginatum* does not represent the best forage (Table 10) but quantitatively it is valuable. The fens also provide the reindeer with a valuable nutrient supply of rhizomes, for which they willingly dig. The plant communities that contain rhizomes for grazing are important, particularly if they contain *Menyanthes trifoliata* (Skuncke 1958).

Wein & Bliss (1974) observed that *Eriophorum vaginatum* fens in Alaska and the Yukon territory have a higher production during the spring than other plant communities. These fens are important for the caribou as it visits them during the calving period. Johnson (1969) found that *E. vaginatum* tufts thaw earlier than other species during the spring because the water runs off them so that they receive more radiation energy. According to Chapin et al. (1980), *E. vaginatum* stores nitrogen in the over-wintering leaves. They consider that this implies that the species can start its development early in the spring. In Atkasook, Alaska, this species has high concentrations of phosphorus and nitrogen during the spring. Fens with *E. vaginatum* are preferred by caribou and ptarmigan (Batzli & Brown 1976).

Apart from the fens, sub-area A is characterized by an undulating topography with dominating hills. The south side of these hills rapidly became snow-free during the years of investigation. Here the reindeer can find *Deschampsia caespitosa, D. flexuosa*, and *Vaccinium myrtillus. D. caespitosa* had one of the highest protein values of the analyzed species. According to Davy (1980), this species is mycorrhiza-forming. Such species have a greater ability to take up nitrogen (cf. 5.2.3) than species which lack mycorrhiza (Miller & Laursen 1978). The low-frequent *D. flexuosa* was also one of the best species as regards quality. This may be more important than indicated by the quantity. It has the lowest biomass m^{-2} of the investigated species but has one of the highest values with regard to content of minerals, as well as a high value for sugar.

Pine forest has relatively good availability of *Stereocaulon paschale* which, according to Steen (1966), has an energy value of 3.32 Mcal per kg DM. This lichen is of importance when the reindeer enter the range in April.

Some of the reindeer grazing on snow-free areas on the range were given supplemental feed during the most critical part of the winter and early spring. They were in good condition when they entered the range, as demonstrated by a satisfactory calf weight (Franzén & Bjärvall 1978).

The area in which the calving took place was within sub-area B (Fig. 2). The reindeer were taken to the range in mid-April (cf. 2.2). Observations during April 1979 indicated low mean weight per shoot and low biomass in g m^{-2} of *Carex bigelowii* within the investigated area. During May there was a marked increase (Fig. 52, 6.2). No investigations of *Juncus trifidus* biomass were made until late May when it was calculated to have 3.3 g m^{-2}. The production of these two species during May must be important as most of the calves are born during this month. The female reindeer do not move over long distances during the calving period, preferring to stay within a limited area for some weeks following calving. A female of normal weight (ca. 70 kg) has a feed requirement of 4.1 Mcal per day during the winter (Steen 1966). The energy requirement increases during the spring and amounts to 8 Mcal during the summer. The grazing available in the form of *Carex bigelowii* and *Juncus trifidus* should be considered of value (cf. 6.2). They early become available for grazing primarily on open south-exposed terrain and on wind-swept patches. However, ice crust may decrease the availability. Nevertheless, this ice crust can be changed to a coarse, granular loose type of snow by the warmth of the sun during the day (Eriksson 1976). In that way the reindeer can dig down to the new shoots, which have higher protein contents than the lichens which primarily consist of *Cetraria nivalis* and *Cladonia mitis* within the area above the tree limit.

Observations at Dörålen, Norway (E. Lyftingsmo, Grazing Consultant, pers. comm. 1971) also indicate that *Carex bigelowii* is important for the female reindeer. My own observations show that the reindeer do not eat only the leaves of *C. bigelowii* but also the rhizomes and roots. This species can be grazed not only in areas that early lost their snow cover but is also dug up before snow-melt in places where the snow is not too deep and compact.

During the snow-melt the reindeer also grazed buds of shrubs and dwarf-shrubs. The calves preferred buds to graminaceous plants. This certainly depends on the buds being more easily available than the young leaves of graminaceous species. In addition, the calves do not require very much forage as they receive most of their nutrients from their mother's milk. Reindeer milk is high in nutrients. According to Ruong (1969) it contains 10.9 % protein, 17.1 % fat and 3.8 % lactose. Klein (1970) reports 10 % protein and 22 % fat.

With knowledge of the reindeer's energy requirement it is clear that the biomass of the investigated species is insufficient to cover the feed requirement. However, the area where the reindeer are present during the spring offers them other grazing species for which the biomass has not been calculated. Thus, with sub-area B (Fig. 2), the reindeer had access, in addition to the above-mentioned species, to *Deschampsia caespitosa, D. flexuosa, Festuca ovina, F. vivipara*, and *Anthoxanthum odoratum*. There are also fens within this area containing primarily *Eriophorum angustifolium* and *Scirpus caespitosus*. Some of the higher altitude fens contain *Eriophorum scheuchzeri*. Samples taken in May of *E. scheuchzeri* from Hardangervidda, Norway, contained 12.4 % protein according to Skogland (1970—1973). Protein-rich grazing is valuable and grazing plants with high nutrient value can compensate for low quantities of grazing. According to Bell (1970), the plant cells generally are thin and easily digestible in the early part of the growing period and the protein content is high.

Snow conditions and rate of snow-melt vary from year to year and naturally influence the availability of the different plant communities for grazing. The factor determining what the reindeer eat during the calving period is which plant community that earliest becomes available for grazing and which plants that first appear from beneath the snow.

Calculations of amounts of feed available to the reindeer at a given time are complicated due to the fact that when the snow has melted in one area, another area at a higher altitude is still melting and the biomass is still low, while it has become higher further down. During the period of snow-melt the reindeer graze the plant communities which have appeared and which offer grazing which is quantitatively limited but qualitatively good. The reindeer prefer newly emerged plant communities and therefore follow the snow line as it recedes.

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