Parmelia enteromorpha is the dominant foliose species and P. physodes and P. austerodes are also constant though less abundant. The small species Parmeliopsis ambigua and P. hyperopta (not included in the records) reach high cover values on basal parts.

Most by far of the upper subalpine stands give very good to excellent range values.

Lower Subalpine Zone

The tree stands are denser than in the upper subalpine zone, though the number of trees is not very high. Subalpine fir is dominant, but Engelmann spruce is more abundant than in the upper subalpine zone. Lodgepole pine may be present in burns.

The lichen loads are usually rather heavy in the old forests, although the branchiness is generally lower than in the preceding zone. The pine stands are always poor in accessible lichen.

One of the most conspicuous differences from the upper subalpine stands is decreased abundance of Alectoria oregana. It seems to be replaced by increased amounts of A. jubata. Among foliose lichens Cetraria glauca is locally abundant, but usually only sparsely present. Cetraria subalpina is sometimes abundant at bases of the shrubs Rhododendron albiflorum and Menziesia ferruginea.

The average range values of the lower subalpine zone are somewhat less than those of the upper zone, being usually from fair to excellent.

Western Hemlock Zone

There are five main types of forest stands in this zone: (1) subalpine fir - spruce, (2) red cedar, (3) hemlock, (4) pine, and (5) aspen stands.

The fir-spruce forests are particularly common in the Murtle Lake area in this zone. Most stands are clearly denser (crown canopy usually 30 to 70 percent) and the abundance of lower twigs is considerably smaller than in the subalpine forests. This means that the amount of lichen is also fairly low. The fruticose species do not attain remarkable abundance near tree bases, except in some localities on lakeshores and margins of open bogs. Alectoria sarmentosa is the major species, A. jubata, A. fremontii, and Ramalina thrausta being abundant, too. However, in most stands the abundance of lichen is distinctly greater on higher twigs, above the reach of caribou. On the other hand, the foliose lichens, particularly Cetraria glauca and more locally Lobaria pulmonaria, are more plentiful in the hemlock zone than in the subalpine zones.

The cedar stands are often extremely dense (crown canopy 60 to 90 percent) and, therefore, the lichen cover is usually less significant.

The hemlock forests are generally still poorer than the cedar stands as to lichen production. On the shore of Azure Lake, however, even hemlocks bear more lichen than in closed forests. Most hemlock stands are very shady and many trees are almost lacking basal twigs.

The pine (and Douglas fir) stands also possess rather insignificant lichen resources. This is mainly due to the scarcity of twigs and to the low age of pine stands. However, occasionally pine trees are rich in available lichen, mainly Alectoria fremontii, rather than A. sarmentosa which avoids excessively dry habitats.

The secondary aspen forests, dominant in the Hemp Creek valley, are extremely poor lichen range. Only on certain shrubs (e.g. Prunus) may be found a few threads of Alectoria or Usnea with Parmelia and Cetraria species.

Summing up, the subalpine fir - Engelmann spruce forests, found in the upper parts of the hemlock zone, represent the best lichen range in this zone. However, their range values vary from poor to excellent. Typical hemlock, cedar, and pine stands have a range value from very poor to poor, but in favourable conditions (which are overrepresented in the sample plot material) higher values may be reached.

3. Phytosociological aspects

As stated in Chapter II, even among epiphytic lichen, vegetation associations and other communities are distinguished and named (cf. Barkman, 1958).

The writer attempted delimitation of some kinds of such units in Wells Gray Park. However, most epiphytic lichen covers in the park give an impression of being very immature. They are growing in ecologically highly variable conditions, and, therefore, the formation of real regular vegetation is not easy. For instance, stems

and branches and other variable qualities of tree species, microclimate of environment changing in small distances, etc., make the variation considerable. The influence of interspecific competition remains weak and surfaces of trees never get completely filled with lichens. Thus, theoretically, most of the epiphytic vegetation may be regarded as poorly developed successional communities or ill-defined groupings of single individuals or, as expressed by Barkman (op. cit.), fragments of plant communities.

However, in the upper subalpine zone the lichen covers are frequently so closed that we may speak about real lichen communities. This is also generally true of the upper parts of trees in the other zones. In valley forests well-developed lichen covers on basal twigs are usually scattered. Crustose lichens do form extensive covers even in lowland forests.

The number of lichen species with strong powers of competition is small in Wells Gray Park. This kind of condition easily results in communities with only one abundant and dominant species. The composition of a few frequently seen communities were analyzed by the author, but since sociology is a question of peripheric interest in this report, only some general features of the communities are outlined here. The following tentative associations may be distinguished:

1. Alectoria fremontii association

Alectoria fremontii is dominant (cover 50 to 90 percent in the writer's records). Other Alectoria and Parmelia species are present in variable degrees. Prefers open, light, and rather dry stations,

being chiefly found on small exposed twigs in the upper parts of trees. In the subalpine forests also present close to the tree bases. It is also common in northern sections of boreal forest in N. W. Europe (Barkman, op. cit. p.476).

2. Alectoria jubata association

A rather common community, probably found in all zones in the park, but often poorly developed or with A. jubata considerably mixed with other Alectoriae. In a broad sense it is this association that is abundant at lower levels on trees in subalpine forests. It varies in composition, but it seems fairly arbitrary to distinguish other associations according to dominant species. However, an Alectoria oregana association might be often distinguishable in the upper subalpine zone on greater parts of lower branches exposed to sun.

3. Alectoria sarmentosa association

Besides Alectoria sarmentosa, Cetraria glauca is typical of this association. Although A. sarmentosa is present in the upper subalpine zone, it is not dominant in any community there. In the hemlock zone the association is rather common in moist and fresh forests. More or less the same association is mentioned by Barkman (op. cit. p.477) under the name Letharietum divaricatae from Europe. According to him it is 'skio-, psychro- and very aerohygrophytic', having 'a strong preference for Picea, particularly the lower, dying branches'.

3. Ramalina thrausta association

Ramalina thrausta, Cetraria Glauca, and Alectoria sarmentosa are characteristic of this association. It is ecologically closely

related to the preceding association, but is confined to still more sheltered and moist forests. In the park it is scattered in rich forests, but largely poorly developed and fragmentary only.

4. Cetraria glauca association

Typical of lower branches of shaded fir and spruce trees in the hemlock zone. Besides Cetraria glauca, Parmelia species are found more or less sparsely, while Alectoria species are very scarce. Common in the park.

5. Parmelia physodes - enteromorpha association

Very common in the hemlock zone, but mainly rather fragmentary. It occurs both on branches and on stems.

6. Lobaria pulmonaria association

Conspicuous but fairly uncommon community of rich and moist forests. It is usually restricted to the very lowest branches near the ground. Some bryophytes are often present with it. In Europe it is confined to humid regions, being very sensitive to drought (Barkman, op. cit. p.523).

4. Relations of availability of lichens and silviculture

Since most of the Wells Gray caribou range is situated in a Provincial Park, logging companies' operations do not greatly affect its range conditions. However, considering some relations between silviculture, fire protection, and caribou range management may be profitable even in this connection.

Clear-cutting and fires are very unfavourable to caribou in this area, as has been demonstrated by Edwards (1954), but selective cutting might be practised within caribou ranges. In Lapland, the

co-operation of logging and reindeer husbandry is generally good because of selective cutting, but in cases when large areas of too old or otherwise undesirable forests have been cut over, conflicts have arisen.

Abundance of Alectoria lichens on trees in boreal or montane coniferous forests primarily indicates old age and slow growth in the trees. This fact means a contradiction between forestry and caribou management.

For instance, old people remember the abundance of "beard lichens" on trees in South Finland at the beginning of this century, but now when the majority of these forests have been changed into so called "economy forests", where no old or poorly growing trees are allowed, the amount of fruticose lichens is not conspicuous at all. Alectoria sarmentosa has particularly suffered from intensive silviculture in N.W. Europe, as was also pointed out by Ahlner (1948). The same holds true with A. fremontii, while A. jubata has somewhat better adapted to the new conditions, being, however, fairly small in size nowadays. Also the general thinning of forests has been often unfavourable to Alectoria species in Finland. They are hygrophious and shade-tolerant to such a degree that thinning makes the forests too dry for luxuriant growth in normal boreal conditions.

Romell (1922) discussed the problem, whether the Alectoria species cause damage to conifers in North Sweden. He came to the conclusion that the damage is evidently negligible. Although this statement may need checking in some conditions, later authors have generally agreed with it.

In British Columbia lowered productivity of lichens is well seen in secondary forests. A decrease of lichen abundance would be also expected to follow intensive silvicultural measures in older forests. However, in very dense stands and on humid sites moderate thinning would improve lichen production. Moreover, in the upper subalpine zone, which is not silviculturally interesting, lichens will remain more abundant than elsewhere for climatic reasons. In that zone lichens possibly hinder the growth of trees to some extent by killing needles, etc.

Cringan's (1957) statement that falling trees would be important to caribou (this was also discussed by Edwards et al., 1960, and Scotter, 1962) does not seem to be generally valid for several reasons. Fallen trees are usually very scattered and most of them are not presumably found by caribou at the time when the lichens on them are still palatable or accessible (note snow conditions!) or when the animals are anxious to browse lichens (with the exception of very limited areas like the Slate Islands, Cringan's study area). Many dried-up trees leaning to other trees have almost totally lost their lichens before falling down. The same kind of condition is true with lichen falling on snow or on ground. Therefore, the importance of the heavy lichen loads above 10 feet from the ground seems to be practically insignificant to caribou. The same opinion was expressed by Scotter (1962).

In most of the lichen stands on trees in Wells Gray Park no browsing by caribou could be assessed. Only at Azure Lake could definite evidence of utilization be seen. Therefore, it seems correct to assume that a considerably higher number of caribou than at present is found there could live on the existing lichen resources. Ranges of

early and late winter, when the animals migrate down to valleys (Edwards and Ritcey, 1959), may be the most critical point to the population. However, it seems that even the valley range, if kept undisturbed, is able to maintain a higher number of caribou over the annually rather brief early and late winter periods.

VII. PALATABILITY AND NUTRITIONAL VALUE OF EPIDENDRIC LICHENS

Observations and experiments made all over the caribou and reindeer districts fairly uniformly give the following order of lichen groups as to their palatability to the animals of the genus Rangifer:

1. Highly palatable

   Reindeer lichens (Cladonia, subgenus Cladina)

   Epidendric 'beard' lichens (Alectoria, Usnea, Evernia)

   Stereocaulon spp. (data on palatability partly contradictory)

2. Fairly palatable

   Most Cetraria species (epidendric and terrestrial species)

   Cup-lichens (small Cladonia species)

   Umbilicaria spp.

   etc.

3. Less palatable

   Peltigera spp.

   Parmelia spp.

   Terrestrial Alectoria species

   etc.

Thus the epidendric Alectoria species, abundant in Wells Gray Park, are classified in the same category as the true 'caribou mosses', which are famous for their high palatability. Two Russian authors (Rabotnov and Govorukhin, 1950) even claim that the reindeer may prefer epidendric lichens to ground lichens. In any event, in most districts epidendric lichens are not abundant enough to support great herds of reindeer or caribou.

The characteristic nutritional properties of lichens are:

(1) scarcity of nitrogenous compounds and minerals

(2) high content of carbohydrates

(3) presence of special lichen substances, many of which are bitter acids

The following data on the composition of lichens is mainly based on the compilation by Rabotnov and Govorukhin (1950) in the Russian handbook "Forage Plants of Hayfields and Pastures in the U.S.S.R.". It is to be noted that the composition of the reindeer lichens is fairly well known, while analyses of epidendric lichens are few and, therefore, partly very preliminary.

Protein content

According to the Russian authors the protein content of different lichen groups is as follows (percent of dry weight):

Epidendric lichens (Alectoria, Usnea, Evernia),	6.8 - 7.8%
Reindeer lichens, average,	2.5 - 2.9
Cetraria islandica and allied species	3.5 - 5
Cladonia gracilis agg. (incl. C. ecmocyna)	4.5

As to species, Rasanen (1928) reported 4.14 and 7.31 percent in Alectoria "prolixa" and Florovskaya (1939) 7.31 to 7.77 percent in A. "chalybeiformis".

In spite of variations we may conclude that the protein content of Alectoria species attains fairly good levels, being two to three times higher than in the true reindeer lichens. However, in most experiments the digestibility of lichen proteins has proved to be

negative or very low (one to two percent). No experiments with solely epidendric lichens are known to the writer, but they are not expected to give results essentially different from the reindeer lichens.

Mineral content

Only one incomplete analysis of epidendric Alectoria is reported by Rabotnov and Govorukhin. It is compared with the reindeer lichens:

	Total Mineral Content per cent of dry weight	Per Cent of Total P_2O_5	Per Cent of Total CaO
Alectoria "chalybeiformis"	1.01	15.0	35.0
Reindeer lichens	1.2 - 2.2	2.8 - 5.4	0.5 - 5.2

Rasanen (1928) determined the total amount of minerals in Alectoria "prolixa" to be 1.0 percent.

These data indicate that the total mineral content in epidendric Alectoriae is about the same or lower than in the ground lichens. On the other hand, the phosphorus and calcium contents are essentially higher in Alectoria than in Cladonia.

The major portion of minerals is formed by silica (SiO_2) and, therefore, the digestibility of minerals is comparatively low. One experiment on this subject in the U.S.S.R. yielded 36.5 percent (in Alectoria ochroleuca, a ground lichen).

In foliose Parmelia species very high mineral contents have been reported.

Carbohydrates

Some Russian analyses are summarized below:

Percent of Dry Weight

		polysaccharids		
	monosacch.	hemicell.	cellulose	total
Alectoria (1 anal.)	0.6	81	1.6	84
Reindeer l.(11 an.)	0.3 - 0.4	56 - 83	4 - 7.3	82 - 93

No great difference is probably found between the two groups of lichens. Lichen is almost pure carbohydrate nourishment, mainly composed of hemicellulose.

In the numerous experiments conducted the reindeer's digestibility of carbohydrates has varied from 60 to 90 percent. For cow and goat their digestibility is considerably lower and still lower for sheep (about 40 percent). For pigs, they are almost indigestible.

Fat content

The amount of "raw fat" given in analyses also includes the often bitter lichen substances. Some Russian data on the quantity of raw fat (percent of dry weight):

Alectoria "jubata"	1.3 - 1.4%
Reindeer lichens	0.4 - 5.5
Parmelia spp.	17. -19.

The amount of fat is usually negligible. There seems to be a positive correlation between low fat content and good palatability. Thus the low palatability of Parmelia species is probably partly caused by their high acid content, which makes these lichens too bitter. The slight bitterness of reindeer lichens and epidendric Alectoriae does not seem to be harmful.

Regional differences have been noted in chemical contents of lichens. Therefore, it is possible that in Wells Gray Park some local peculiarities might be revealed. Especially Alectoria oregana and A. sarmentosa, which probably have not been analyzed before, may yield results different from the above values.

VIII. OCCURRENCE OF GROUND LICHENS IN THE PARK

Ground lichens, the staple food of caribou in most caribou districts, are very poorly represented in Wells Gray Park. However, they are not completely lacking there.

The reindeer lichens (Cladonia, subgenus Cladina) were found in all zones, but only very locally. In the hemlock zone Cladonia arbuscula spp. beringiana (concerning the nomenclature, see Ahti, 1961) was found on the Murtle River at Mushbowl and Helmcken Falls, at Hemp Creek (very sparsely), on the edge of the Clearwater Canyon south of the park, on Azure Lake, on Murtle Lake, and at Blue River. Cladonia rangiferina is frequently associated with it, but sparser. Cladonia mitis is present at Murtle Lake and Stereocaulon paschale at Murtle Lake and at Azure Lake. However, only at Azure Lake and in the rock-beds on south slope of Ramsay Mtn., Murtle Lake (plus in lodgepole pine stands at Blue River, outside the park) do reindeer lichens attain some abundance.

The last-mentioned places (except Blue River) are also grazed by caribou. On the rock-beds of Ramsay Mtn. only some scattered lightly grazed patches were found, while near the middle of the southern shore of Azure Lake a few small rock outcroppings, 100 to 200 yards in from the lake, are heavily grazed. It is apparent that the caribou feed regularly on the lichen mats of these outcrops every year (in fall and spring).

The subalpine zone is also very poor in reindeer lichens. Scattered patches of Cladonia mitis were in meadows near Fight Lake, and

Battle Mountain, but were not found at all on Fish Lake Hill. In subalpine meadows and open woodlands the gray cup-lichen, Cladonia ecmocyna var. intermedia, is common and often abundant. In dry subalpine meadows Cetraria subalpine, C. islandica, and C. crispa are common. All these lichens are certainly palatable for caribou, though no signs of grazing were seen in them. It should be noted that the subalpine ground lichens are accessible to caribou chiefly in summertime (cf. Edwards and Ritcey, 1959), when the animals prefer vascular forage richly available in the same meadow habitats.

In the alpine zone many ground lichens are found. The major species include Cladonia ecmocyna var. intermedia, Cetraria islandica, and C. crispa. Cladonia mitis and many other species are sparsely present. The importance of alpine lichens to caribou seems to be insignificant.

The main reasons for the scarcity of ground lichens in the park are undoubtedly due to a fertile soil and sparsely revealed bedrock. The reindeer lichens are most abundant in areas with sandy or granitic ground and with cool climate (Ahti, 1961). Also, in Wells Gray Park the growing period of reindeer lichens is short because of thick snow cover, long winters and rather dry summers.

IX. SUGGESTIONS FOR CARIBOU WINTERING RANGE MANAGEMENT

With more intensive land use in the future special management of lands used by mountain caribou may prove to be necessary. Silvicultural measures are often essential to wildlife management. Being a climax animal the caribou is easily influenced by the activities of man. Fires and clearcut logging could never favour caribou which live on arboreal lichens in winter. The elimination of these two factors in caribou ranges is of primary importance for successful caribou management. Some other general principles are outlined below:

1. The upper subalpine zone should be entirely protected from cutting since the regeneration of forests is very slow in that zone. Destroying timberline stands probably results in permanent meadows, which may be good summer ranges but of no use in winter time. In many countries timberline forests have been designated as shelter forest belts, where commercial cutting is prohibited by law. In British Columbia such areas might act as excellent caribou game preserves.

2. In the lower subalpine zone and in the upper hemlock zone selective cutting might be allowed. It may even improve the production of arboreal lichens to some extent, if the ages of tree stands are not lowered too much.

3. In general, the great density of forests in Wells Gray Park is one of the most important conditions limiting the abundance of lichens on lower twigs. Therefore, moderate thinning of forests by selective cutting would be profitable for both lichens and trees. Even in the upper

subalpine zone cautiously conducted thinning could prove to be useful.

4. However, thinning should not be made according to purely silvicultural principles. It seems to be advisable not to take out all dead or old trees, particularly such trees that are rich in lichens and are thus centres of dispersal. It is subalpine fir and spruce that have lower twigs and thus lichens near the ground in greater amount than other tree species. Richly branched individuals of fir and spruce might be left growing.

5. Any disturbance of critical points on major migration routes, as, for instance, the area where caribou cross the Murtle River, should be avoided. The wintering districts situated in the valley floors (Murtle Lake, Azure Lake) should be also preserved in undisturbed condition as much as possible.

6. The forests of lower hemlock zone (Hemp Creek, etc.) do not seem to offer much potential for winter food for caribou. Therefore, the upper and lower subalpine zones may be regarded as optimal, the upper hemlock zone as submarginal and the lower hemlock zone as marginal range for mountain caribou.

7. Experimental cutting plots may prove to be useful in studies on productivity of lichens. Such plots should be situated in each wooded zone and in different habitats. The effects of various intensities of thinning, dispersal of lichens from lichenous trees, changes in lichen cover on artificially dried-up trees, falling of basal branches in different light conditions, etc., are suitable objects for study in these plots. Other silvicultural and wildlife management experiments might be included in the same program.

X. SUMMARY

Distribution and abundance of lichens on trees in Wells Gray Park were the main objects of the present study.

The upper subalpine zone proved to be richest in epidendric lichens, which condition is due to the slow growth, the great age (4 - 250 years), the high summer humidity and the low density of its forests. The tree species, subalpine fir and Engelmann spruce, with their numerous basal twigs, are also favourable to the occurrence of lichens. The most abundant fruticose species are Alectoria oregana, A. "chalybeiformis" (identification as yet tentative), A. jubata, and A. fremontii. Winter food resources for caribou in this zone are excellent and, therefore, availability of food is no restricting factor to considerable increase of the number of caribou. So far these forests are under very light grazing.

The lower subalpine zone is fairly rich in lichens, and the species composition is much the same as in the preceding zone, but other circumstances like the abundance of thicket-forming shrubs (particularly Rhododendron albiflorum) make it less favourable as caribou range.

The western hemlock zone, where the caribou also frequent in wintertime, possesses much lower amounts of available lichen than the subalpine zones. High density of forests, their good growth, and the high frequency of tree species that are poor sites for fruticose lichens result in low value of the hemlock zone as caribou wintering range. When compared to the subalpine forests it is also evident that the

number of lower twigs on trees is much smaller in the hemlock zone. However, there are localities like lakeshores, riversides, bogs, moist forests, etc., which may produce considerable amounts of available lichen. The most abundant species include Alectoria sarmentosa, A. jubata, A. "chalybeiformis", A. fremontii, Ramalina Thrausta, and Cetraria glauca. Even in this zone tops of trees usually carry heavy loads of lichen (mainly A. fremontii), which is not accessible to caribou in great quantities.

According to data found in literature the palatability and nutritional values of the abundant fruticose, epidendric lichen species of Wells Gray Park are not lower than those of the true reindeer lichens growing on ground. The mineral and protein contents of the epidendric lichens are frequently even higher than those of the reindeer lichens.

Ground lichens are fairly scarce in the park. However, locally (at Azure Lake) they have some importance for caribou in winter-time. The major species are Cladonia arbuscula ssp. beringiana and C. rangiferina.

As to range management it is suggested that the wintering grounds of caribou, i.e., the upper subalpine zone and some parts of the valleys (Murtle Lake, Azure Lake) should essentially be protected from cutting, fires, and excessive human influence. In the lower subalpine zone selective cutting may be practised, at least locally. Most of the hemlock zone is very marginal as caribou range and generally insufficient production of lichen in this zone cannot be improved to any great extent. However, since some parts of this zone are necessary for migrating and wintering caribou, local management is useful. Certain