26 Subarctic Lichen Woodlands
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Introduction

Between the tundra and the closed-canopied boreal forest is a vast region of largely undisturbed, open-canopied conifers with a ground cover of lichens (Figure 26.1). This region has been called various names in the North American literature: subarctic forest, lichen woodland, hemiarctic, and spruce woodland. Refer to Löve (1970) and Blüthgen (1970) for the semantics of these terms.

The subarctic woodlands are primarily climatic in origin, occupying the transitional areas between the summer location of Arctic airstreams and more southern airstreams. As in all transition zones, small variation in the primary forcing variable changes the vegetation composition and structure. This change in airstream position interacts with the available plants, landforms, elevations, substrates, and fire regime to create a vegetation mosaic reflecting past and present interactions.

The North American subarctic woodland is one of the last remaining extensive and continuous ecosystems (Figure 26.2a). It covers approximately 2 million square kilometers, most of which is without roads or permanent settlements. Hunting, trapping, and some mineral extraction are the primary land uses. The subarctic has a population of indigenous people whose way of life is still strongly related to the land. Furthermore, during part of the year it is the home of caribou (Rangifer tarandus), the last large migratory ungulate herd in North America.

Distribution

The subarctic woodland in North America (Figure 26.2a) occurs from the northern interior of Alaska, cutting through the Richardson Mountains and north of the Mackenzie Mountains, to the south end of Hudson Bay, East of Hudson Bay, the woodland extends north toward the coast of Labrador and Quebec.

The general position of the subarctic woodland coincides with the mean position of the Arctic front in summer (Figure 26.2b). The Arctic front separates maritime and continental Arctic airstreams from Pacific, Atlantic, and tropical airstreams. This baroclinic structure is a characteristic of the mean westerly air flow and influences the large-scale dynamics of climate, particularly precipitation, and temperature patterns. Thus, the subarctic is positioned between the colder, drier climate of the tundra and the warmer, wetter climate of the boreal forest (Bryson 1966; Barry 1967; Krebs and Barry 1970; Barry and Hare 1974).

Although large-scale climate patterns determine the general distribution pattern of the subarctic woodland, regional features also have an effect (Figure 26.2a). The woodland does not reach the west coast in Alaska, which is covered instead by cool, wet tundra due to the influence of the cold, extensively ice-covered Bering Sea. Similarly, the subarctic zone narrows and is forced southward around Hudson Bay because of the influence
of this large, cold mass of water. East of Hudson Bay, the woodland extends northward in Quebec and Labrador due to the diminishing effect of the cold water and due to the maritime influence of the north Atlantic. The influence of mountain ranges is indicated by the bend in the subarctic zone around the Northern Cordillera in the Northwest Territories.

In delineating the subarctic woodland, an important consideration is its transitional nature from forest to tundra. For example, Timoney et al. (1992) used the ratio of trees to upland tundra cover to define the northern section of the subarctic. Most “tree line” maps generally are based on this approach. Hustich (1966, 1979), for example, defined transition from forest to tundra in terms of the economic forest line (limit of sexually reproducing trees), the physiognomic forest line (limit of vegetatively reproducing trees), the tree line (limit of tree growth form), the tree species line (limit of all species that normally grow as trees), and the historical tree line. The physiognomic forest line, tree line, and tree species line are observable on air photos and are persistent because of tree longevity, whereas the economic forest line changes from year to year. The historical tree line is determined from paleoecological evidence such as macrofossils and microfossils (Payette and Gagnon 1979; Ritchie 1984, 1987).

For convenience, the divisions of the subarctic recognized by the Ecoregions Working Group (1989) are used here. This classification (Figure 26.2a) is a compromise between a large number of divisions needed to reflect the transitional nature of the region and a...
Figure 26.2. (a) The range of the subarctic lichen woodland in Canada. (Redrawn from Ecoregions Working Group 1989.) (b) The coincidence of the subarctic lichen woodlands with the summer position of the Arctic front. (Redrawn from Barry 1967.)
reasonable number of easily mappable units. The classification recognizes a high, mid, and low subarctic with two smaller subunits on the east coast – the maritime mid-subarctic and Atlantic low subarctic. The mid-subarctic is not recognized in western North America, where the transition from high to low subarctic is extremely narrow. In the east (northern Quebec to Labrador), the transition region is broad, and the mid-subarctic can be recognized as a distinct unit. The boundaries of these regions are based on density and height of trees, and on the decrease from north to south in the amount of tundra vegetation, particularly on exposed hilltops.

Community Composition and Structure

The upland community on cool, mesic sites of the high subarctic consists of an open forest of black spruce (*Picea mariana*), tamarack (*Larix laricina*), white birch (*Betula papyrifera*), and some white spruce (*Picea glauca*). The ground cover is composed of feather mosses (*Pleurozium, Hylocomium*, and *Dicranum*), ericaceous shrubs (*Ledum groenlandicum* and *Vaccinium vitis-idaea*), and lichens (*Cladonia* and *Peltigera*). Warm, dry sites support open forest of white and black spruce and a ground cover of bearberry (*Arctostaphylos uva-ursi*), crowberry (*Emetrium nigrum*), mosses (*Polytrichum*), and lichens (*Stereocaulon* and *Cladonia*). Dwarf birch (*Betula glandulosa*) and willow (*Salix spp.*) with mountain avens (*Dryas integrifolia*), sedges (*Carex spp.*), and lichens (*Stereocaulon* and *Cladonia*) characterize areas of shrub tundra.

The mid-subarctic is represented best in northern Quebec and is characterized by a higher density of trees than the high subarctic (e.g., Payette 1976). Within the low subarctic, cool, mesic sites support closed-canopied stands of white and black spruce containing ericaceous shrubs and feather mosses. Cool, dry-mesic sites are covered by open-canopied stands of black spruce and white birch with ericaceous shrubs and lichen (*Cladonia*), whereas warmer dry sites have open-canopied jack pine (*Pinus banksiana*) and black spruce woodlands with a ground cover of lichen (*Stereocaulon*).

Regionally, the composition, structure, and floristic range of the subarctic vegetation reflect a south-to-north decrease in temperature and a maritime-to-continental decrease in precipitation. A large number of species reach the limit of their geographic range within the subarctic and no species is endemic to the subarctic (Rousseau 1968; Cody 1971). Morisset, Payette and Deshaye (1983) noted that floristic changes from subarctic to Arctic result from a decrease in the number of boreal taxa, rather than an increase in the number of Arctic taxa.

The two most common patterns in species geographic ranges are Arctic circumpolar (e.g., *Salix arctica*; Figure 26.3a) and boreal circumpolar (e.g., white birch, black spruce, and tamarack; Figures 26.3b, c, d). Although the ranges of most species are circumpolar, a smaller number of plants, both boreal and Arctic, are either amphibious or amphibian-Atlantic. Boreal trees also show some regional variation in their northward extension; for example, tamarack extends further north in Quebec than it does in the west (Figure 26.3d).

The changes in tree density and growth form across the region correspond to the climatic gradient. In the low subarctic, tundra vegetation is limited to exposed hilltops and high plateaus. Northward within the high subarctic, the tundra progressively extends to lower elevations within the landscape until trees are restricted to wet sites, usually in protected areas along incised drainages. Growth form changes along a gradient of increasing cold and blowing snow, and a concomitant increase in forest fragmentation (Figure 26.4). Tree structure changes from a symmetric, open growth form through a progressive series of flag, vertical, skirted, fruticoid, and mat growth forms (Payette 1974).
Locally, the principal topographically related factors affecting vegetation composition, canopy structure, and species diversity are moisture, nutrients, and heat (Maikawa and Kershaw 1976; Payette 1976; Payette and Gagnon 1979; E. A. Johnson 1981; Ritchie 1984; Ecoregions Working Group 1989; Timoney et al. 1992). At the moist, high-nutrient, low-heat end of the gradient are found closed black and white spruce stands with a ground cover of sphagnum, feather mosses, and lichen (*Cladonia rangiferina*). These stands often are relatively rich in species, containing both tundra and boreal representatives because of the high availability of nutrients. The sites tend to be located at the base of north-facing slopes that occasionally contain permafrost. On slightly drier but still cold sites, closed black spruce and white birch stands occur with a ground cover of feather mosses and ericaceous shrubs. Stands are found on sites that generally are north-facing on bottom to mid slopes, have fine- to moderate-textured soils, and lack permafrost. Warm, low-nutrient sites found on mid to top slopes, or on level plains with course-text-
tured, sandy soil, support open-canopied stands whose composition varies, depending on site moisture. Black spruce is found throughout the range of sites, but jack pine occurs only on dry, warm, low-nutrient sites. The dominant lichen composition also changes along a moisture gradient from mesic to dry as follows: Cladonia rangiferina—Cladonia alpestris to Cladonia mitis to Cetraria spp.—Stereocaulon pascale.

**Ecosystem Dynamics**

**Climate**

The subarctic is related to the summer contact zone between the cool, stable, Arctic airstream and warm, unstable, maritime Pacific or tropical airstreams (Bryson 1966; Barry 1967; Krebs and Barry 1970; Barry and Hare 1974). In turn, these airstreams pass over, and interact with, surfaces that change the airstream characteristics (Hare and Ritchie 1972; Szeicz, Petzold and Wilson 1979). This airstream boundary abruptly delineates two climatic regimes. In summer, the maritime Pacific air is cloudy and warm with moderate wind. Across the boundary in the Arctic air, the temperature is cooler and there are noticeably fewer clouds. The boundary between the two airstreams at a height of 2,000 m often is very narrow, on the order of meters, whereas on the surface, ground friction stretches the boundary width to kilometers (Bryson 1966).

Over the long term, the location of this airstream boundary is relatively dynamic. During a period of general climatic cooling from 1425 to 1850, the Arctic front was further south than today (Lamb 1977), and during the brief warming at the turn of this century, the Arctic front advanced northward into the tundra (Jones, Wigley and Kelly 1982). These climatic changes have affected the recruitment of seedlings and mortality of plants, most conspicuously trees. Having established during warmer periods in the past, black and white spruce survive in what is currently tundra, although they are not producing seed (Payette and Lajeunesse 1980; Payette and Filion 1984; Payette and Gagnon 1985). On the other hand, tundra plants such as Diapensia lapponica can be found over 50 km south of present tree line on eskers and ridges, where they appear to have survived in the subarctic from the 1500s, when this forested area was tundra.

**Fire**

The other main force in the dynamics of subarctic vegetation is forest fire. Generally, these fires are quite large, measuring in thou-
sands of hectares, with intensities greater than 4,000 kW m\(^{-1}\) and relatively rapid rates of spread (tens of meters per minute). This fire behavior results from the open forest canopy, which leads to relatively high winds at the surface (Szeicz, Petzold and Wilson 1979) and rapid drying of surface fuels, relatively low precipitation, and the long day length during the summer fire season. The low crown base of the open grown trees (Figure 26.5) leads to passive crown fires. Lightning is the major cause of fire, accounting for approximately 85% of fires and 99% of the total area burned (E. A. Johnson and Rowe 1975).

Fire is less frequent in the high subarctic than in the low subarctic (E. A. Johnson and Rowe 1975; E. A. Johnson 1979; Payette et al. 1989). E. A. Johnson (1979) showed a decrease in the expected fire cycle (time required to burn an area equivalent to the study area) from 100 years at 100 km from the black spruce tree line to 50 years at 400 km from the tree line. Payette et al. (1989) found a decrease in number of fires as well as a 100-fold decrease in fire size from the low to the high subarctic.

In general, subarctic forests are open forests. Closed canopies are present on certain sites with higher nutrients and moisture, as noted earlier. Of the tree species, black spruce, white birch, trembling aspen (Populus tremuloides), and balsam poplar (Populus balsamifera) have the capacity for vegetative regeneration, whereas jack pine, white spruce and tamarack do not. All of these species are capable of living several hundred years, either as trees, krummholz, or vegetative sprouts.

The age distributions of these upland subarctic tree populations are remarkably similar (Figure 26.6). In all cases, the stands have one or more age classes of trees separated by age classes with either no or few individuals. The challenge is to understand how this pattern developed as a result of the forces that operate on the recruitment and mortality of the individual tree species populations. The regeneration cohort of a local population is a group of individuals recruited at approximately the same time and generally experiencing a similar mortality schedule. A local population is made up of one or more regeneration cohorts. These cohorts form a population that contributes seed (along with long-distance dispersed seed) to produce new cohorts. Consequently, the dynamics of a local population are based on the mortality rate of these cohorts and the original recruitment number. Unfortunately, age distributions do not indicate the number of individuals recruited in a cohort, the rate of cohort mortality, or if cohorts have become extinct (E. A. Johnson, Miyashita and Kleb 1994). Despite these limitations, ecologists have gained a reasonable understanding of
the tree dynamics in the subarctic.

Generally, large numbers of seedlings establish after a disturbance (usually fire) that removes the herbaceous and lichen cover and exposes large areas of mineral soil (Cowles 1982; Thomas and Wein 1985). Effective germination and early seedling survival tend not to occur on intact forest floors, probably because of low moisture supply caused by drying of litter, duff, and lichen layers (Kershaw 1977). Low moisture and heat, as well as a limited seed supply, lead to low seedling density, even when there is a mineral soil surface. Many seeds germinate in the burned-out bases of trees (C. E. Van Wagner, unpublished manuscript). The number of seedlings recruited after a fire depends to a large degree on the regional climate; cooler episodes lead to few or no recruits, whereas warmer periods have a greater number (e.g., Payette and Filion 1984). Cohort survival varies depending on the specific historical sequence through which the cohorts live. Trees recruited in the cool period of the 1400s were subjected to a different mortality schedule than those recruited in the warm period of the early 1900s. However, mortality of established trees generally seems to be low. Persistence of a cohort also will be influenced by fire frequency and species maximum life span. Black spruce appears to live well over 400 years, whereas white birch rarely lives
more than 150 years and jack pine rarely more than 200 years. Exceptions, of course, do occur. Individual trees of black spruce persist by layering around the base. This also allows them to increase their density, at least locally, and to modify their microclimate.

Climate–Fire Interaction

Explanations of the low tree density and open canopy of the subarctic vegetation have primarily centered on the interaction of fire and climate. Maikawa and Kershaw (1976) and Kershaw (1977) took a traditional successional view that tree regeneration after fire was a slow process, requiring a long period for development of a self-reproducing closed-canopy forest with a feather moss ground cover. Closed-canopy forest was thought to be rare, because the harsh surface conditions of high temperature and low soil moisture immediately after fire (Rouse and Kershaw 1971; Rouse 1976) lead to poor tree establishment but abundant regeneration of mosses and lichens. However, the few trees that are established ameliorate the high summer temperatures and low soil moisture, thereby allowing increased vegetation cover. Canopy closure was thought to be retarded by the inhibitory effect of lichens on tree seedling establishment and on the recurrence of fire.

However, this traditional view of succession is not well supported by detailed studies of forest dynamics. Studies of tree regeneration patterns in open- and closed-canopy boreal forest indicate that most regeneration occurs in the few years after a fire (Black and Bliss 1980; E. A. Johnson 1981; Cogbill 1985; Carleton and Wannamaker 1987; Bergeron and Dubuc 1989; Morneau and Payette 1989; Siros and Payette 1989; E. A. Johnson 1992). In the subarctic, the stressful environment and low seed rain following a fire limit seedling recruitment (Siros and Payette 1989, 1991). Furthermore, after this limited postfire seedling establishment, regeneration is reduced because the lichen mat prevents seeds from making contact with mineral soil. Any germination that occurs is associated with "cracks" in the lichen mat that allow seeds to penetrate to mineral soil (Cowles 1982). These few seedlings also are subject to high mortality. In fact, most regeneration occurring 30 or more years after fire is by vegetative means. Black spruce reproduces by layering, and white birch by basal sprouts. However, vegetative reproduction does not progressively create a closed canopy but instead results in a balance between production of new vegetative stems and mortality of older ones.

Recurrence of fire determines the frequency of periods during which the seedling recruitment "window" is open, and climate determines the seed bed condition. Furthermore, since there is no soil seed bank (E. A. Johnson 1975), tree seeds must come from prefire trees. Serotinous cones of jack pine and semiserotinous cones of black spruce release viable seeds for several years after the tree has been killed by fire and heat from the fire has opened the cones (E. A. Johnson and Gutsell 1993; J. S. Johnson and Johnson 1994). The number of seeds from these aerial seed banks depends on the density and fecundity of the prefire trees. White spruce and tamarack have no serotinous cones and, consequently, the trees must either survive the fire or their seeds must disperse into the burned area from unburned edges.

In the high subarctic, fires are infrequent, and tree seed crops are small and highly variable. Furthermore, conditions for tree establishment are generally poor. Consequently, when a fire occurs there is a high probability that tree density will decrease and forest fragmentation will increase. The persistence of old trees in the high subarctic is probably a result of the long interval between fires. On the other hand, in the low subarctic—with its more frequent fires, larger seed rains, and
Figure 26.7. Location of some of the major caribou herds in North America. (Redrawn from Bergerud 1978.)

generally better tree establishment conditions – there is a greater probability of maintaining existing areas of forest at their current density (e.g., Sirois and Payette 1991). If the Arctic front were to move south and produce a cooler period in the mid and low subarctic, fire could have a greater impact. Increased forest fragmentation resulting from reduced postfire tree regeneration during this cooler period likely would persist for some time.

Caribou

The subarctic forest is occupied during part of the year by large migratory herds of barren-ground caribou (Rangifer tarandus var. groenlandicus) and woodland caribou (Rangifer tarandus var. caribou) (Figure 26.7; Bergerud 1978). These are the last migratory herds of free-ranging ungulates in North America. Caribou spend the summer on the tundra. Females, yearlings, and calves form large herds for insect abatement and protection from predators while males are in smaller, bachelor herds. In August, as insect pests decline and calves become larger, the herds break into smaller groups. By September, they have moved south into the subarctic forest; the males move first, followed by the females and young. The rut occurs in October and November. The first heavy winter snow results in movement of the caribou deeper into the forested region, where food is easier to obtain.

Winter is spent close to large lakes, which provide escape from wolves, and in upland areas, where lichen, herbaceous, and shrub browse are available and accessible due to the reduced snow cover. Caribou dig small holes with their hooves to reach browse. Food apparently is detected below the snow by odors diffusing up along the branches of
shrubs extending above the snow. Thus, conditions of food availability and snow depth largely dictate the location and dispersion of herds.

In April, the caribou migrate northward toward tundra. Traditional routes are used because they are generally snow free early. Pregnant females lead the migration to reach their calving grounds by late May to early June. Caribou reproduction rate is low, with one calf per female being the rule. Female pregnancy rates vary by age, but for mature females (3-4 years old) the rate is around 80% (Bergerud 1980). Calf death rate is high, with weather and predators accounting for most of the mortality (F. L. Miller 1974; F. L. Miller and Broughton 1974). Calves are particularly vulnerable in their first few weeks, with 50%-90% mortality in areas where wolf density is high. Mortality of adults is 4%-15% annually, depending on predator density. Caribou are not particularly effective in escaping predators. Their general strategy is to run from the forest to hard snow and ice on large lakes, where they can see the predator and try to keep a safe distance. However, wolves are successful in more than 50% of the chases (Haber 1977).

Until the last few decades, the estimated number of caribou has been based on speculation. For the three large herds in Ungava, Northwest Territories, and Alaska, estimates of population size vary considerably but are thought to be between one and two million (Bergerud 1974). Herd size probably has decreased in the last 100 years or so. The extent to which the herds have declined is a politically volatile question. Several explanations for the decline have been proposed: (1) overhunting, (2) predators, particularly wolves, and (3) decrease in carrying capacity of the winter range due to destruction of the lichens by an increased frequency of forest fire.

Despite the low number of indigenous hunters, overhunting probably has been an important factor in the decline of caribou. Most hunting occurs during winter, when caribou are in the forest and native hunters are on their trap lines. The introduction of the high-powered repeating rifle has made caribou herds particularly vulnerable. Because the normal response of a herd to danger is to run onto a frozen lake and mill around looking for the predator, shooting from a distance is easy. Caribou, like bison, seem to have no adaptive behavior to respond to a hunter who can kill from a distance. These facts suggest that hunting probably was important in reducing the caribou population during this century.

Predators seem to be particularly effective in harvesting caribou. With the low population growth rate of caribou, it appears that in the past a delicate balance existed between recruitment and mortality from predators. Moreover, a case can be made that multi-equilibria exist, depending on hunting pressure and predator density (Haber 1977; Haber and Walters 1980). An understanding of caribou population dynamics and impacts of predation and hunting requires not only an estimate of birth and death rates but also metapopulation estimates of dispersal between herds. If calf mortality due to predators is consistently high (assuming predator densities normal or high), then an above-normal adult mortality (e.g., by hunting) will result in a decrease in population. However, a decrease in a local population could be prevented by immigration of animals from another herd.

The suggestion that the carrying capacity of caribou winter range in the subarctic forest has been reduced significantly (Scotter 1967) is based on several premises, none of which seem to have much support (Bergerud 1974; E. A. Johnson and Rowe 1975; D. R. Miller 1980). The first premise is that caribou are climax forest animals that depend on lichens (Cladonia rangiferina and Cladonia alpestris) found only in climax forest. However, compared to other ungulates, caribou have highly variable diets, of which lichens are only one
part (Murie 1935; Scoog 1968; Bergerud 1974; D. R. Miller 1980). It has been reported that caribou feeding only on lichens lose weight (Bergerud 1974). The second premise is that climax (old-growth) forest stands of the subarctic have been replaced largely by younger, successional stands due to fires set by Europeans (Scoter 1967, 1971). Evidence from subarctic forest fires does not support the suggestion that human-caused fires account for much area burned (E. A. Johnson and Rowe 1975; Payette et al. 1989). For the last 300 years, fire frequencies have changed due to climatic shifts associated with the Little Ice Age and not humans (Payette et al. 1989; E. A. Johnson 1992).

Also, there is no documentation that reduced range quality has resulted in changes in birth or death rates in caribou (Bergerud 1974). The only possible effect of fire is local and short term, causing caribou to seek older, unburned forests, which contain more lichens rather than younger, recently burned stands (Klein 1982).

Native People

Indigenous hunters have always occupied the subarctic seasonally, usually during winter when caribou migrate into the woodland. Bands of hunters migrated south into the boreal forest or north onto the tundra during the summer, and into the subarctic in the winter, after the caribou arrived. The prehistoric era (prior to 1680) was, in the context of the time, a period of plenty for the subarctic people (Yerbury 1986). Most took advantage of the summer abundance of caribou, fish, and waterfowl on the tundra. Winters were spent in the subarctic lichen woodlands, fishing and hunting caribou, moose, and smaller game (Jarvenpa 1980). Food generally was reliable and plentiful (Helin 1965; Smith 1975; Yerbury 1986).

The beginning of changes in migration pattern caused by the evolution to a more trading-trapping economy occurred during the protohistoric era (1680–1769) (Bishop and Ray 1976; Yerbury 1986). During this period, little direct contact occurred with European traders, but goods were passed along through native middlemen. Although the mark-up by middlemen on European goods was high because of their technological superiority, the trade was not initially exploitive of the fur resource for two reasons: the difficulty of transport by the middlemen, and cultural wealth accumulation not being part of the native culture (Ray 1974; Ray and Freeman 1978). However, to keep fur supplies at satisfactory levels, the European traders resorted to even higher mark-ups, which then were passed along to native trappers. Furthermore, hunting of food animals, including caribou, increasingly occurred to provision the fur traders and not simply to provide for the subsistence of the local people.

Further changes in the human population and in their location took place during the historic era (1770–1890) due to the increasing importance of the fur trade and due to secondary effects such as disease (Bishop and Ray 1976; Yerbury 1986). Many tribes were forced into the low subarctic, either from further south or from the tundra. The low subarctic is not as good a subsistence habitat as the high subarctic and tundra. This forced relocation of people, together with the increasing fur trade economy, meant that hunting/trapping pressure increased on the populations of caribou and fur-bearing animals. Particularly during the period between 1763 (Treaty of Paris) and 1821 (merger of the Northwest and Hudson Bay companies), fur and game animals over increasing areas of the boreal forest were exploited with little concern for conservation. Fur animals were exhausted commercially in many areas (Ray 1974). The beaver, which was the mainstay of the early fur trade, was completely eliminated from large areas. Since beaver feed on birch, aspen, and balsam poplar, and build dams that modify the water table, their elimination probably had a major effect on the
local vegetation and hydrology. As exploitation progressed, trapping activity moved west and north, allowing the “trapped out” parts of the southern and eastern subarctic time to recover.

In both prehistoric and historic times, caribou had a cultural and survival (food, shelter, clothing) significance to native hunters. However, caribou have been severely hunted, particularly in recent times. The indigenous people seemed to take the existence of caribou for granted. When caribou were abundant, large numbers were killed and only partially used. Periodic shortages were attributed to changes in migration routes due to snow conditions or to the necessity of trapping in areas where there were no caribou. It appears that in traditional resource utilization, indigenous people under-utilized available resources due to the unimportance of accumulating wealth and the reciprocity of exchange within kinship groups.

Summary

Despite the occurrence of fire and the presence of large grazing herds of caribou in the subarctic, the major factor determining the open-canopy nature of the subarctic spruce–lichen woodland is climate. Thus, unlike other transitional open-canopy vegetation such as pine barrens and oak openings, the lichen woodlands would not be converted into closed-canopy forest in the absence of disturbance by fire or grazing. The location of the subarctic woodlands is closely related to that of the Arctic front in summer, which is determined by large-scale atmospheric (climatic) processes. Changes in the average location of the Arctic front in summer occur over long time scales due to long-term climatic shifts. Also, fires in this region are primarily influenced by large-scale atmospheric processes. Furthermore, because of the extremely low human population density, the subarctic woodlands have not suffered the fragmentation that has occurred in other transition vegetation, such as temperate oak savanna. As a consequence, natural large-scale processes continue to be the dominant influence on the extent, location, composition, and structure of the lichen woodland.

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