

*A. M. Marshall*

**The effects of fire  
on the ecology  
of the Boreal Forest,  
with particular  
reference to  
the Canadian north:  
a review and  
selected bibliography**

**by John P. Kelsall, E. S. Telfer  
and Thomas D. Wright**

**Occasional Paper  
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### Abstract

This review analyzes literature relevant to effects of fire on the Boreal Forest, and on its related wildlife resources, with particular reference to the Canadian North. The selected bibliography contains the more recent and historically important references and is not all-inclusive. Be-

cause of a paucity of material pertinent to the forests of the Northwest and the Yukon territories, it has been necessary to extrapolate information from other areas. Alaskan publications have been particularly useful.

It was concluded that fire is the most important factor influencing the ecology of the northern Boreal Forest; that fire and the resulting forest mosaic are natural features of long standing; and that the Boreal Forest can be characterized as a fire-dependent ecosystem. Trees, other plants, birds, mammals, and other animals of the forest have evolved in response and adaptation to the frequency, extent, and intensity of fire. With some possible exceptions, a mosaic of varied successional stages in the Boreal Forest provides a richer habitat for a more varied and abundant fauna than does the monotypic spruce forest characteristic of unburned areas. Specific attention is given to fish, birds, and mammals — particularly to important species of game and furbearers — and to such characteristics of the northern forests as the presence of permafrost, the soils, and the characteristics of unique vegetation. The basic characteristics of different types of fires are also described.

### Résumé

Cette étude analyse les publications traitant des répercussions des incendies sur la forêt boréale et sur la faune qui y habite, plus particulièrement dans le contexte du Nord canadien. La bibliographie choisie, sans être exhaustive, comprend les références les plus récentes et les plus importantes du point de vue historique. A cause de la rareté des documents qui portent sur les forêts des Territoires du Nord-Ouest et du Yukon, il a été nécessaire d'extrapoler à partir des renseignements tirés d'autres régions. Les publications de l'Alaska se sont révélées particulièrement utiles.

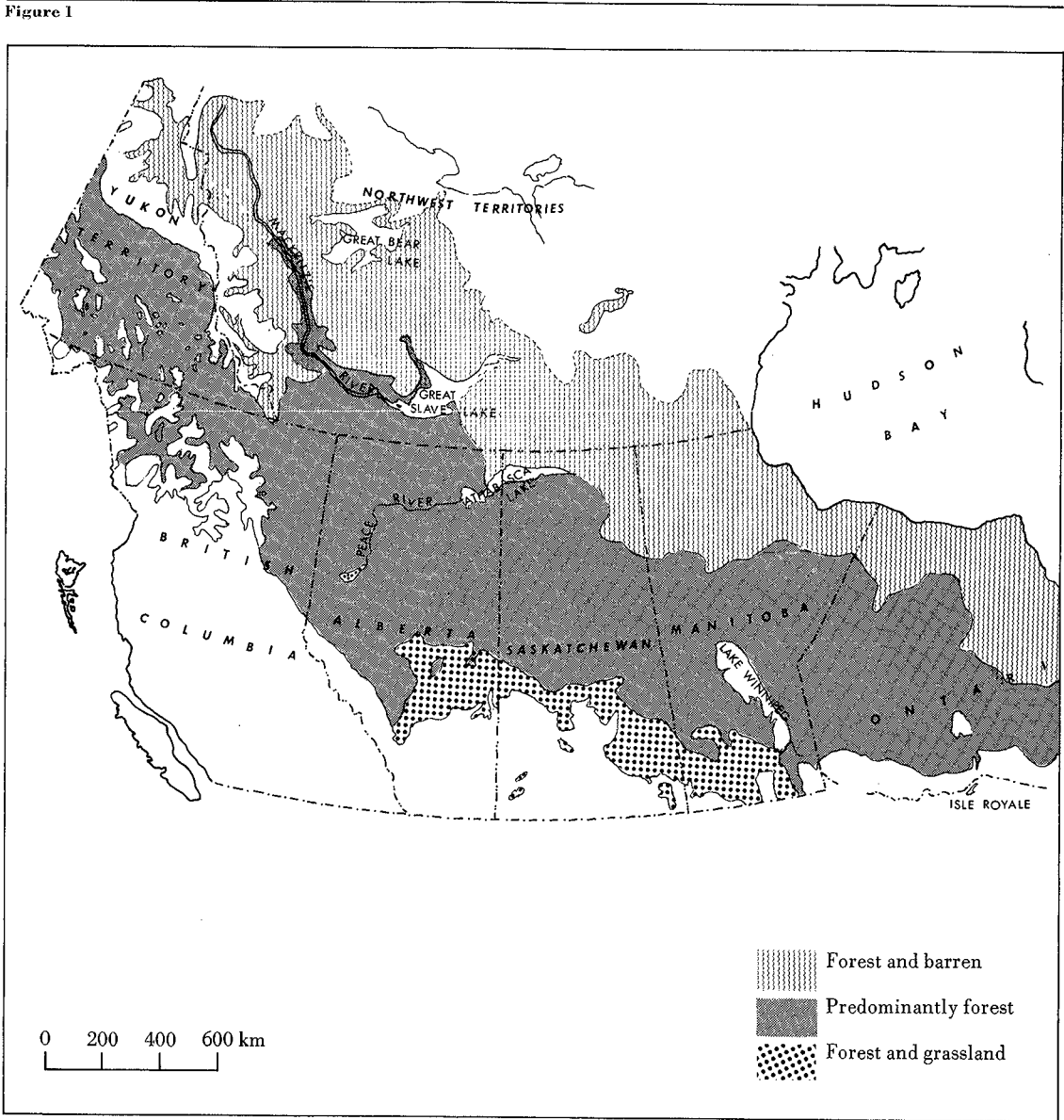
# Introduction

On a conclu que les incendies de forêt étaient le facteur le plus important de l'écologie de la forêt du Nord au peuplement boréal; les incendies et la sylve en mosaïque qui en résulte sont des caractéristiques naturelles permanentes; la forêt boréale peut donc se définir comme un écosystème en fonction du feu. La flore et la faune y ont évolué en réagissant et en s'adaptant à la fréquence, à l'étendue et à l'intensité des incendies. Sauf pour quelques exceptions possibles, l'ensemble des divers stades de la succession des peuplements végétaux y fournit à une faune plus variée et plus abondante un habitat plus riche que ne le fait le peuplement homogène d'épinettes caractéristique des zones qui ont échappé au feu. On consacre une attention particulière aux poissons, aux oiseaux, aux mammifères, et tout particulièrement aux espèces importantes de gibier et d'animaux à fourrure ainsi qu'aux caractéristiques propres des forêts nordiques comme la présence de pergélisol, la pédologie et la végétation unique. On décrit également les caractéristiques fondamentales des différents genres d'incendie de forêts.

The development of a soundly formulated basis for management of the Boreal Forest of northern Canada (Fig. 1), specifically the Northwest and Yukon territories, has long concerned federal and territorial agencies and the public sector. Although most of this forest is slow-growing, open-canopied or dispersed, and of doubtful large-scale commercial value, its various resources have benefited man both in prehistoric and historic times. Since prehistoric times, the fauna typical of the northern Boreal Forest have supplied indigenous man with food, clothing, and other necessities of basic survival. In historic times, this forest has provided firewood for regional consumption, lumber for a small-scale forest industry, furs for trade, and game species for sport and for a continuing domestic economy. Areas within the Boreal Forest of northern Canada support stands of timber-sized trees that are potentially valuable as pulpwood or sawlogs, and the waters of this forest support fish in numbers sufficient not only for domestic use but also for both a commercial fishery and an increasingly popular sport fishery.

Federal and territorial agencies concerned with the Boreal Forest and its resources have attacked many research and management problems, with varying degrees of success. Because most approaches to these problems have been unilateral and discipline oriented, there is a great need for a more comprehensive ecosystem approach to the Boreal Forest of the northern territories, to consider the relative values of its various components, and on these bases to commence or recommence (where necessary) the development of management priorities. As a matter of national interest, this task should rank high. The Boreal Forest of the Northwest Territories and of the Yukon Territory occupies approximately 1 036 000 km<sup>2</sup>, an area that includes an immense — though in places thinly scattered —

**Figure 1**  
The boreal forest of western Canada  
(after Rowe 1972)





# Sources of information

quantity of renewable resources. The value of wildlife in all its forms must generally outweigh the direct commercial value of the forests and, in the long term, of any other presently conceivable form of widespread land use.

In the review that follows, we have attempted to synthesize into one document the most reliable current and historical information on the effects of fires on northern forests. Throughout, we have adopted the assumptions (relatively new in some quarters) that the Boreal Forest of the Canadian north is a fire-dependent ecosystem, and that the flora and fauna of this region have evolved in response and adaptation to forest fires.

We do not claim that this review is exhaustive or that the bibliography is complete. Rather, our specific objectives have been to find the most recent and authoritative references available under each pertinent topic, to include the best of the older literature, to include references to appropriate analogous situations, and to interpret the results in view of our own research, interests, and experience. Most of our bibliographic references are mentioned in the text, but a few are not. Ultimately, we hope that this review will serve as a starting point for a progressively fuller understanding of the close relationships between forest fires and the dynamic ecological character of the Canadian north.

Sources of information are listed in the attached selected bibliography. Most items are specialized references that deal with narrow aspects of the general subject. Sources of information that were thought worthy of specific mention are summarized immediately below.

## 1. Symposia

Four recent symposia provide overviews of the role of fire in forests. "The role of fire in the intermountain west" (Intermountain Fire Research Council 1970) and "Fire in the environment — symposium proceedings" (North American Forestry Commission 1972) both include references that directly apply to coniferous forests and the northern environment. Of special interest is "Fire in the northern environment — a symposium" (Alaska Forest Fire Council 1971) and a special issue of the journal *Quaternary Research* (Volume 3, October 1973). The former is devoted largely to fire in the Boreal Forest, both to ecological relationships and fire control. The latter is devoted to ecological considerations; its individual articles, their bibliographies, and the symposium summary (Wright and Heinselman 1973) are all of value. A recent volume, "Fire and ecosystems" (edited by Kozlowski and Ahlgren 1974), is topical throughout and contains a particularly informative review by Bendell of effects of fire on birds and mammals.

## 2. Bibliographies

We found five bibliographies containing at least a few titles that are pertinent to this review and many that are peripheral to its primary interest. One of these (Wood 1966), though not well known, is partially annotated; of the 354 titles included in it, 44 pertain to "animal life". Barney and Dils's (1972) "Bibliography of clear-cutting in western forests", which contains approximately 720 titles, was useful because of the

analogies between clearcutting and forest fire. A 350-page "Annotated bibliography of permafrost — vegetation — wildlife — landform relationships" (Roberts-Pichette 1972) deals mainly with the Canadian north but includes few references of direct relevance to wildlife and fire. "Fire in the northern regions — a bibliography" (Larson 1969) contains only 198 titles, many of which discuss fire suppression. An extensive annotated and summarized bibliography (317 titles) by Gibbons and Salo (1973) deals with the effects of logging on fish of the western regions of the United States and Canada.

In summary, the bibliographies, though they contain a wealth of reference material for those interested in peripheral subjects, are relatively unhelpful as guides to material that directly concerns fire-wildlife relationships in the Boreal Forest.

### 3. Systematic reviews

We found several papers that systematically cover the ecological effects of fire on northern regions of North America. They should, in our opinion, be required reading for anyone contemplating major research or work on this subject.

Ahlgren and Ahlgren (1960) deal primarily with east-central North America. Their discussion, however, transcends narrow geographical lines and the publication itself is of value because of its 358-title bibliography, which contains many historical references. The dissertation by Hansen *et al.* (1973) on fire and wildlife in the limited Boreal Forest of Isle Royale, in western Lake Superior, also contains a useful section of literature citations.

Four comprehensive discussions of fire as an ecological factor in the Boreal Forest of Alaska deserve special mention: Lutz (1956, 1960*b*), Komarek (1971), and Viereck (1973*b*). The most valuable of these are by Lutz (1956), who gives

a long and historical overview of the subject, and Viereck (1973*b*), who provides a recent and comprehensive discussion of the effects of fire on soil, plants, and animals.

We found only two comparable treatments of the role of fire in the Boreal Forest of Canada: a brief general review (Kayll 1968) that accents effects on soils, and a longer and more comprehensive treatment (Rowe and Scotter 1973) that focuses on effects in the northwest.

"Some implications of large-scale clearcutting in Alberta — a literature review" (Johnson *et al.* 1971) also deserves mention. This 114-page report discusses clear-cutting under six major topics, each of which includes a reference section. The hydrology section of this report (see Hillman 1971) was particularly useful. This publication contains no specific discussions of wildlife, and fire is not included as a topic. It is of interest, however, because the effects of logging and burning are in some cases analogous.

### 4. Computerized searches

We employed computerized searches through the University of Alberta library in an attempt to find references pertinent to specified topics. Because the searches yielded few results, we recommend that before much trust is placed in future searches, their efficiency be tested on subjects where key references are well known.

A computerized bibliography relating solely to fire in the environment is being compiled at the School of Forestry of the University of Montana. We are advised that it will be primarily used for local purposes. However, a 246-title printout of fire-wildlife material, which was used in the preparation of our review, was kindly supplied to us.

# The boreal forest

## 1. Climate

Climatic descriptions of particular forest sections can be extrapolated from the "Climatological Atlas of Canada" (Thomas 1953), which includes country-wide maps of temperature, precipitation, windspeed, and other factors of interest. For many specific places within the northwest the series "Climatic normals" (Canada Department of Transport 1968*a-f* and Environment Canada 1973*a, b*) gives a complete coverage of all the factors normally measured at weather stations. Rowe (1972) summarizes factors of ecological importance to Canadian forests, and Kelsall (1968) summarizes the climatic character of the range of the barren-ground caribou, which includes most of the Boreal Forest Region in the Northwest Territories. A recent publication on the climate of the Mackenzie Valley - Beaufort Sea area covers most of Mackenzie District and eastern Yukon Territory (Burns 1973).

Although climatic conditions throughout the Boreal Forest Region of Canada — an area ranging from Newfoundland to the Rocky Mountains and Alaska — vary widely (Rowe 1972) the portion within the Northwest Territories has a relatively uniform climate. There the summers tend to be moderately warm, sunny and dry, and the winters to be long and cold. Mean annual precipitation ranges between 25 and 36 cm — only slightly above values typical of true deserts. Of this precipitation, a little less than half falls as snow. Mean annual total snowfall is remarkably uniform, varying between 102 and 127 cm throughout most of the northern Boreal Forest. Westward of the Rocky Mountains, snowfalls that measure 150 cm and greater occur. Many lakes and ponds are present in the northern forest — despite limited precipitation — because the brief summers do not permit massive evaporation and because permafrost, which is widespread in the northern territories, greatly inhibits drainage.

Mean annual minimum temperatures are remarkably uniform, at approximately  $-45^{\circ}\text{C}$ ; somewhat lower minimums occur in the mountainous regions. Maximum summer temperatures vary only slightly above or below  $30^{\circ}\text{C}$  regardless of whether the location is far north of the Arctic Circle in the Mackenzie Delta, at Yellowknife on Great Slave Lake, or further south at Stony Rapids, in northern Saskatchewan.

The growing season in the Boreal Forest is short. On its southern fringes in central Ontario and in the middle portions of the prairie provinces, the mean annual length of the growing season is 160 days. In the Northwest Territories the length of the growing season varies from approximately 80 days in the Mackenzie Delta to between 120 and 140 days in areas approaching the provincial boundaries.

Studies by Bryson (1966) have shown that the edge of warm, moist, unstable Pacific air masses pushes northeast in summer to occupy a modal position near treeline at the northern edge of the Boreal Forest. As winter approaches, the boundary between Pacific and cold, dry, continental arctic air moves south to the southern edge of the Boreal Forest.

Winds and thunderstorms we shall discuss below; here we shall simply point out they have a direct and important relationship to fire.

## 2. Topography

The northern Boreal Forest includes four of Canada's major physiographic regions (Rowe 1972). In the Yukon Territory and the Northwest Territories westward of the Mackenzie River is the Cordilleran Region, which is the northern extension of the Rocky Mountains. This area, composed primarily of sedimentary rock, includes both minor and major mountain ranges, deep valleys, high plateaus with glacial till, and low altitude plains.

To the east lies the Interior Plains Region, extending to the Slave River, the north arm of Great Slave Lake, the east side of Great Bear Lake, and northward to the portion of the Arctic coast near Paulatuk. In this area, Precambrian rock is overlain by limestones, shales, and sandstones that gradually increase in depth from east to west. The portion of perhaps greatest economic interest, the Mackenzie Lowlands, includes extensive muskeg interspersed with low, rugged mountain ranges and localized delta formations.

Eastward again and extending to the coast of Hudson Bay lies the Canadian Shield. The Shield is mostly Precambrian rock — granites, quartzites, and others — frequently covered with only a shallow layer of glacial till. Topography is often rugged and ranges from sea level to over 760 m in elevation. There is an extremely extensive network of streams, lakes, and small water bodies of various shapes and sizes.

South of the border between the Northwest Territories and Manitoba and along the Hudson Bay coast lie the Hudson Bay Lowlands, which also contain Boreal Forest. The Lowlands are covered with unconsolidated glacial and post-glacial deposits and are underlain by Palaeozoic limestones over Precambrian rock. Having little relief, they are poorly drained and have numerous bogs and shallow lakes.

The topography of the northern Boreal Forest cannot be described in general terms. This topography ranges from high mountains to low and gentle plains. Almost everywhere, however, are rivers, streams, lakes and ponds. Glacial till covers much of the country, and residual glacial features such as eskers, drumlinoid ridges, and evidence of glacial scouring are oriented along lines of glacial movement, and in some areas there are numerous long, narrow parallel lakes in troughs scraped by glaciers (Kelsall 1968).

### 3. Soils

Rowe (1972) briefly describes soils in the Boreal Forest. Soil profile development is rudimentary or absent in the northernmost sections and becomes progressively more advanced away from the tundra — although peat development can occur anywhere in this forest region. Profiles are poorly developed, and the natural decomposition of litter by bacteria and fungi is extremely slow. In the northernmost section of the Boreal Forest, soil development is further inhibited by the proximity of permafrost near the surface. Rowe (1972) shows that most of the Boreal Forest has a mixture of rock and frozen organic and sporadically frozen brunisolic and gleysoilic soils, with some regular occurrence of podzols, chernozems and regosols in the Cordilleran Region.

### 4. Vegetation

Rowe (1972) has subdivided the Boreal Forest region of Canada into "forest sections", several of which occur in the Yukon and the Northwest territories. Viereck and Little (1972) have provided a similar classification for Alaska. Much research on the role of fire in Alaskan forests is directly applicable to the Canadian north and can be related to the classification of the just-mentioned authors. Composition of the flora of the Boreal Forest of Canada has been described by LaRoi (1967) and Rowe and Scotter (1973); Lutz (1956, 1960b) and Viereck (1973b) have described the flora of the Boreal Forest of Alaska.

Throughout this review, nomenclature used for trees and shrubs primarily follows Rowe (1972); for species not mentioned by Rowe, nomenclature follows Viereck and Little (1972).

The Boreal Forest of the Northwest Territories consists primarily of open stands of slow-growing black and white spruce (*Picea mariana*

# Fire

and *P. glauca*) and of a ground cover of lichens and/or mosses, which becomes quite dense as the stands age. This forest is interspersed with many treeless bogs that are often fringed by larch (*Larix laricina*) and by occasional dense and tall forest stands. In the southern portions of the Northwest Territories, jack pine (*Pinus banksiana*) is common on sandy soils and some uplands. The common deciduous trees, often prominent following fire, include trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and white birch (*Betula papyrifera*). These deciduous species occur particularly in the Northwestern Transition Section (Rowe 1972) which extends eastward from the Mackenzie River and Slave River systems. To the west in the Upper Mackenzie and Lower Mackenzie sections, lodge-pole pine (*Pinus contorta*) and Alaska birch (*Betula neoalaskana*) are locally prominent.

Similar flora dominate the Boreal Forest in the Yukon Territory and Alaska. In the Alaskan forests in particular large areas of birch occur.

The authors cited above note an increasing northward trend toward domination by black spruce and by the various bogs that occur throughout the Boreal Forest. These range in constitution from rich grass (*Gramineae*) and sedge (*Carex* spp.) to more numerous oligotrophic sphagnum (*Sphagnum* spp.) mosses. Particularly prominent are tussock sedge areas with sphagnum moss and many low ericaceous shrubs.

Among the more ubiquitous plants of the northern Boreal Forest are the dwarf birch (*Betula glandulosa*) and Labrador tea (*Ledum groenlandicum*), both common to bogs and upland sites throughout the north. Several species of willows (*Salix* spp.) occasionally cover large expanses along rivers, around bogs and marshes, and (in the Yukon and Alaska particularly) on benches and gentle slopes at high elevations.

Rowe (1970) states that "Fire is an integral feature of the northern forest environment" and that "the widely distributed boreal broad leaf trees and conifers are well adapted to it". Mutch (1970) develops the hypothesis that certain plant communities (of which the Boreal Forest would certainly be one) have evolved in association with fire; moreover, he supports the rationale that the continued incidence of fire maintains a "natural and balanced condition" in such plant communities. Rowe *et al.* (1975) suggest that fire is an active and essential "resource" in the diversification of ecosystems and that the intervals between fires control the evolution of such systems.

Authorities agree that fire is a natural agent influencing the Boreal Forest. Mutch's hypothesis suggests that this forest is a fire-dependent system that would lose its character, vigour, and faunal and floral diversity in the absence of fire. Many of the references cited below adopt similar hypotheses concerning the relationship between fire and the ecological character of the Boreal Forest.

## 1. History of fire

Rowe (1970) regards the ubiquitous layers of charcoal found in the soils of northern forests as clear evidence of the universal, historical presence of fire. This history of extensive fires is evident, according to Lutz (1956), in the Canadian north and also in Alaska, European Russia, Siberia, and the Scandinavian countries. Fire can be traced as a frequent occurrence in some North American forests far into prehistory (Loope and Gruell 1973).

Swain (1973) traced the history of fire in northeastern Minnesota from charcoal layers in lake sediments and concluded that fire "had always been a factor" in these forests. Fire, he found, occurred on average every 60 to 70 years

within an approximate range of 20 to 100 years. More charcoal was found in sediments 1000 to 500 years in age than in those 500 years or less in age, but the frequency of fire was approximately the same during both periods. That there were no major pollen changes following any charcoal peaks showed that the same cycle of succession had extended far back into prehistory with the same plant species.

Recent studies (Lewis, in press and pers. comm.) have shown that both Cree and Athabaskan Indians in Alberta regularly conducted controlled burning to improve wildlife habitat, to reduce fire hazard near camps, to assure a future supply of dry fuelwood, and (among other reasons) to dry out trails through muskeg. Their well-developed knowledge of fire management indicates a long history of trial and error. Such burning continued until it was outlawed by provincial fire regulations.

Because lightning and man were as able to start forest fires in early times as they are today, fires have probably occurred regularly in the northern Boreal Forest since the last glaciation (Barney 1971a).

## 2. Causes of fire

Scotter (1972) points out that 72% of forest fires on the winter range of barren-ground caribou were apparently caused by lightning and comments that "most fires caused by man occurred near the centers of population". Scotter's data cover 1961 to 1964, a period during which it is improbable that all fires on the caribou range or their causes were recorded.

According to Barney (1971a, b), and Barney and Comiskey (1973), the percentages of lightning- and man-caused fires in Alaska are almost the reverse of these percentages in the Canadian north. He summarized the causes of fire in interior Alaska between 1940 and 1969: 70.5%

caused by man and 29.5% by lightning. These figures possibly reflect the larger size and the relatively greater mobility (particularly along networks of highways and secondary roads) of the human population in Alaska. Regional differences in meteorological conditions during summer may also be a contributing factor.

Johnson and Rowe (1975) studied an area of 105 000 km<sup>2</sup> south of Great Slave Lake, in the Northwest Territories. Between 1966 and 1972 lightning caused 85% of 273 reported fires, and lightning-ignited fires covered 99.9% of the total burned area. Rowe *et al.* (1975) reported that 97% of the area burned in the Mackenzie Valley from 1971 to 1974 was the result of lightning-caused fires.

According to Requa (1964), 76% of fires in the Yukon were ignited by lightning (quoted by Kiil (1971)). Johnson and Rowe (1975) found that 39% of fires, which accounted for over 50% of the burned area, were started by lightning on protected areas in the Northwest Territories. Most protected areas adjoined settlements.

That man can cause serious fires in the Boreal Forest is shown by the extensive conflagrations in May, 1968, in central Alberta. Kiil and Grigel (1968) showed that the numerous outbreaks all started from smouldering settler fires associated with land clearing. Fire hazard was extremely high at the time because of the very dry air and the prevalent southwest winds. Also, large volumes of highly flammable materials occur in the forests of central Alberta. In a 15-day period, 250 fires burned 380 000 ha of forest despite intensive fire control efforts.

These last observations agree with Leopold and Darling (1953), who remark that fires increased after settlement in Alaska, and with Kellsall (1968) and Scotter (1964) who believe that fires in the north have increased, at least in local areas, with intensive technological use by both

white man and Indian. It is the opinion of Lacate *et al.* (1965), however, that lightning is probably the main cause of fire in the lower Peace River area and that it undoubtedly is the main cause of fire in remote areas throughout the Canadian northwest.

Kourtz's (1967) study, which described conditions under which strikes by lightning were apt to occur and the types of trees struck, showed that evergreens are far more flammable than deciduous trees. Komarek (1968) and Habeck and Mutch (1973) also outlined the conditions for lightning-fire occurrence. A prerequisite of such a fire is a build-up on the ground of large accumulations of organic litter, which provide a ready fuel source. Such build-ups are common in northern coniferous forests. According to Rowe (1969), who documented lightning-caused fires in the grassland area of Saskatchewan, fire probably maintains some grasslands at the expense of shrubs and trees. Also, it is probable that forests can be opened or destroyed completely by fire at treeline, at high elevations, and at high latitudes. DeBock (1970) found that fire had provided open range lands preferred by mountain goats on Mount Wardle in Kootenay National Park, at the expense of forests. Wein and Weber (1974) noted that tree seedlings were not invading 5-year-old burns at treeline. They also cite Russian and other circumpolar literature that suggests that burns can drive treelines southward for extended periods.

Occurrences of thunderstorms and lightning are in some measure predictable. From "Climatic normals, Volume 3" (Canada Department of Transport, 1968c), which shows the seasonal occurrence and frequency of thunderstorms at selected meteorological stations through the Boreal Forest, it can be seen that such storms are more frequent in some areas than in others. This fact, viewed in relation to forest fire statistics and

prevailing forest fire hazards, can provide a basis for prediction of the probable times and locations of lightning strikes that could cause fire. On this basis, Johnson and Rowe (1975) drew isolines of the fire-size expected to recur on the average of every 5 years in their study area.

Weather is probably the most important factor influencing the behaviour of fire. Kiil and Griegel (1968) described the daily variation of fires in the northern Boreal Forest of Alberta, and their responses to climatic factors, during a 1968 period when all factors favoured extremely high rates of fire spread. During this period, the stage was set for fire by a prolonged prevalence of dry air and southwest winds. Once ignited, fires smouldered at night and increased during the daylight hours to a point where they crowned at approximately noon. The fires were capable of crowning at any moment when winds reached velocities of 24 km/h or greater.

### 3. Areas burned

Most of the historical references to the extent of destruction of forests by fire in the northern hemisphere are extremely general. Mozeson (1961), for instance, states that "about one-fifth of Yakutia shows traces of recent fires". Lutz (1956) recorded many of the noteworthy fires in Alaska from the mid-1800's onward, together with estimates of their extent.

Accurate records were not possible until the use of aircraft and the development of accurate map sheets permitted burned forests to be surveyed and mapped. Records have been kept in Alaska since 1940 (Barney 1969, 1971) and are available for shorter periods and in less detail for the Canadian northwest (Kelsall 1968, Scotter 1970). In Alaska, from 1940 to 1969, lightning fires covered 78% of the burned state-wide area (5 321 641 ha), and man-caused fires covered the balance (1 428 613 ha). Lightning-caused fires are

generally more extensive (average coverage of 3522 ha) than man-caused fires (average coverage of 679 ha) — probably because man-caused fires are detected soon after they start and can often be quickly controlled.

The above-cited studies of Barney showed that the number and extent of fires in Alaska is extremely variable and unpredictable from year to year. Despite many man-caused fires in Alaska and the excellence of the statistics, Barney points out that "it is hard to say with certainty whether or not we are experiencing more fires now than we did in the past".

In the Northwest Territories and the Yukon Territory the recorded loss of forests to fire was 238 120 ha annually between 1948 and 1957. However, in 1958 the loss was 655 878 ha. Between 1952 and 1957, recorded fires in Wood Buffalo National Park — for many years the only extensive area in the Canadian North to receive regular protection — burned 451 441 ha, more than one-tenth of the total area of this park. Annually during this 5-year period, fires covered over 2% of the total park area (Kelsall 1968). Kelsall (1957a) measured fire damage in a 23 864 km<sup>2</sup> area of caribou winter range that contained no settlements and that was located approximately midway between Great Slave Lake and Great Bear Lake. It was not possible to classify burns by age, but the majority had occurred within the previous 20 years and were in early stages of post-fire succession. It was calculated that 29% of the land area had been burned. The best caribou range, the dry upland spruce-lichen forests, were reduced by more than 29% because unchecked fire had been more destructive to them than to the damper habitats, which are less valuable to caribou. Kelsall (1960) also reported on the examination of another winter range of barren-ground caribou, an area of 43 020 km<sup>2</sup> surrounding the east end of Lake Athabasca and

Black Lake, in northern Saskatchewan. Of this area, forest that appeared to be at or near maturity totalled no more than 777 km<sup>2</sup>.

On the basis of Simard's (1973) recent analysis of "fire weather" data, Canada has been map zoned for liability to fire. The region surveyed by Kelsall was found to be one of the most fire-prone in Canada. Also included in the region of "high" fire potential were the study areas of Johnson and Rowe (1973, 1974, 1975), Kershaw *et al.* (1975) and Kershaw and Rouse (1976). Scotter's (1964) study area was zoned "moderate" risk but adjoined the "high" risk zone in a region where meteorological data are scarce. Both Wood Buffalo Park and the Yukon interior are rated by Simard as "high" or "very high" fire-risk areas.

The statement of Rowe *et al.* (1975) that the probability of recurrence of fire in the high-risk zone approximates a Weibull distribution suggests that the older the stand the more susceptible it is to burning. As elsewhere, bad fire years and periods have been detected in the northern Boreal Forest (Rowe *et al.* 1974). Large-scale fires in the northern Mackenzie Valley in recent years were believed to have been partially due to large areas of "old growth" forests that resulted from fires in the 1800's.

For the period 1961 to 1964, Scotter (1970) provides detailed statistics on the number of fires and the area burned in the winter range of barren-ground caribou in northern Alberta, Saskatchewan, Manitoba, the District of Mackenzie and Wood Buffalo National Park. The large annual variation in the extent of burning underlines the need for long-term and accurate fire statistics. In 1962, only 9569 ha were recorded as burned. In the previous year, 1 081 578 ha were burned, and nearly the same number of hectares were burned in 1964. Scotter (1964) calculated the average annual rate of forest destruction by fire on winter



# Effects of fire on soil and hydrology

range of barren-ground caribou in northern Saskatchewan. He found that from 1945 to 1959 fire destruction had increased 1.4 times over the period 1885 to 1944 and 3.1 times over the period 1840 to 1884. The average annual destruction of forest in his study area was 2639 ha during the period 1840 to 1884 and 8312 ha during the period 1845 to 1959. Scotter pointed out that the increases were coincident with mining activity and white settlement. Armstrong and Vines (1973) have shown historical evidence of periodicities in weather patterns that would produce periodicities in extent and severity of fires. Thus long periods of drought would coincide with periods of severe fire. Johnson and Rowe (1973) showed that the average rate of burning calculated by Scotter does not exceed approximately 1% of the total forest annually. The recent work of Johnson and Rowe (1975) showed that stand-age determination in the taiga is more difficult than was previously thought. They suggest that no firm conclusions can be drawn as to whether fire incidence has increased in recent decades.

## 1. Soil nutrients

It has been stated that fire generally has a beneficial effect on the soils in coniferous forests. In warm climates, particularly where there is ample moisture, bacteria and fungi decompose organic litter that accumulates on the ground. This decomposition releases minerals into the ecosystem for future plant growth. In northern areas, and in coniferous forests in particular, natural decomposers are not efficient and a build-up of litter inhibits plant growth (Kilgore 1973). Fire acts more rapidly than other natural agents to decompose ground litter and to release minerals and other nutrients.

The effects of fire on nutrients have been discussed by Uggla (1958) in regard to Sweden, by Yancey (1964) in regard to marshes, by Lutz (1956) and DeLeonardis (1971) in regard to interior Alaska, and by Scotter (1963), Smith (1968), Armson (1969), and Kayll (1968) in regard to the Boreal Forest in various parts of Canada. Fires in the north usually consume only part of the surface organic layers and do not expose much mineral soil. Removal of large quantities of organic litter, however, improves conditions (e.g. soil temperature and nutrient conditions) for young tree growth. All nutrients show an immediate increase in concentration because of the deposition of ash from burned organics on the soil surface. Calcium, phosphorus, potassium and trace minerals generally increase following fire. Total nitrogen can decrease, but the amount available for recycling generally increases.

As Smith (1968) points out, however, a relatively large-scale loss of nutrients can occur after a fire. He found during the first year after a fire on jack pine barren in Ontario losses due to erosion included 93% of potassium, 80% of calcium, and 91% of extractable phosphorus. Kershaw *et al.* (1975) and Kershaw and Rouse (1976) also concluded that burning degraded soil fertility in

their study area in a section of the Northwest Territories north of Uranium City. To explain the varied results from nutrient analyses following fire, they advanced the following tentative hypotheses: that soils with a high content of clay and a "substantial" humus content in the A horizon will lose only a "minimal percentage" of potential nutrients through burning; that, in contrast, soils low in clay or humus depend on the humus (L, H and F) layers for their moisture and nutrient-holding capacity; and that burning alters physical and chemical properties of such deficient soils and leads to increased density, lower moisture-holding capacity and reduced fertility. Fire effects vary depending on the characteristics of individual sites.

According to Scotter (1963) and Kayll (1968), there is a marked and beneficial reduction in acidity following fire in Boreal Forest. Armson (1969) found that following fire the pH of the upper horizons increased from 4.3 to 5.2. Behan (1970) states that "Burning of the forest litter generally increases the pH of the forest floor". He adds that increased pH may permit accelerated decomposition of the remaining litter through enhanced microbial activity. Kershaw *et al.* (1975) also found pH to increase from 3.7 to 4.8 but believed that their results indicated soil degradation.

According to Behan (1970), wildfires cause major depletions of nutrient capital, and nitrogen and potassium in particular are volatilized and lost to the atmosphere. In light burns, however, soil concentration of available phosphorus, potassium, magnesium and calcium are generally increased. The amount lost to leaching appears to be a function of the temperature of the burn and of the degree to which soil, organic matter, humus, and total plant cover were destroyed. His results confirmed a loss in total nitrogen after light burning, but he found that available nitro-

gen for plant growth increased. His general conclusion is that low temperature burns are beneficial to forests but that hot fires can deplete minerals at a disastrous rate.

Wein and Weber (1974) studied post-fire conditions at treeline northeast of Inuvik, Northwest Territories. They found that available phosphorus and nitrogen were increased and that the active layer thickened by 50%. They also found, however, that after 5 years only 5 to 10% of the plant mass had recovered and that tree seedlings were not invading.

Scandinavian foresters have had lengthy experience with effects of controlled fire as a land-management tool (Viro 1974). According to Viro, "The effect of burning on availability of nutrients is entirely positive". He does note slight leaching of magnesium, potassium and phosphorus but regards these losses as apparently unimportant because the mica-rich parent material supplies these nutrients in adequate amounts. That addition of these nutrients in fertilizer has caused only slight improvement in growth of vegetation further indicates that leaching losses were minimal.

In Scandinavia, burning after logging is prescribed for sites with thick humus mats, where the soil has good water-holding capacity (Viro 1974). Burning is not recommended for sites on coarse, excessively-drained water sediments such as eskers or sand out-washes because such sites become very dry, and survival of young trees is therefore inhibited. If dry sites are to be burned, fire should be quick and of low temperature, should kill the vegetation, but should leave the humus intact. On more moist and fertile sites, foresters often err by not burning deeply enough.

The effect of fire on soil nutrients depends not only on temperature of the burn but also on the topographic aspect of individual sites and on the soil parent material. Heilman (1966, 1968),

in his study of distribution and availability of nutrients in forest succession in interior Alaska, found that after burning nitrogen goes deep into the ground, that on exposed north slopes it becomes incorporated in permafrost, and that under these conditions it is no longer available for plant growth. This accounts for slow growth of stands of black spruce, frequently accompanied by the invasion of sphagnum moss, on north slopes. On the other hand, on warmer sites, where birch does best, nitrogen remains in upper soil layers and is available to vegetation. Nitrogen is not the only nutrient that declines with black spruce bog formation on north slopes. Phosphorus and potassium are likewise affected. Heilman (1968) considered that the establishment of sphagnum indicated a large drop in forest productivity due to the loss of nutrients.

In northern soils, certain physical conditions that appear related to fire can affect both nutrient status and overland flow. Johnson and Rowe (1973, 1975) have reported that "water repellent" soils are wide-spread east of Great Slave Lake. These authors reviewed pertinent literature and concluded that this condition, although poorly understood,

- a) was usually associated with fire-prone vegetation;
- b) can cause overland flow and accompanying erosion;
- c) can conserve nutrients; and
- d) can favour growth of shrubs in other regions.

Kershaw *et al.* (1975) noted that burning produces hardened layers, known as "crustmor" in the mineral soil; these layers exhibit a coarse mineralized humus fabric. Crustmor probably results from thermal stress and oxidation of organic matter during fires and is also influenced by freezing and thawing. Sims (1976) has described the effect of prescribed burning on a

number of soil properties in jack pine sites in a paper of interest to those wishing to pursue the subject.

## 2. Permafrost

In recent years, interest in permafrost has increased in northern Canada in response to development of modern towns, industry, and major construction projects such as pipelines and highways. The effects of fire on permafrost in interior Alaska (e.g. DeLeonardis 1971, Viereck 1973*a, b*) and in northwestern Canada (Mackay 1970, Bliss and Wein 1971, Heginbottom 1973*a* and 1973*b*, Strang 1973, Crampton 1973, and Zoltai and Pettapiece 1973) have been studied. Zoltai and Pettapiece state that the most important function of vegetation in areas of permafrost is insulation of the surface from heat transfer. They point out that vegetation re-establishes rather quickly after fire but that the pioneer vegetation is a poor insulator and that thermal subsidence occurs. The frequent formation of ponds with more thermal subsidence further alters the thermal conductivity and leads to increased melting. Rowe *et al.* (1974) have further documented occurrence of subsidence on medium and fine-textured soils. Coarse soils, they found, were relatively stable after thawing. Kershaw *et al.* (1975) and Kershaw and Rouse (1976) found that soil temperatures at the surface on new and 1-year-old burns were in the optimum range for germination of spruce seeds. It is possible then, that burning insures subsequent establishment of spruce south of the treeline.

However, opinion is not uniform on the effects of forest fires in permafrost areas. Heginbottom (1973*a, b*) states that forest fires do not seriously disturb permafrost — although he does point out that the active layer is thickened and that the incidence of slope failure increases. On the basis of their studies, Kershaw *et al.* (1975)

predict that burning would cause "strong" summertime melting for at least 23 years.

The literature contains several statements to the effect that use of fire-fighting methods, particularly of heavy equipment such as bulldozers to create fire lines, frequently causes far more damage to the environment than fire itself (e.g. Lotspeich *et al.* 1970, Lotspeich and Mueller 1971, and Lotspeich 1972). Crampton (1973) stresses that effects of fire on permafrost vary with site characteristics.

Sykes (1971) points out that the extent of disagreement regarding the effects of fire on permafrost and on the degradation of the environment is to be expected because of the different effects of fire on different sites. The precise effect of a fire on permafrost would depend on presence or absence of a humus layer following the burn, the type of permafrost (whether or not it was rich in water), the slope of the land, and the nature of the substrate.

In summary, the disagreement in the literature as to whether forest fires seriously damage the land in areas where permafrost is near the surface is primarily focused on the degree of damage possible. There seems to be consensus that fire, by removing insulation in the form of living vegetation, litter, and humus causes soil temperature to rise and the thickness of the active layer to consequently increase. This is sometimes beneficial, enabling plant roots to reach nutrients that would otherwise have been locked in permafrost, and without damage to the landscape.

### 3. Fire in rocky areas

Site diversity is responsible for the occasional total destruction of soil by hot fires in areas (such as the Precambrian Shield) where bedrock is near the surface (Lutz 1956; Kelsall 1960, 1968). In Kershaw's study area, for in-

stance, an upland site was burned 2 years in succession, resulting in much greater loss of humus than only 1 year's burning, and in extensive exposure of mineral soil and boulders (Kershaw *et al.* 1975).

Some of the islands in the east arm of Great Slave lake have been denuded by fire. Following the passage of fire, heavy rains wash what soil and ash remain on the rock surface into gullies and frequently into water courses; consequently, these materials are completely lost to the land. Kelsall (1960, 1968) believed that this process had seriously reduced barren-ground caribou winter ranges in some portions of Mackenzie District.

### 4. Effects of fire on hydrology

It is evident from the literature that the effects of forest fires on hydrology depend on variables that include size and characteristics of the watershed and its water bodies, the site characteristics of the burn, the presence or absence of rainfall shortly after the burn, and intensity and size of the fire.

Connaughton (1972) and Sheridan *et al.* (n.d.) are among the few who mention the loading of streams with debris from burned and fallen trees. Although it is probable that only small waterways would be seriously affected in this manner, such waterways are often extremely important components of watersheds.

Erosion can also cause severe siltation of streams (Brown 1972). Hillman (1971) mentions increased erosion and siltation rates as one of the results of clearcutting large blocks of Boreal Forest in Alberta. Lutz (1956), Lotspeich *et al.* (1970) and Lotspeich (1972), however, conclude that erosion occurring in burned northern forests is relatively slight despite the apparent susceptibility of the soil properties to erosion. Similarly, Methven *et al.* (1975) did not note any pronounced down-slope movement of mineral soil

even after intense burning had exposed large boulders and sheets of bedrock. Lutz suggests that the lack of extensive and severe erosion is due to the prevailing low precipitation, the low intensity of rainfall in individual storms, the long annual period during which soils are frozen, and the rapid re-vegetation of burned lands.

Johnson and Needham (1966) studied the ionic composition of a stream through a coniferous forest in California for 2 years following fire. They found no specific effect on the ionic composition and speculated that as the ash constituents were dissolved by light rainfall they leached into the permeable forest soil. Because the soil was acidic, the dissolved cations were absorbed on the exchange complex rather than being washed directly into the stream.

Rises in water temperatures have been documented in cases where fires have removed shade trees from the margins of small rivers and lakes. Hillman (1971) concluded that such temperature rises occur when stands are clearcut to the stream-edge, and Levno and Rothacher (1969) found that water temperatures increased by 6.7 to 7.8°C during summer months following slash burning, which directly exposed the water to the sun. Berndt (1971), however, found relatively little fluctuation in extreme temperatures following fire in the Pacific northwest. In the north, where ambient temperatures are lower and ground water is often in contact with permafrost, less fluctuation in water temperatures would be expected in response to fire. Following fire or logging, the rate of snow melt (Berndt 1971, Hillman 1971), the rate of stream flow, and the possibility of flood hazards can increase (Brown 1972). These effects would be most pronounced where large portions of drainage basins are burned.

James (1956) calibrated four streams in southeast Alaska in order to measure the effects

of logging on them, and James (1957) and Meehan *et al.* (1970) reported the results pertinent to two of these streams. The rate of stream flow did not change although flooding was more rapid; suspended sediments increased but not significantly; and summer temperatures increased by a mean of 2.2°C. They concluded that salmon habitat was not adversely affected.

As was mentioned above, erosion and lasting damage to landscapes are more likely to result from fire-fighting activities (e.g. bulldozing of rights of way and fire breaks) and control measures than from fire itself. The study by Lotspeich *et al.* (1970) of effects of large-scale forest fires on water quality in interior Alaska is applicable to the probable effects of fire on water quality in the Canadian northwest. They examined not only the physical characteristics following the fire but also the macrofauna portion of the benthos and concluded that "Fire control methods may cause more serious long-lasting damage to the aquatic ecosystem within the burned area than the fire itself".

To summarize, large fires can cause increases in snowmelt rate, rapidity of runoff, flooding and erosion. These effects can in turn cause heavy sedimentation and siltation of streams. However, such sedimentation and siltation are not likely to be extensive following fire in northern Boreal Forest areas unless fire fighting activities have damaged the land. Stream temperatures can be expected to rise in areas where trees that provided a substantial measure of shade have been destroyed. The ionic composition of the stream studied by Johnson and Needham was not altered following a fire in the coniferous forest area that included this stream.

# Effects of fire on vegetation

Wildfire partially or fully destroys forest communities and extensively changes the vegetative structure and occasionally the plant-species composition of such communities. Pioneer species of plants that regenerate in or invade burned areas are frequently short-lived in comparison with the long-lived climax species (white and black spruce in the north), and pioneer species tend to produce light, easily disseminated seeds in numbers that favour colonization of burned tracts (Lutz 1956). Whether such changes are positive or negative depends on man's view of the primary values of forest areas. Where forestry practices prevail, fires are generally viewed as bad; where hunting and trapping is of greatest importance, fires are viewed as beneficial when replacement species are of greater value than those that were present before the fire.

## 1. Types of forests burned

Balbyshev (1964), in his study of the comparative resistance to fire of trees of the taiga zone in Asia, found that coniferous trees were less fire resistant than deciduous trees and that larch, pine, cedar, fir, and spruce were progressively less resistant. Among deciduous species, birch was somewhat less fire resistant than aspen. Balbyshev stated that the inability of spruce, cedar and fir to withstand repeated fires causes a shrinking of forest areas dominated by these species.

Rowe and Scotter (1973) reported that of the types of trees that burn in the Boreal Forest region of Canada stands of jack pine and lodgepole pine were the most susceptible in all seasons to both surface and crown fires. Surface fires are initiated with greater difficulty in white and black spruce stands than in pine stands; but when weather favours "crowning" both types of stands are probably similar in flammability. Aspen, birch, and larch litter provides excellent fuel for ground

fires during the spring, but fires only crown in these species under exceptionally dry weather conditions. Rowe and Scotter point out that "In mixed broadleaf-needleleaf stands, the hazard increases as the proportion of the evergreen tree species increases".

It is apparent from the studies by Balbyshev (1964), Scotter (1964, 1970, 1972), Kiil and Grizel (1969), Kelsall (1968), and Johnson and Rowe (1973) that the most flammable forests consist of coniferous trees and contain a high accumulation of organic litter. Spruce-lichen forests on dry upland sites are, therefore, very flammable; the least flammable Boreal Forest types are aspen and poplar in early stages of succession.

Rowe and Scotter (1973) further point out that there is no reason to believe that age brings increasing vulnerability to fire and that some of the oldest forests in the north consist of white spruce over 300 years in age. Most old forests occur on moist flood plains of river valleys. It is possible that a high humidity below the canopy and an understory of green shrubs that do not burn well deter fires in such areas. However, Rowe *et al.* (1975) have suggested that in some northern areas older stands are more likely to burn. Old dry upland forests have a much higher fire frequency than adjacent forests in river valleys. In the mountain valleys of the Cordilleran region, fire is, by contrast, most frequent in valley bottoms probably because precipitation increases up slope and valley bottoms are relatively dry.

Barney (1969) states that most fires in the interior of Alaska start on southern exposures, which are drier and hence more flammable than northern slopes. Countryman (1972) points out that variations in topography cause drastic changes in fire behaviour as the fire progresses over the terrain. Topography changes quickly in horizontal space in some parts of the Boreal Forest —

particularly in the more rugged portions of the Precambrian Shield and in the mountainous country to the west. Sesukov (1970) studied the rate of fire spread relative to topography in the far eastern sections of the Soviet Union. He concluded that owing to increasing flame contact and to a simultaneous increase in the depth and linear rate of combustion the rate of fire increases with slope gradient. With increasing fire intensity, the flames lengthen and thus make more effective contact with their fuel. Rowe *et al.* (1975) state that creeping ground fires are "common" in the "subarctic" and Wein and Weber (1974) found that as little as 400 g/m<sup>2</sup> of fuel would carry fire in the forest-tundra. Rowe *et al.* found that such fires would skirt lichen patches but would burn ericoid shrubs — perhaps because they had higher lipid and caloric content.

To facilitate fire-control in Alaska, the vegetative types of the Boreal Forest have been categorized as *conifers*, *conifer-broadleaf*, *broadleaf*, *tundra*, and *other* (mostly brush) (Viereck 1973b). According to estimates of the proportions of these various cover types that have been burned since 1900, conifers have accounted for 35.9% and the conifer-broadleaf category for 15% of total burning. Broadleaf forests, the least flammable, accounted for only 1.8% of total burning; but 47.3% of the total burned area consisted of tundra and brush-type vegetation. It is probable that the mountainous terrain of Alaska, due to site characteristics, provides a much greater interspersed of unforested tracts within the forest proper than is generally found through the Canadian northwest. Viereck considered that approximately one-quarter of the total area burned since the turn of the century was what he called "virgin forest". Fires in Alaska occur primarily in tundra, bog, and non-commercial forest sites; little timber of commercial value or land capable of producing commercial timber

has been burned. This is probably also true of northern Canada.

## 2. Forest succession

Succession is the process whereby a forest generates or regenerates itself. "Primary" succession occurs on previously unvegetated land, and "secondary" succession follows fire or other disturbances (such as clearcutting) in previously vegetated land. The common view regarding post-fire succession in northern Boreal Forests is that white and black spruce are the end products of many years of forest development and that burned stands eventually revert back to these conifers. When spruce stands burn, the sites are first dominated by growths of liverworts, mosses, and herbacious plants; these species are followed by young birch, aspen, and willow, which eventually mature and give way to the re-establishment of conifers.

An examination of the literature, however, suggests that although this relatively uncomplicated cycle does at times occur, it does so with many complex variations. Lutz (1956, 1960b) has described succession in the Boreal Forests of interior Alaska in great detail. He has suggested, in general, that black spruce forests tend to revert to black spruce following disturbance. Similarly, aspen, birch, and balsam poplar forests tend to regenerate themselves with an admixture of white spruce following a single moderate fire or several light fires. White spruce will revert to white spruce following moderate burning and will revert to aspen, birch, poplar, or spruce following single severe fires. After repeated severe fires, all these forests revert to herbacious or shrubby communities.

Lutz (1956) regarded white spruce as the climax species in Alaska and maintained that all forests, excepting black spruce on poorly drained areas, will become dominated by white spruce

provided they are not subject to repeated severe burnings. Direct analogies can be drawn between what he describes for interior Alaska and the Boreal Forest of northern Canada. Recent studies of post-fire succession in northwestern Ontario (Methven *et al.* 1975) have confirmed that burned stands regenerate to the same species that were dominant before the fire; this, as Methven *et al.* point out, implies "that cycling by fire rather than succession is the basic mechanism in this forest". They do note that aspen and birch can invade burns and establish themselves in greater densities than formerly, especially if seed sources are nearby; but they also note that the deciduous seedlings will remain subordinate to the conifers.

Viereck (1973b) provides a summary of current thinking on succession in northern Boreal Forests. He first divides northern forests into dry sites typified by south-facing slopes and by coarse river benches, where permafrost is either absent or far from the surface. Depending on the severity of fire on such sites, the usual succession is re-invasion by liverworts, seed plants such as fireweed (*Epilobium* spp.), and shrubby willows of several species, which are almost immediately replaced by tree species. Both aspen and birch, where originally present, will regenerate either by sprouting or from root suckers. White spruce will also invade within a year or two of the fire when a seed source is available. Because seed is usually not available after extensive fires, and because white spruce only produces abundant seeds approximately once in 12 years, aspen and birch tend to dominate south-facing uplands following fire. They are eventually replaced by spruce, but the process is a slow one. Few aspen stands are over 100 years old, and they generally have an understory of white spruce. Paper birch lasts somewhat longer, and mixed stands of birch and of either black or white spruce of up to 150 years of age are common on uplands. Viro (1974)

stated that in Fenno-Scandia the climax stage "is an old spruce stand of poor growth; this can rightly be called the stage of degradation of the stand". His suggested treatment was logging followed by burning of debris and litter.

Where white spruce stands are long lasting — not a common occurrence on dry upland areas — they may develop a moss layer that occasions a rise in the permafrost level. The white spruce stands can then be replaced by black spruce and bog formations. Occasionally, where black spruce has developed on coarse alluvium or thin rocky soils, replacement by aspen can follow a severe fire. The black spruce can reseed at the same time as the aspen, but because of the rapid growth of the latter, the spruce can exist for a long time only as a low understory.

On wet, poorly drained, and permafrost sites, forest succession differs according to Viereck (1973b). Such sites, which are occupied primarily by black spruce, muskeg, and bogs, and which are widespread both in the interior of Alaska and in the Canadian north, are frequently burned (in Alaska at least). However, Kershaw *et al.* (1975) state that in their study area fire was confined to dry spruce-lichen forest on drumlins and that fire only occasionally burned some of the drier parts of adjacent bogs. Even though it may be hot enough to kill the trees, fire does not penetrate deeply because permafrost is close to the surface of the ground. There is generally a rapid recovery of the shrubs, sedges and grasses that existed in the stands before the fire. Birch, where it was originally present, will often develop from root sprouts.

Such forests provide much of the winter range of the barren-ground caribou, and recovery of the lichen layer, especially of the preferred species of fruiticose lichens, is slow. According to the literature, estimates of 50 to 150 years for recovery of a full lichen mat are common. Large



quantities of spruce seed that germinate quickly are generally present in crowns of unburned trees that have been killed by fire. The pattern is one of rapid replacement of the black spruce by another dense black spruce stand. When fire is not repeated in later stages of black spruce development, sphagnum moss develops, and the forest may become an open black spruce – sphagnum moss stand or even an open bog with scattered spruce, larch and birch.

When repeated fires occur on such sites, a nearly permanent grassland of *Calamagrostis canadensis* and herbaceous plants such as *Epilobium angustifolium* can develop. Near treeline and in wetter sites, repeated fires can result in shrub thickets of alder (*Alnus crispa*), willows of various species, and dwarf birch (*Betula glandulosa*).

Cody (1964, 1965) studied a 1954 fire of natural origin that burned a 2123 km<sup>2</sup> section of the winter range of the Canadian reindeer herd east of the Mackenzie Delta. This is an area in which permafrost occurs near the surface and that would be expected to revert to either black spruce or tundra-shrub land depending on the severity of the fire. It is on the extreme northern edge of the Boreal Forest. In 1963, the spruce that had originally grown there were mostly dead; but willows, dwarf birch, and shrubs of the genera *Rosa*, *Ledum*, and *Vaccinium* were all suckering. Grasses, sedges and forbs were also "returning fairly well", but mosses and lichens were still virtually absent. Cody emphasizes that the regeneration of winter lichen range so important to reindeer was so slow that every effort should be made to control and prevent fire in such areas. Cody's observations contrast with those of Kiil and Grizel (1969), who noted that green vegetation far to the south of Cody's study area was general in all burned areas within one month of huge fires that burned Boreal Forest in northern Alberta in 1968.

The northernmost forests are predominantly black spruce and tend (even following fire) to have relatively few deciduous trees. Rowe (1970) stated that black spruce is better adapted to fire than white spruce. It is less selective in regard to sites, produces seed at a younger age, and retains semi-closed cones for several years. White spruce survives best in localities where intervals between fires are relatively long; such places typically occur on humid alluvial lowlands along rivers.

Viereck's (1973b) previously cited description of post-fire succession in interior Alaska is consistent with commonly observed conditions in the Canadian north.

Wagg (1964) and Lacate *et al.* (1965) found that the highly productive stands of white spruce that flourish on the alluvial soils of the lowlands of the Peace River and the Slave River owe their structure to either a history of fire, which prepares suitable seed beds, or periodic flooding, which deposits rich sediments. Similar sequences were reported where large stands of white spruce were present on alluvial soils in Alaska (Viereck 1970).

Jack pine is a locally important component of northern forests in limited areas of the southern Mackenzie District, and it is somewhat more common in the adjacent forests of northern Saskatchewan and Alberta. Scotter (1964) studied various jack pine stands, as did Dix and Swann (1971), in Saskatchewan. Jack pine forests characteristically occur on dry upland sites that have been repeatedly burned. They tend to be self-perpetuating because jack pine seed cones are resistant to fire and because there is no lack of seed. Because jack pine stands are more flammable than other stands, this species may have adapted to facilitate fire spread.

Methven and his co-workers also studied a southern Boreal Forest area where permafrost was not present. They advanced the following

hypotheses regarding post-fire succession (Methven *et al.* 1975):

a) Fire is a normal and necessary component of the Boreal Forest, and its exclusion is unnatural.

b) Fires in the Boreal Forest always result in the re-establishment of forest.<sup>4</sup>

c) Whether the same species predominates after fire as before depends partly on the fire frequency and partly on the proximity of other seed sources.

d) Seeding-in is completed quickly, and all individual young trees capable of taking part in the stand development are present from the start. There is no succession in the normal sense of the term, only a cycling of the forest by fire.

### 3. The mosaic effect

The traditional concept of primitive North American forests is one of huge expanses of monotypic, self-perpetuating climax stands. Disturbances such as fire were thought to be at the most a minor influence on otherwise widely stable ecosystems.

Current thinking suggests that few stable climax forests exist anywhere except under special and local conditions, and this thinking is especially relevant to the northern Boreal Forest. Heinselman (1970) exemplifies this trend in his statement that "The primeval landscape was a vast mosaic of stands in various age classes and successional stages following fires, interspersed with recently burned areas". It is his opinion that whole ecosystems have evolved in response to fire.

Kilgore (1973), who also believes that coniferous forests are dependent on fire, maintains that fire initiates new succession and produces

"the mosaic of vegetation that supports animal components". Wright and Heinselman (1973) point out that the historical overview of coniferous forests provided by such tools as tree-ring, charcoal and pollen analysis adds a new dimension to the old concept of climax forests. In a fire-dependent coniferous forest, fire is the principal long-term environmental factor of influence. In the short-term, the climax stage is occasionally approached in local elements of the mosaic that have escaped fire for a long time (such as islands in lakes). Continuation of present, widespread policies of fire suppression would increase the probability of the attainment of climax-forest in many areas.

Most forests of the holarctic region seem to be fire-dependent. Fire has, according to Uggla (1958), always determined the extent and composition of Boreal Forest in Sweden. Concerning Minnesota, Frissell (1973) claims that pre-settlement forest communities were predominantly sub-climax and fire-dependent. Frissell is among the increasing number of recent authors who carefully point out that man's forest protection activities have interfered with natural processes. He states that successional development to climax will reduce both vegetational variety and ecological niches and that it will, consequently, reduce diversity of wildlife species. If the natural biotic community is to be restored in the protected forests of Minnesota that he studied, fire must be allowed to return to the ecosystem. Heinselman (1970), in exactly the same vein, points out that entire ecosystems, including their wildlife components, have evolved in response to fire. He favours either suppressing all fires from natural causes and replacing them with controlled burns or, as an alternative, allowing lightning fires to burn and prescribing additional controlled fires where necessary to maintain a natural fire regime.

<sup>4</sup>Note, however, Viereck's (1973a) comment (above) on the effect of repeated burning in the far north.

Loope and Gruell (1973) trace the history of fire in northwestern Wyoming back to the 1600's and 1700's. Following fire in this area, fir invades and causes a great increase in coniferous cover and, ultimately, a relatively sterile forest as far as wildlife is concerned. Loope and Gruell recommend prescribed burning to restore the natural mosaic effect in such places as Grand Teton and Yellowstone National Parks, where intensive fire suppression has been in effect for many years and where coniferous forest is assuming dominance.

Taylor (1973) studied biotic succession in lodgepole pine burns in protected forest areas of Wyoming. Numbers of plant, bird and mammal species increased during the first 25 years after fire; following this period, however, all species decreased in numbers. Taylor concluded that suppression of fires would reduce or eliminate species that are present only in early or open-canopy forests.

The natural mosaic of the northern Boreal Forest results from the effects of forest fires but also from variations in site. Lutz (1956) and Viereck (1973) discuss factors that are influential in the interior of Alaska, and Rowe and Scotter (1973) discuss the Boreal Forest in general, but many of their remarks pertain directly to the forests of the Canadian northwest. Kershaw *et al.* (1975) note and illustrate with aerial photographs the patchwork of different-aged burns on drumlins northeast of Uranium City. Miller (1976), referring to northern Manitoba, notes that it is difficult to find an area of homogeneous cover of more than 4 ha.

Available evidence shows that the forest mosaic is dynamic: that in the short term, succession proceeds on each area that is burned or otherwise subjected to a major disturbance. There are, however, a variety of ways in which succession can occur, and the mode of succession de-

pends on characteristics of individual sites (see section on Succession). Studies of pre-history have shown that in the long term periods of intensive burning have often been succeeded by periods of little or no fire. There are, therefore, both short-term and local changes and long-term and widespread changes in forest composition.

To summarize, forest succession has been intensively studied both in the northern Boreal Forest and elsewhere. Although there are general similarities, the mode of succession that can occur in each individual area depends on several factors that include the type of fire, the type of forest burned, presence or absence of permafrost, extent and quality of fuels on the forest floor, presence or absence of suitable seed for forest regeneration, topography and exposure. Many northern forests do not necessarily revert to deciduous growth following the burning of conifers. Black spruce in particular tends to be self-perpetuating and to dominate the northernmost Boreal Forest areas of Canada.

It is probable that the northern coniferous forests are fire-dependent, in that fire provides for a dynamic ecosystem, much richer in plants and animals than it would be otherwise. The interspersed forests of many different ages into a widespread mosaic is a natural feature. Where fire suppression is particularly efficient and long-lasting, the natural mosaic can be lost unless other factors replace fire as a disturbance factor. Forests that are protected with optimum efficiency will proceed to a relatively sterile and homogeneous climax of conifers or, where permafrost is near the surface, to a black spruce forest that may ultimately develop many sphagnum bogs. Examples of such climax associations are sufficiently rare that their composition and dynamics are not well known. They may "cycle" to young growth by wind, disease or insects in the absence of fire or logging.

# Effects of fire on wildlife

The literature contains many references to the effects of fire in Boreal Forests on fur and game mammals and their habitats and some references to the effects of fire on game birds such as grouse and waterfowl. However, except for studies of moose (*Alces alces*) and barren-ground caribou (*Rangifer tarandus*), there has been little research on fire-wildlife relationships in the Canadian northwest. General relationships for most of the important species can, though, be deduced from analogy.

In the following sections, nomenclature follows Crossman and Scott (1973) for fish, Godfrey (1972) for birds, and Burt and Grossenheider (1964) for mammals (except where otherwise noted).

## 1. Fish

The literature contains little that is directly pertinent to the effect of wildfire on fish, particularly on species of the Canadian northwest. Crossman and Scott (1973) provide descriptions of all the freshwater fish of Canada, and their text includes notes on the distribution, biology and importance of each species. McPhail and Lindsay (1970) provide similar coverage but specifically for northwestern Canada and Alaska.

Fish, their habitats and their susceptibility to disturbance caused by construction in the Mackenzie River Valley have recently been described by Hatfield *et al.* (1972), Dryden *et al.* (1973) and Stein *et al.* (1973). They itemize distribution and abundance of the various species in the Mackenzie River system (in the Northwest Territories) and provide notes on water quality, food habits and recommendations for the protection of fish in the event of highway or oil-pipeline construction. Jessop *et al.* (1973) conducted intensive studies of the fish resources of the Rat River and the Rabbitskin River. The aquatic ecology and fish resources of the Yukon Territory have been

investigated by Bryan (1973) and Bryan *et al.* (1973).

The few direct references to the effects of fire on fish are typically more provocative than informative. Thus Ahlgren and Ahlgren (1960), for instance, state that fish are frequently killed because of the wash of ash into the lakes and streams after fires; and Davis (1959) maintains that the "lye" leaching from the ashes of larger fires can kill whole fish populations. These authors may have been following Leopold (1923), who recounts that in 1900 many dead fish were found in the Saco river in New Hampshire following a severe fire (itself followed by heavy rain). The fish were "presumably killed by the alkaline ashes washed into the water". Hakala *et al.* (1971) record that salmon mortality was extensive immediately following a 34 400 ha fire on the Kenai Peninsula in Alaska in 1969; the causes of this mortality were unknown. However, there were no long-term effects. Most recent literature provides little cause for alarm concerning the possible effects of fire on fish in the Boreal Forest (see below and earlier section on Hydrology).

According to Sheridan *et al.* (n.d.), siltation and debris from logging in Alaska affect fish populations, especially salmon and trout, not only by destroying spawning beds, for which clean gravel is required, but also by destroying bottom populations of aquatic insects. These authors mention cutthroat trout (*Salmo clarki*), rainbow trout (*S. gairdneri*), pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), king salmon (*O. tshawytscha*) and Dolly Varden (*Salvelinus malma*). McPhee (1969) discusses siltation in some detail although not specifically in fire-related context. Siltation caused by deposition of ash and other airborne debris and perhaps by burned trees falling directly into water bodies could occur where terrain conditions are suitable

and when the burn is sufficiently intense. This would be followed by erosion during the first rains following the fire. Severity of erosion would depend on slope, soil structure and texture, proportion of drainage basin burned, and intensity of rainfall (Rutter 1968).

Most fish are tolerant of only a narrow range in temperature. Levno and Rothacher (1969) measured changes in stream temperatures after slash burning in an experimental watershed. They found that following burning, water temperatures increased by 6.7 to 7.8°C as a result of direct exposure to the sun in areas where shade had been removed. Such temperature increases would affect fish and the aquatic organisms on which they depend for food. However, Meehan *et al.* (1969) and Meehan (1970) found that although removal of shade trees from streams in southeast Alaska resulted in increases of water temperature the increases were not sufficient to affect fish.

Lotspeich and Mueller (1971) suggest that fire is often far less damaging to the aquatic environment in the taiga than are fire fighting activities. The use of heavy machinery can strip the land and result in serious erosion, and the commonly used phosphate-base retardants used in fighting fire possibly contribute in a minor way to the eutrophication of small lakes. Martin *et al.* (1969) demonstrated a rise in pH from 4 to 5 in unburned pine litter and humus, to 6 to 7 in partly burned stands, and to 9 to 13 in completely burned forest. Although they did not relate their findings to hydrology or fish, it is possible that if rains were to cause a heavy runoff of ash with extremely high pH values into smaller streams and lakes, fish mortality could result either directly or as a consequence of a sudden reduction in food organisms not adapted to alkalinity. Knight (1965) suggested that a pH in excess of 10.7 may be harmful to speckled trout (*Salvelinus*

*fontinalis*), but Welch (1952) did not consider pH to be a limiting factor for many fresh water organisms.

Brown (1972) studied effects of a severe fire on the hydrological characteristics of two streams in New South Wales (Australia) and concluded — as do most American hydrological studies — that the amount of runoff was significantly greater for at least 4 years following the fire, that sediment loads carried by both streams were much greater than before the fire, but that there was a progressive reduction in all the effects with the passage of time. His conclusions were similar to those of MacPhee (1969), and it seems probable that increased runoff and sedimentation could produce adverse conditions for fish for at least several years post fire.

In a study of benthic macro-organisms present following large fires in interior Alaska, Lotspeich *et al.* (1970) concluded that effects were negligible or of such short duration that benthos returned to normal in the brief time before evaluation started. There may have been fleeting effects on aquatic organisms as a result of increased turbidity in the streams caused by erosion from bulldozed fire lines. In addition, these authors state "Even though we have been able to show some changes in the chemical make-up of the water, especially some of the nutrients and potassium, these changes must have been below the magnitude necessary to effect a change in the portion of the aquatic population we examined. To further substantiate this hypothesis, fish collected from the burned area were no more difficult to obtain than from outside the area and were in good physical condition, feeding voraciously on the aquatic insects from the streams."

Meehan *et al.* (1969) studied the effects of clearcutting in southeast Alaska and, on the basis of the return of pink salmon and chum salmon,

concluded that such cutting, although it caused small changes in water quality, did not adversely affect the spawning habitat of these species.

To summarize, we found suggestions in the literature that fire can be detrimental to fish populations under some conditions. Davis (1959), for instance, puts it very strongly in his statement that "The effects of fire on fish populations are consistently adverse; prescribed use of fire seems to have no place (in fish management)". Adverse effects can result from increased flow rates, from siltation, from sedimentation in streams, from increased erosion from the surrounding land, and perhaps from a change in water quality due to the runoff of ash, which has a high pH. Fish are known to be intolerant of temperature changes, and forest fire could raise the temperature of small streams and rivers by removing shade trees.

However, these factors may not be as serious in the Canadian northwest as elsewhere. Most studies show that effects of fire and logging on aquatic organisms in northern ecosystems are negligible. It would seem wise to assume that the organisms in large streams, rivers and lakes are probably not affected except under unusual conditions but that effects could follow in an increasing order of magnitude with decreasing size and flow rate in water bodies involved. Erosion and increased sedimentation could be detrimental wherever they occur.

## 2. Birds

Wildfires affect waterfowl both directly and indirectly. Although Leopold (1923), Ahlgren and Ahlgren (1960) and Ward (1968) point out that fires raging through a marsh in spring will destroy nests and young of waterfowl and of other birds (e.g. red-winged blackbirds (*Agelaius phoeniceus*)), the consensus seems to be that the burning of marshes is beneficial in the long run.

The deliberate burning of marshes has a long history in North America. Fire rids marshes of dead grass, sedges, and shrubs and makes new shoots available to cattle, furbearers, and waterfowl. Furthermore, burning releases nutrients from organic litter — usually potassium, calcium, phosphorus, magnesium and chlorides (Yancey 1964).

Davis (1959) and Ward (1968) agree that fire opens up dense marsh growth to a degree that suits feeding waterfowl. According to Ward, in fact, "Unless the large marshes of Manitoba are managed for waterfowl with fire as a major tool they will cease to serve their primary purpose. Indeed, within a short time they may cease to exist as marshes". This situation would result because the heavy growth of marsh vegetation would literally produce, within a few years, a litter of organic material that would completely block and fill in shallow waters.

Ward (1968) concluded that fires before April 20 would be too early to affect nesting waterfowl at Delta Marsh in Manitoba (on the edge of the Boreal Forest). Summer fire would probably damage plant roots, and its possible long-term benefit would be greater because it would create more open areas and edges.

In dry summers, peat marshes can burn down to the point where new water bodies are created (Davis 1959, Ward 1968). Productivity of marshes within the northern Boreal Forest in Canada could probably also benefit from occasional burning, particularly in dry periods. Klein (1971) states that the productivity of several major waterfowl areas in interior Alaska seems to be maintained by two natural factors, periodic flooding and periodic fires.

Erskine (1971) points out that buffleheads (*Bucephala albeola*), common goldeneyes (*Bucephala clangula*) and Barrow's goldeneyes (*B. islandica*) usually use the holes of flickers

(*Colaptes auratus*) for nesting. Suitable nests are usually found in poplar trees during successional stages following fire. The large dead stumps of fire-killed spruce and poplar are particularly useful to flickers and hence to buffleheads and goldeneyes.

Willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*L. mutus*) regularly migrate into the northern Boreal Forest in winter (Godfrey 1972). These species are ground-loving birds that feed during winter almost exclusively on willow and birch buds and dried berries, where they protrude through the snow. Because they confine their activities to forest edges and to the young and shrubby plants that succeed following fire, they benefit from wildfire in the northern forests.

Blue grouse (*Dendragapus obscurus*) occur within the Boreal Forest at the extreme eastern edge of their range in Mackenzie District, and in the Yukon Territory. It was long thought that the blue grouse was a fire-dependent species, but Redfield *et al.* (1970), after 20 years of study, have concluded that this is not the case. They found that wildfires were not necessary for high blue grouse populations, that grouse densities were not improved when burning reduced forest land to earlier stages of succession, and that fire may well have inconsequential immediate effects on these birds. Bendell (1974), who generally concurred with these findings, cited studies that showed that intraspecific competition between territorial males was the proximal regulation of blue grouse numbers. However, he believed that very large burned-over areas (> 12 000 ha) would support denser populations of this species.

Three widespread species of grouse that inhabit the Boreal Forest year-round are the sharp-tailed grouse (*Pedioecetes phasianellus*), the ruffed grouse (*Bonasa umbellus*), and the spruce grouse (*Canachites canadensis*). Cringan (1958) and Aldrich (1963) have expressed the generally held view that sharp-tailed grouse in the northern

forests require recently burned areas. Supporting this view is the well-known preference of this species for open and shrubby areas over dense forest. Ruffed grouse appear at the sapling stage following burns, and spruce grouse appear at the polewood stage in aspen succession, approximately when sharp-tailed grouse begin to disappear. As succession proceeds from aspen to conifers, ruffed grouse diminish in numbers and spruce grouse increase. Johnsgard (1973) reported that spruce grouse in Alaska seem to prefer white spruce and birch uplands for summer use and pure coniferous forest in winter. Though ruffed and spruce grouse may have common ranges, the former prefer deciduous growth during both winter and summer. Paper birch and aspen are the major winter foods of both ruffed grouse and northern sharp-tailed grouse, but the latter prefer early stages of forest succession. As Johnsgard (1973) points out, the northern races of all these birds have received little study.

Hakala *et al.* (1971) noted that grouse re-invaded the area of a great 1969 fire on the Kenai Peninsula in Alaska the year following the burn. In Minnesota, however, burns are occupied by ruffed grouse 4 to 12 years following fire; the birds thrive for 10 to 15 years, until the number of stems in the maturing forest drop below 800/ha (Johnsgard 1973). Sharp (1970) believed ruffed grouse to be a fire-climax species that benefits directly from recurring fires. He points out that the key food plants are fire induced and further suggests that nesting sites, which are usually devoid of low vegetation, indicate a specific adaptation to fire.

Doerr *et al.* (1970) conducted an intensive and seminal study of the effects of a 1968 forest fire on a ruffed grouse population in the Boreal Forest of north-central Alberta. They found that reproduction during the year of the fire was almost a complete failure because eggs and nests

were burned, and grouse did not re-nest. Doerr *et al.* also noted that immediately after the fire the numbers of grouse in the burned area decreased by 50%; this, they point out, was due not to fire-caused mortality but to large-scale egress of hens and adolescents of both sexes. Grouse were, in fact, observed avoiding the flames with ease.

Large-scale egress of hens and immature ruffed grouse also explains the abnormally high ratio of males to hens that persisted for 2 years following the fire. The males, because of their territorial-oriented breeding instinct, remained in the vicinity of the burn. (Several studies remark on the fixation of the cock grouse to his drumming log and on the more transient characters of the hen and the immature grouse). As a result, normal numbers of cocks were available to serve a drastically lower than normal number of hens; this overbalance in the breeding population caused 2 years of low grouse production. Apparently, over the 2 years following the fire, vegetative recovery had not been sufficient to attract or hold female grouse. The gradual attrition of males and the reluctance of newly mature males to claim vacated drumming sites in the area of the burn were also evident. Hence, by 1970, the number of drumming males on unburned areas was three times greater than that on the burn — although pre-fire densities had been similar.

Gullion (1970), in a review of the ecological impact of fire on ruffed grouse and their habitat, concluded that these birds derive "seven distinct and important benefits, . . . from occasional fire in the forest". Gullion's paper is important to this discussion because it lends support to Cringan and Aldrich and by implication sets itself in partial opposition to Doerr *et al.* In agreement with Cringan and Aldrich, Gullion argues that ruffed grouse thrive well "in subclimax forest

situations" and that they fare poorly in unbroken or mature coniferous stands. In support of this popular view, he refers to reports that date back to the last decade of the 1800's and to the mid-1900's and that "point to a scarcity of Ruffed Grouse" in "unbroken coniferous forest regions".

Of particular interest here is Gullion's suggested attribution of the contemporary decline in ruffed grouse populations in his study area and in the Minnesota Boreal Forest in general to "increasingly efficient fire suppression by the state and federal forest services". Though these improved suppression measures have "sharply reduced the menace of extensive and catastrophic fires in Minnesota's forested regions", fires do not, Gullion speculates, directly threaten the well-being of resident ruffed grouse. As he puts it, "fire might be the missing ecological catalyst needed to produce higher density grouse populations". To Gullion then, it appears "that there is a strong positive correlation between the extent of forest fires in northern Minnesota and the abundance of Ruffed Grouse".

However, the findings of Doerr *et al.* raise doubts that ruffed grouse are a fire succession species that derive both immediate and midterm benefits from burning. Their observation of the post-fire reduction in the density of the ruffed grouse population in the burned-over Rochester (Alberta) study area — a reduction that persisted over 2 years — supports the conclusion that burned areas, despite the extent and nature of improvements brought about by fire, must be able to compete in attractiveness with adjacent unburned range before they can reclaim hens and immature young that have left after burning. For those who advocate fire as a blessing to ruffed grouse, the drawback is, simply, that improved habitat cannot benefit an absent grouse population. To date, the long-term impact of burning



on grouse in northern Boreal Forest remains unclear.

We know of no studies of song birds in relation to fire in the north, but Emlen's (1970) study of a coniferous forest in Florida provided possibly applicable results. After the forest had been burned deliberately as a management procedure, bird counts were conducted both in the burned areas and in immediately adjacent and ecologically similar unburned areas. During the first few months following the fire, numbers of birds were essentially the same in both areas. Emlen attributed this to the home-range attachments of the individual birds and to the brevity of the disruption caused by the fire. Bendell (1974) analyzed 11 studies of species composition and population densities of birds before and after burning in a number of regions. Populations showed little change, but Bendell pointed out that the data were often from short-term studies and that the studies included small samples.

It seems probable that in northern forests, where most bird species are migratory and are hence absent for a large part of the year, changes would be evident over both short and long periods. Following burning of a white spruce forest in Alaska in 1948, only 19 birds of 7 species were seen during 20 hours of observation. By 1957, nearly 200 birds of 19 species were seen. By 1961, only 16 species were present; woodpeckers were particularly well represented because of insects in the fire-killed spruce (Klein 1963).

Telfer (1973) has shown that the habitat requirements of 21 species of wood warblers common to the Canadian Boreal Forest vary extensively. Thus, although the Tennessee (*Vermivora peregrina*), magnolia (*Dendroica magnolia*), chestnut-sided (*D. pensylvanica*), blackpole (*D. striata*), yellow-throated (*D. dominica*), mourning (*Oporornis philadelphia*), Connecticut

(*O. agilis*), and Wilson's (*Wilsonia pusilla*) warblers all prefer early successional stages of forest growth, many others prefer mature forest. A few, in particular the northern waterthrush (*Seiurus noveboracensis*) and yellow warbler (*Dendroica petechia*), prefer a medium successional stage of small tree growth. It is evident from Telfer's list that a homogeneous forest, whether coniferous or deciduous, would have a lesser variety of warblers than one having a mosaic of varied successional stages.

Komarek (1969) has pointed out that hawks and eagles are attracted to fire because they find ready prey among small birds and mammals displaced by the flames.

To summarize, the available evidence suggests that fire provides a diversity of habitat which, in turn, provides for a diversity of avifauna. When fire burns a mature coniferous forest, the numbers of spruce grouse diminish because their optimum habitat is destroyed. At the same time, however, new habitat is created for sharp-tailed grouse and, eventually, for ruffed grouse. The succession of trees in a forest is followed at each stage by a succession of bird species particularly adapted to the conditions of the moment. The evidence also suggests that although nests and young birds in forests and marshes may be lost to fire during the nesting season, the longer-term effect is generally beneficial.

### 3. Mammals

Much has been written about the effects of forest fires on mammals. The classic picture, often referred to as the Smokey Bear Complex, shows terrified animals either running for their lives before a raging fire or burning to death. A review of current research and thinking suggests that the perpetrators of this sort of fire-prevention publicity have consistently misinformed and misled the public. Handley (1970) is one of many

who suggest that because many forests are extremely subject to fire, mammals have evolved with and are, therefore, adapted to fire. Some habitats, particularly some grasslands, are in fact perpetuated by fire. Komarek (1969) points out from personal observation that mammals do not seem to fear fire. They often find refuge within it and, failing that, do not generally flee ahead but simply move to one side or the other. Buckley (1958) adds that "The direct destruction of animals by fire is probably never of lasting importance; the more subtle effects, exercised through changing hydrologic relations and vegetative composition, are far more significant".

Edwards (1954), in his study of the effect of wildfire on dense Columbian Forest in British Columbia, demonstrates that habitat change, although it adversely affects some mammals, benefits others; he further comments that ecosystems are probably never stable and that the world would probably be a much less interesting place if they were. The fire observed by Edwards destroyed the climax habitat used by marten (*Martes americana*) and hence removed these mammals for decades; this fire also greatly restricted grizzly bears (*Ursus horribilis*) and wolverine (*Gulo luscus*). Woodland caribou (*Rangifer caribou*), which range in mature forest for part of the year, declined. There were, however, spectacular increases in the numbers of mule deer (*Odocoileus hemionus*) and of cougars (*Felis concolor*) and coyotes (*Canis latrans*), which prey upon these deer. Beavers (*Castor canadensis*) and ground squirrels (*Citellus* sp.) increased, as did black bears (*Ursus americanus*) that moved in to take advantage of berry-producing shrubs. Mountain goats (*Oreamnos americanus*) were above the fire on high ground and were little affected. The most important consequence was the invasion of moose, which, though previously unknown to the area, became common, as did

wolves (*Canis lupus*), their major predators. Changes of this sort — though not always on such a pronounced scale, can be expected wherever Boreal Forest is subjected to wildfire.

### 3.1. Small mammals

Edwards (1954), Hakala *et al.* (1971), and Kayll (1968) point out that burning either benefits small mammals or causes only temporary declines in their populations. Because vegetative recovery enormously increases biomass on the burned area, these declines are more than compensated for in a short time. Howards *et al.* (1959) conducted experimental and observational studies of behaviour of vertebrates during controlled burning. They found that small mammals remained calm and managed to avoid hot spots and the heat of fires by running, burrowing a short way, hiding in rock outcrops, or seeking unburned patches. The results of 11 studies cited by Bendell (1974) showed that populations of 80% of the species did not change with burning but, rather, "carried on as usual".

Several studies conducted in coniferous forests elsewhere are relevant to fire in Boreal Forests. It should always be kept in mind, however, that the severe winters and special conditions that occur in the northern part of the Boreal Forest may create a situation that differs from situations in other forests. Tevis (1956) investigated whether or not slash burning following logging would reduce populations of forest mice. Before burning, 41 mice of several species were trapped, tagged and released on a 6.5-ha area. Three weeks following the fire, only 13 mice were taken; but in two and a half months, after the first rain had washed away the heavy deposition of ash, 72 mice were taken. Tevis concluded that slash burning does not control mice.

Ahlgren (1966) compared small mammals for 4 years in logged, unlogged, and burned jack

pine areas. He found that deermice (*Peromyscus* sp.) recover immediately after fire because burning makes the seeds on which they feed more available. Fire opens cones and uncovers seeds that have been buried under organic litter. Red-backed mice (*Clethrionomys* sp.) and chipmunks (*Tamias striatus*) appeared during the first season after the burn and became abundant during the third year. Ahlgren (1966) concluded that chipmunks need vegetation and fruit as well as seed for food and that they need taller vegetative cover than the small mammals. The results of the study conducted by Sims and Buckner (1973) in burned jack pine in Manitoba were similar. Over a 3-year period, populations of deermice (*Peromyscus maniculatus*) increased well beyond pre-burn levels while other species recovered slowly.

Hooven (1969) found that wildfire selectively reduced populations of small mammals in coniferous forest in western Oregon. Like others, he also found that recovery, particularly of deermice, was rapid. He believed that such recovery resulted mainly from re-invasion of the burn and found that within 14 months small mammals were more abundant on the burn than on comparable unburned forest. This he thought was due to the diversity of vegetative succession, which provided a greater diversity of food and cover than was previously available.

Cook's (1959) study of the effects of fire on a population of small rodents in an area of mature grassland with scattered brush showed effects quite different from those observed when forests were burned. Cook found that there was an initial annihilation of small mammals either directly because of the fire or indirectly because of removal of food and cover. Apparently, this annihilation occurred because the grassland area was homogeneous, with a deep layer of organic litter that burned down to the mineral soil. Re-

covery, when it occurred in the second year following the fire, was spectacular: six species of four genera of small mammals were present in great numbers. Cook observed that the species composition of the population shifted with recovery. Because there was little or no brush left on the area, grass-dwelling mice became the dominant forms.

To summarize, there is consensus that forest fires do little permanent damage to small mammals, who do not seem to fear fire and efficiently find refuge within it. They survive forest fires well and recover quickly. They do not, however, cope successfully with fires on grassland, where deep homogeneous organic litter may cause hot fires that burn down to the mineral soil. Species composition tends to shift following fire, with deermice assuming dominance in the initial stages of recovery. Conditions in the northern forests probably differ somewhat from those in the studies cited. With shorter breeding seasons, recovery could be considerably slower than reported elsewhere, particularly if fires burned Boreal Forest late in the summer.

### 3.2. Furbearers

Most writers agree that wildfires are beneficial to the beaver and muskrat (*Ondatra zibethica*). Deliberate burning has played a major role in the management of muskrats in the southern and Atlantic states of the United States for generations (Errington 1963, Yancey 1964, and Ward 1968). According to Errington (1963), Davis (1959), and Kayll (1968), burning keeps marshes at a subclimax state that is most productive of food such as *Scirpus* sp.; burning also removes grasses that could crowd out useful plants and, eventually, muskrats as well. Opening marshes by fire and creation of ponds in burned peat benefits muskrats and waterfowl. Errington further considered natural fire "to have been a

permanent factor in the ecology of the marshes". Klein (1971) believed that furbearers benefited directly from wildfire in major marshes of the Boreal Forest of interior Alaska.

Patric and Webb (1953) and Heinselman (1970) point out that the beaver is best adapted to early stages of forest succession. Beaver depend primarily on deciduous trees for food and for necessary building supplies; in the north these trees are aspen, poplar, birch and willow. Aspen is preferred wherever it is found. It and birch are almost always a component of new succession following fire in the north. Beaver are virtually absent from many areas where coniferous forest dominates late-succession stages.

Coniferous forests do, however, maintain large populations of red squirrels (*Tamiasciurus hudsonicus*). Ahlgren and Ahlgren (1960) found that squirrels were eliminated for 10 to 25 years following burning in southeastern forests. It seems probable that these squirrels would be absent for periods of similar duration following the fires in the north.

It is a common assumption that marten prey to a great extent on red squirrels and that their populations fluctuate according to available numbers of these squirrels. However, this assumption (which may be valid in southern forest) is contradicted by studies of marten in Alaska and Siberia, conducted in areas of similar habitat to that which prevails over much of the northwestern Boreal Forest of Canada. According to Lensink *et al.* (1955), 72% of the diet of marten in Alaska consists of redbacked mice and meadow voles (*Microtus* sp.), 17% of berries and other vegetation, and the rest largely of birds. Their quantitative findings were similar to those of researchers in Siberia, whom they quote.

There seems to be no doubt that late succession forests with large trees provide more denning holes and better general habitat for both marten

and fisher (*Martes pennanti*) (DeVos 1951). According to DeVos, both species are virtually absent from recent burns or logged areas, and the fisher does better in second growth than marten.

Lensink (1953) concluded that the distribution of marten in Alaska was decidedly coincident with that of spruce forests, which were the most important component of their habitat. Treeless areas and areas on which aspen and birch dominate following fire are abandoned by marten. The management of marten habitat, according to Lensink, requires control of forest fires.

The effect of fire on snowshoe hares (*Lepus americanus*) in north central Alberta was studied by Keith and Surrendi (1971). This study was particularly thorough because the population involved had been the subject of intensive research before the fire and because many animals had been marked. The burned area included diversified Boreal Forest cover ranging from bog to dry upland sites. There was no evidence of direct mortality due to fire — although hares abandoned severely burned sites. They remained in areas that were not damaged or only moderately damaged. Pregnancy rates and numbers of juveniles were reduced immediately after the fire. It was thought that young animals probably left in greater numbers than adults: the younger animals would be forced out because of reduction in area of available habitat. Complete reoccupation of the area occurred in the second summer following fire, when brush cover had again developed.

In summary, the effects of fire in the Boreal Forest on furbearers depend on the species involved. Red squirrels are reduced where coniferous forest is severely burned and cannot reoccupy an area in large numbers until conifers are established again. Neither marten nor fisher do well immediately following fire — although there is evidence that both species can thrive in

late stages of succession, when conifers once more dominate the landscape. Most other fur-bearers probably benefit from fire. It is probable that the herbivores, muskrat, beaver, and hares, find food sources more abundant shortly after fire. Small carnivores, such as weasels (*Mustela* sp.), benefit from the increased biomass of prey species that almost always results when fire creates faster growth and a greater diversity of plant species.

### 3.3. Caribou

Though woodland caribou have received little study, those of the Boreal Forest in northern Ontario have been investigated by Peterson (1955) and Cringan (1958). Heinselman (1973) discussed a decline of woodland caribou in and their subsequent disappearance from Minnesota. These authors agree that woodland caribou require lichens for winter food. Cringan and Peterson believed that caribou decrease with burning of forests and destruction of food sources and are replaced by moose. Cringan pointed out that as Boreal Forest matures and moose decrease, woodland caribou slowly increase. Stelfox and Taber (1969) concluded the same for coniferous forests of the northern Rocky Mountains. Under fire suppression, "grass and shrublands reduce as plant communities advance toward maturity", and "Favourable caribou habitat will develop where fir and spruce are the climax species".

Although young seral stages favour deer, wapiti (*Cervus canadensis*) and moose, Heinselman thought that the picture was not quite so simple. In Minnesota, the time of caribou disappearance did not everywhere coincide with a period of heavy burning of forest. He believed that two factors were involved: the destruction by fire of arboreal lichens in mature forest and of ground-growing lichens on open ridges, and increasing hunting pressure. However, the recent discovery

that caribou and reindeer are extremely susceptible to *Paraelaphostrongylus tenuis*, a parasite of white-tailed deer (*Odocoileus virginianus*) (Anderson 1972), raises the possibility that caribou decreases may be related to the northern extension of white-tailed deer.

Banfield and Tener (1958) discussed distribution and condition of Ungava caribou, which Banfield (1961) considered members of the woodland group. Forest fires, they believed, were a primary influence on the depressed Ungava caribou populations. They found that the ranges of central and eastern Ungava were relatively intact but that the western ranges "have suffered great destruction" from forest fires, with up to 25% of the mature forest having been burned.

The barren-ground caribou of the western Canadian Boreal Forest and of adjacent tundra have been the subject of one of the most comprehensive and continuous research programs devoted to major mammals in North America. Studies have been continuous since 1947. However, the resulting reports and publications, and comparable studies in Alaska, present a picture that is not as clear as might be expected.

Banfield (1954), in reporting the first Canadian studies, stated that destruction by fire of the larger part of the winter range of caribou would result in starvation and consequent reduction of the caribou population. In his statements, there seems to be an implication that man was largely responsible for extensive recent burning of the winter caribou range. He noted, as have all the biologists who followed in his footsteps, that caribou apparently avoid burned areas in winter and that during their winter wanderings they at times take circuitous routes to avoid such areas.

Courtright (1959), in a thesis which deserves to be better-known, concluded that fire in Alaska was much more destructive to lichens than grazing. Repeated burning may result in permanent

replacement of lichen forest by grasses, sedges and other plants. He thought that fire, logging and air pollution (to which lichens are most intolerant) have reduced the extent and continuity of lichen cover.

Kelsall (1957*b*, 1960, 1968) enlarged on Banfield's (1954) studies. He concluded that although barren-ground caribou depended on lichens for only about 40% of their winter food they nevertheless had a strong predilection for mature spruce-lichen forest, using it, where available, to the exclusion of earlier stages in succession.

During the time of Kelsall's studies, caribou numbers were believed to be the lowest in recorded history. Kelsall concluded the following: that the limiting effects of forest fires had been negligible on the caribou population only because the numbers of animals were low and declining, that fire had increased in recent times due to human technological activities on the ranges, and that an increasing caribou population would be limited to a level well below what might have been possible only 40 to 50 years previously.

During this period in Alaska, similar opinions were held by Leopold and Darling (1953) and Lutz (1956). It was believed that in interior Alaska fire was principally responsible for greatly reduced numbers of caribou. Much evidence suggested that fires had increased in size and frequency following settlement and gold-rush days and that not more than 20% of the original white spruce forests remained. On the credit side, it was invariably noted that fires, which had eliminated lichen ranges for caribou, had created extensive areas of good browse for moose. Leopold and Darling (1953) suggested that moose, caribou and reindeer could be regulated through strategic control of forest fires.

Pruitt (1959) studied snow as a factor in the winter ecology of barren-ground caribou in

northern Saskatchewan. He noted that caribou avoided burned areas and that although food might be absent the quality of the snow cover prevailing in most burns might be an overriding factor. Particularly during middle to late winter, the depths, densities, and hardnesses of snow in burned areas exceeded the limits that barren-ground caribou were conditioned to. It is entirely possible, therefore, that caribou avoid burned-snowed-over areas because more suitable snow conditions are available in nearby unburned forest.

Scotter (1964, 1967, 1970, 1972) conducted intensive studies in the winter range of barren-ground caribou in northern Saskatchewan and in the southern portions of the Mackenzie District, in the Northwest Territories. He concluded that "an increased rate of forest destruction by fire has accompanied settlement and exploitation, and possibly changes in summer weather patterns". In northern Saskatchewan, he found that the area burned per year by forest fires during the 15 years before 1963 increased 1.4 times when compared with the previous 60 years, and 3.1 times when compared to the period 1840 to 1884.

However, Johnson and Rowe (1975) believed that the data available to Scotter may have been subject to interpretations that would not support a change in burned area. Kelsall (1960) reported that the mapping of an area of over 43 020 km<sup>2</sup> in northern Saskatchewan had showed that only 2% of the country had not been burned in comparatively recent times. Scotter estimated that both the quantity and quality of caribou forage, principally lichens, had been reduced. He determined that the regrowth of forage lichens, though variable, is extremely slow — some might take 90 to 120 years to recover. Uggle (1958) found that similar species in Sweden took over 40 years to recover after fire.

Scotter (1967) found that although moose extensively used early sub-climax forests on burned upland sites on the barren-ground caribou winter range the biomass of caribou per unit area of mature forest was apparently higher than that of moose in early succession areas. Thus, in terms of meat production, upland forests would be best suited to winter use by caribou. It must be remembered that caribou are present on their winter range for only part of the year and that during other seasons vast areas contribute to the support of their biomass. In contrast, moose are year-round residents of a particular range. Scotter concluded that "there can be little doubt that forest fires have been one of the principal causes of the (caribou) decline". He felt that the reduced carrying capacity of the forests did not appear at the time of his study to have been the factor limiting caribou but that it might well have been the factor responsible for "the reduction". He also felt that control of fire would be desirable for that reason. Despite this, Scotter (1972) also acknowledged that "fire may serve a vital role in ecosystem functioning through periodic energy conversion".

Skoog (1968), in a report of the results of a long and comprehensive study of the ecology of the caribou in Alaska, concluded that reduced numbers of caribou were not the result of burning of forests. Alaskan caribou are not dependent on lichen growth in spruce forest for winter food. They use extensive sedge forage on tundra, alpine meadows, bogs and lakeshores. Caribou will winter in such lichen-poor areas year after year even though lichens may be available elsewhere within the range of a given herd. Unlike Leopold and Darling (1953), Lutz (1956) and Courtright (1959), Skoog feels that fire, although it may influence population shifts among caribou, has probably had little influence on the fluctuations in the numbers that have occurred. He

excepts the caribou that once inhabited the Kenai Peninsula, where the population may have been marginal at best and where fire may have been the primary factor that destroyed the herd.

Kelsall (1957*b*) cited an example of a herd of barren-ground caribou that wintered in an area in the Mackenzie District that had been burned only 12 to 15 years previously. These animals prospered even though they were forced to eat plants that they would not have used had their preferred winter range on spruce-lichen uplands been available. It is worth noting, according to Kelsall (1968), that the diet of barren-ground caribou, even on good spruce-lichen winter ranges, only contains 40% lichens. Sedges make up over 20% of their diet, Labrador tea over 10%, and a variety of low shrubs and other plants make up the balance. It is probable that the adaptability of barren-ground caribou to young stages in forest succession needs deliberate study, and such study can only be conducted by finding and observing herds that are wintering in these habitats.

A second matter in need of elucidation is the extent to which barren-ground caribou rely on arboreal lichens during winter. Scotter (1964, 1970) places great stress on the abundance and potential of arboreal-growing lichens in the north, but the literature does not indicate that the barren-ground caribou of the north-central Canadian mainland make extensive use of them. They are palatable to caribou because they are almost invariably eaten from wind-fallen trees (Kelsall 1968), but caribou have not been seen to systematically graze them from standing trees.

Johnson and Rowe (1973, 1975) have studied the wintering ecology of one of the major barren-ground caribou herds. They have examined all aspects of the role of fire in the ecology of caribou. In some respects their conclusions are at variance with those of earlier authorities, and they ask some pointed questions. For example,

they present figures that question the thesis that the present rate of forest destruction by fire exceeds what might "normally" be expected in such an ecosystem. They use Scotter's (1964) data to suggest that rates of burning are close to 1% of the area per year. Therefore, because Scotter (1970) has also shown that intensive use of forests by barren-ground caribou commences approximately 50 years following fire, it follows that an annual burning of approximately 1% of a total forest would probably not be detrimental to them. They also question that fires caused by man have expanded the recent destruction of forests. (It is worth noting that Barney (1971b) found, on the basis of reliable statistics, that although humans in Alaska started 70.5% of fires in the forest, these fires accounted for only 20% of the area burned).

All writers agree that fire is a natural phenomenon on the range of the barren-ground caribou, that it extends far into prehistory, and that these animals have adapted to it. Johnson and Rowe (1975) reflect current thinking that the northern Boreal Forest may well be a fire-dependent ecosystem that depends, for maintenance and for diversity of fauna and flora, on a mosaic of succession. If this is correct, and the evidence is compelling, barren-ground caribou are probably not as endangered by wildfire as has been previously thought. Nevertheless, the views of Johnson and Rowe are based on extensive review of the literature and should be considered a stimulating hypothesis for field testing.

Bergerud (1974), who has reviewed the declines in North American caribou, has rejected the belief that winter food scarcity has limited this species. In his opinion, over-hunting and local increases in wolf predation have been responsible for the decrease in caribou. He suggests increases in numbers of wolves following increases in prey species — moose and deer — following

forest fire. Bergerud also stated several hypotheses and suggested field studies to determine actual relationships between lichens, predation and caribou. Miller (1976) who studied the Kamouriak herd of barren-ground caribou on their winter range in northern Manitoba, concurred with the opinion that winter food does not limit caribou numbers. He calculated an annual rate of burn of 0.17% of the area, approximately one-fifth that calculated by Scotter (1964) for a region of northern Saskatchewan. Miller also found more lichen regrowth on burned land than was reported by Scotter (1964).

Reference to Simard (1973) shows that both Bergerud's and Miller's studies were conducted in regions with low fire-weather ratings but that Scotter's and Kelsall's studies were conducted in areas with higher fire-weather indices. The number and extent of fires can not only be greater where fire-weather indices are high but intensity of burning may also be much greater. For instance, fire intensities in Kelsall's study area between Great Slave and Great Bear lakes may be 10 to 36 times greater than in much of Manitoba (Simard 1973).

Some statements by Johnson and Rowe (1973, 1975) that rates of burning may not be excessive need qualification, although ongoing research by those authors may answer some questions that might be asked (Rowe, pers. comm.). Studies such as those cited by Kelsall (1968) and Scotter (1964 and elsewhere) show that in areas of major settlement and of major mining exploration and development, fires have been so universal in recent times that they have left virtually no mature forest over huge areas. A widespread, random sampling of the seral conditions of forests on caribou winter range is required in order to determine the extents, ages, and frequency of burning of these forests.



Johnson and Rowe (1973) believe that programs of fire suppression in the north should be gradually redirected to programs of fire management. They feel that there should be greater emphasis on studies of fire history, on understanding fire behaviour, and on the influences of fire on terrain, water bodies, plants and animals. Klein (1971), in a similar statement pertinent to Alaska, said much the same and stressed that a change from fire suppression to fire management should be preceded everywhere by the setting of priorities and by careful planning.

### 3.4. Moose and deer

Much North American literature — little of which pertains to Boreal Forest — shows that white-tailed deer do best in early stages of succession following fire. Davis (1959), Ahlgren and Ahlgren (1960), and Heinselman (1970) all discuss this fact. Cringan (1958) points out that in places where fire suppression is efficient and where there are no logging or destructive insect outbreaks, the carrying capacity of forests for both moose and deer decreases as the forest proceeds towards maturity. Deer will decrease more rapidly and earlier than moose. Deer have neither the height to reach browse on maturing trees nor the weight to bend trees over or break them off as moose do. They are also less efficient in feeding on bark in times of stress.

Lyon (1969) discussed the range of the mule deer and Stelfox and Taber (1969) the ranges of deer, wapiti and moose in the Rocky Mountains, where fire protection has been shown to result in long-term deterioration of wildlife habitats. As trees there increase in size and tend toward a coniferous climax, shrubs, forbs and grasses diminish.

Fire creates a favourable environment for preferred deer foods: young poplar, birch, shrubs of a number of species, and grasses. Stelfox and

Taber (1969) report that following clearcutting of a white spruce forest, a process not unlike burning in its effect, browse for deer and other large herbivores increased from 5.50 kg/ha to 213 kg/ha during 1 year, to 437 kg/ha during 5 years, and to 2464 kg/ha during 10 years.

The quality of the food produced after fire tends to be high. DeWitt and Derby (1955) showed that the protein level in four important deer foods increased for 1 year following a "low-intensity" fire and that this increase continued for at least 2 years following a "high-intensity" fire. Taylor (1956) quotes studies that show that preferred deer foods contained 12.1% protein on a 3-month old burn in contrast to only 6.8% protein among the same food species on a 6-year old burn. Cowan *et al.* (1950) found that the contents of ascorbic acid, ether extracts, carbohydrates and protein in moose forage in young forest was superior to those in older stands.

Moose (*Alces alces*) range in western Canada has recently been defined by Kelsall and Telfer (1975). In the northern Boreal Forest, these mammals range north to tree line and slightly beyond in a few places where heavy willow growth provides winter food. Many authors, including Kelsall and Telfer, have discussed the distribution of moose within their North American range. Cringan (1958), Kayll (1968), Mech (1966), Heinselman (1970) and Hansen *et al.* (1973) have discussed the distribution of moose in Ontario and in adjacent portions of the United States. Spencer and Chatelain (1953), Leopold and Darling (1953), Lutz (1960a), Spencer and Hakala (1964) and Hakala *et al.* (1971) are among many who have discussed moose distribution as it relates to fire in Alaska. Scotter (1964 and elsewhere) has contributed to our understanding of the use of succession and mature forest by moose in the Northwest Territories and in adjacent parts of northern Saskatchewan. Peterson

(1955), Geist (1971) and Krefting (1975) have described moose distribution in terms that are generally applicable across North America.

There is consensus that moose are generally present throughout the Boreal Forest in North America but that their abundance varies considerably with the successional stages of forest areas. Mature coniferous forest supports few moose. Successional growth that is rich in aspen, birch and willow supports many moose, particularly in early and middle stages of growth. According to Cringan (1958), fire protection allows forest areas to mature, and such maturation causes moose to decrease. Krefting (1975), among others, considers wildfire the most important factor influencing moose distribution presently and for at least several hundred years previously. He also points out that forest fire protection reduces moose habitat, that moose habitats are unstable, and that population fluctuations are inevitable. Lutz (1960) suggests that moose in Alaska have long been present in greatly fluctuating numbers that depend on various factors. In his opinion, the most important factor is fire, which often, though not always, sets the stage for an invasion by moose or allows an increase if they are already present.

Coady (1973) found that the effects of fire on the Tanana Flats in interior Alaska have been variable. Early seral stages have frequently not developed or have been of short duration and of minor importance to moose. However, a burn in 1957 exposed mineral soil, reducing permafrost levels; for several years the burned area has supported large growths of willow, birch, aspen poplar and a sizeable moose population. Bendell (1974) has examined data on fire occurrence and fluctuations of moose populations in the Kenai region of Alaska. He describes the histories of three large fires and of two moose population peaks and shows that only after the 1947 fire,

when browse supplies were at a maximum, did a moose increase occur. Although a large burn in 1929 apparently had no effect on the numbers of moose, an increase had occurred in 1920 long after browse abundance had peaked in response to a fire around the turn of the century.

Spencer and Chatelain (1953) and Peterson (1955) have described the response of moose to a huge 1947 forest fire that burned 116 000 ha of black spruce in south central Alaska. Moose invaded the area rapidly; the numbers present have been estimated as 273 by 1950, 334 by 1951, 618 by 1952, and 1111 by 1953.

Pertinent information allows the conclusion that in Alaska (at least) increases in moose numbers will not occur in mature coniferous forests and will not invariably occur following extensive burning. It is probable that fires of different intensities cause varying response by browse-yielding plants. Browse availability is mediated by snow cover.

Mech (1966), in reference to Isle Royale (in Lake Superior), explained that trees in an area extensively burned in 1936 were fast growing out of the reach of moose. He predicted that within the next decade populations of moose and of their only major predator, wolves, would decrease.

Lykke and Cowan (1968) report that forest fires in Scandinavia, because they cover relatively small areas, are not important to moose. However, clearcutting, which covers approximately 1% of total forest annually, acts in place of fire as a factor that creates superior moose habitat.

According to Geist (1971), moose habitat is relatively lacking in permanence, most of it being in areas that are subject to frequent disturbance (e.g. alluvial flats along rivers and margins of lakes and muskegs). He believed that moose have evolved behavioural characteristics that enable them to colonize new habitat as it becomes available following fires. Young moose, especially

yearlings, disperse widely and find and colonize new areas. Peek (1974) recorded such colonization in a burned area in Minnesota. The pre-fire moose population in this area had been 1.6/1000 ha. Two years after the fire, densities had risen to 9.8/1000 ha. A nearby unburned area did not show a corresponding increase. Yearling bulls constituted 41% and 30% of the bulls counted in the burned area during the first and second winters following the fire; in the unburned area, such bulls constituted 27% and 20% during the above-mentioned winters. It is also possible that yearling females ingressed into the burned area.

Scotter (1964, 1970) counted moose pellets and barren-ground caribou pellets in forests of all ages and compositions in the Northwest Territories and in adjacent parts of Saskatchewan. Moose were entirely absent from jack pine forests, although caribou made some use of them because of forage lichens on the ground, when the trees were at least 35 years old. In black spruce – white birch forests, moose pellet groups were more abundant than those of barren-ground caribou from 1 to 30 years following fire. From 31 to 120 years or more after fire, moose pellet groups became progressively scarcer. Scotter calculated that although moose were abundant in the younger stages of seral succession in the northern Boreal Forest, their biomass did not exceed that of wintering barren-ground caribou in mature coniferous forest on upland sites. He concluded that such upland sites with mature spruce-lichen forest should be maintained for the benefit of caribou.

To summarize, moose occur throughout the northern Boreal Forest. In mature coniferous forests, their numbers are few and are entirely dependent on the quantity and quality of deciduous, browse-producing shrubs and trees along forest edges. Moose can move into burned coniferous forest as soon as shrubs and deciduous

trees have achieved sufficient growth to provide food, but such ingression may be delayed or ineffective. On the basis of Scotter (1964, 1970) and Kelsall (1968), we conclude that the optimum successional stages for moose occur between 11 and 30 years after burning. The exact stage of optimum habitat would depend on characteristics of the individual site. Scotter suggests that prime upland sites within the northern Boreal Forest are more valuable in terms of biomass when maintained as wintering grounds for barren-ground caribou than as optimum habitat for moose.

### 3.5. Goats and sheep

The range of the mountain goat extends only marginally into the northern Boreal Forest: along the northern extension of the Rocky Mountains and from the border of the Northwest and Yukon territories to approximately the latitude of Great Bear Lake. Because mountain goats live primarily on treeless alpine ranges it is probable that fire never endangers them physically.

Edwards (1954), in his description of a forest fire in British Columbia that affected many species of wildlife, commented that mountain goats lived above the range of the fire and were not affected by it. This comment, however, does not apply to mountain goats everywhere. DeBock (1970) intensively studied the mountain goat population in Kootenay National Park in British Columbia. The study area, Mount Wardle, had been severely burned in the 1920's to an elevation of approximately 2135 m. The resulting vegetation was that which is commonly associated with fire succession and dry situations. Much of the winter goat range, which extends from approximately 1220 m to 2590 m, owed its existence to the fire; otherwise, this range would have consisted of mature coniferous forest. DeBock, in a personal communication, speculates that had it

not been for the fire, goats might not have inhabited the mountain.

Dall sheep (*Ovis dalli*) occur throughout the mountainous regions of the western Northwest Territories and the Yukon Territory. According to Geist (1971), sheep habitat is characterized by "an open landscape and stable plant communities in which grasses or sedges predominate". He noted, however, that some grasslands occupied by sheep are created by forest fire and these grasslands slowly revert to climax forest. Habeck and Mutch (1973) point out that burning at timberline in the northern Rocky Mountains is not uncommon. When such burning occurs, alpine vegetation would be extended downward, and both goats and sheep would benefit. Fires at high altitudes (e.g. near treeline) would create new habitat if the forests had been dense and would improve existing habitat if they had been open-growing.

### 3.6. The larger carnivores

Black bears are ubiquitous in the northern Boreal Forest. Grizzly bears occur along the forest-tundra edge from Great Slave Lake to the north and west, west of the Mackenzie River, and throughout the mountainous areas of Mackenzie District and the Yukon Territory.

According to Leopold (1923), fire benefits black bears primarily because it stimulates the growth of berry-producing shrubs. Such stimulation was one of the few beneficial effects of fire on wildlife that was recognized at the time of Leopold's study. Edwards (1954) described a spectacular increase of black bears in the succession that followed the extensive burning of a large area of Columbian Forest.

Black bears are omnivorous, eating whatever plant or animal material is readily available at the moment. Berries are, however, a staple on which these animals seem to depend in autumn. Hatler

(1972) studied the food habits of black bears in the Boreal Forest of interior Alaska. He confirmed that old burns produced excellent crops of blueberries, which made up 49% of the fall food for bears. Hatler stated that many of the important bear foods are products of mixed forest areas that have a great deal of edge and a large faunal and floral biomass.

With the exception of Edwards' (1954) observation that fire in a mature Columbian Forest restricted grizzly bears, we found no reference to the effects of fire on that species. Grizzly bears are also omnivorous, and it is well known that they are fond of small mammals and berries. It is probable that they, too, would benefit from rich, young and medium-aged succession.

Coyotes are uncommon in the northern Boreal Forest even though they occur sporadically throughout nearly the whole forest region. Because their food consists predominantly of small rodents and hares (Burt and Grossenheider 1964), they prosper in mixed forest with early stages of succession, where small mammals are most abundant.

Wolves are found everywhere in the north. In southern Boreal Forests, they are dependent on deer and moose for food (Mech 1966, Heinselman 1970). Following fire in the Boreal Forest, moose and deer almost invariably increase in response to the development of deciduous succession of a size sufficient to provide browse. As the herbivores increase, so do their predators. As forests reach maturity both game mammals and wolves decrease.

The situation of game mammals in the Northwest Territories is somewhat different. Although white-tailed and mule deer are found in local areas, they are not a major prey species for wolves in these areas. Caribou, rather, are the usual winter prey of wolves over most of the northern Boreal Forest. Kelsall (1968) has de-

## Summary and discussion

scribed the results of wolf control measures that resulted in the taking of hundreds of wolves in the Mackenzie District between 1953 and 1961. He found that there was little profit in setting baits for wolves in forested areas — with the exception of those occupied by barren-ground caribou. For example, in the winter of 1955–56, 29 poison baits set in areas where caribou had not been present produced only two dead wolves. During the same winter, 28 baits set in areas occupied by caribou produced 67 dead wolves, and an additional 23 live wolves were seen about them.

Many of the wolves taken during such operations were tundra wolves that had followed caribou into the forests for the winter, but some were resident timber wolves. During summer, timber wolves must rely on moose and small game for sustenance. Without caribou, they would do best in burned areas from about 10 to 30 years after the fire, where moose are most abundant (Scotter 1967). When caribou are present, however, the wolves depend on them absolutely; wolves travel long distances to find caribou and keep pace with them in their migrations (Kelsall 1968).

In summary, relatively little is known directly about the effects of fire in the Boreal Forest on the larger carnivores. However, all carnivores do best where there is an abundance of food. Because early stages that succeed after fire provide food (both vegetable and animal) in greatest amounts, it is probable that most of the larger carnivores will prosper best during early succession. An exception in the north are wolves, which depend wholly on barren-ground caribou (when they are present) and which, consequently, occur in winter with the caribou in mature coniferous forests. It is also probable that timber wolves, which stay in the forest the year round, must find mixed forest or early succession areas for denning and summer use.

This paper has attempted to develop, on the basis of a review of pertinent and analogous studies, an overview of the effects of fire on the ecology of the Boreal Forest. Because of the primary extent to which fire determines the ecological character of the Boreal Forest, throughout this review this type of forest has been regarded as a fire-dependent ecosystem. This means that the forest trees and other plants, and its birds, mammals, and other animals have evolved largely in response and adaptation to the frequency, extent, and intensity of fire. Past evidence of fire in North American coniferous forests is evident in burn scars on trees, charcoal layers in soil horizons, and pollen layers. The presence of fire can be traced far back into prehistory.

With some exceptions, the forests most subject to burning are those on dry upland sites, where coniferous trees have long been present and where there is an abundance of highly flammable fuel (organic litter, dry lichens and mosses) on the ground. The decomposition of litter is a slow process in the north, and to some extent fire acts in place of decomposition to return nutrients to the soil and to provide energy sources for new growth. Opinions differ regarding the effects of fire on both nutrients and soils, but such differences are to be expected in view of the wide variety of situations that have been studied.

The effects of fires on permafrost have been of particular interest in the north; in regard to these effects, opinions also differ. The most widely held opinion is that unless a fire is hot and exposes the mineral soil, effects on permafrost are not great or long lasting. With a loss of insulation, a slight increase in the depth of the active layers will occur as soil temperatures rise, but this rise tends to encourage the regeneration of vegetation. The effects of fire fighting in permafrost areas, particularly the bulldozing of fire

lines and supply lines, are shown to be often far more destructive in terms of erosion and surface subsidence than the effects of the fire.

Although there is evidence that fires can sometimes seriously affect hydrology and aquatic organisms (including fish), such effects are seemingly unusual in the northern Boreal Forest. There are some records of fish populations having been killed following fire — presumably because rains have washed large amounts of alkaline ash into streams and lakes and changed the quality of the water for a brief but probably lethal period. However, studies in the Boreal Forest show little effect on watersheds following fire. Results are not conclusive in all respects, and the subject merits further investigation.

As might be expected, fires in the forest benefit some birds and harm others. Waterfowl usually benefit because marshes are opened up, nutrients are supplied from the burned debris, and food plants become more abundant. In the forest itself, birds such as the spruce grouse, which find optimum habitat in mature conifers, disappear when the forest is burned, but they are replaced first by sharp-tailed grouse, which do best in early stages of forest succession, and then by the ruffed grouse, when birch, poplar, and willow are present. Many varieties of smaller birds are similarly specialized in their requirements. Particular species of wood warblers, for instance, occur during nearly every stage of succession.

In general, small mammals and furbearers benefit from fire and from the renewed vigour of well fertilized plant succession that follows. All evidence suggests that numbers of small mammals recover quickly (within a few months) following fire. Species composition, however, may change drastically. There is reason to suspect that speed of recovery in the north would be dependent on the time of year at which burning occurred.

Among the furbearers, muskrat and beaver benefit from fire because they prosper best in early stages of succession. On the other hand, marten, an important economic resource in the Canadian north, seem to do best in mature coniferous forests. Reasons for this are not entirely clear because the marten preys mostly on small mammals, which are abundant in burned areas. One authority believes that the marten's preference for mature coniferous forests is largely explained by the presence of trees sufficiently large to contain denning holes.

Moose and deer both prosper best in forests where there is ample deciduous growth for winter browse. Permanent moose and deer habitat occurs along forest edges and lake and river margins. When fires occur, and when succession reverts from coniferous to deciduous forest, moose are often quick to capitalize on an opportunity to invade new habitat. There are many places in the northern Boreal Forest where this sequence occurs (and many where it does not). Studies have shown that moose reach highest numbers in deciduous successional forests between 10 and 30 years following fire. Thereafter they decline rather quickly.

Within its range, the barren-ground caribou is the most important game mammal. The effects of fire on this species and its ranges remain controversial. It has long been thought that the destruction of coniferous forest invariably causes the destruction of caribou range for a period of 50 to 100 years or more. It has been suggested that the recent decline in numbers of the barren-ground caribou herds of the central Canadian mainland has resulted directly from the destruction of their winter ranges by fire. Although this extreme view is not universally shared, most authorities suggest that the number of fires on the range of the caribou have increased, at least locally, with settlement and exploitation by pros-

pectors and developers<sup>5</sup> and that this species has not been able to recover its primitive numbers, partly because of new limitations placed on its winter range.

It is true that the barren-ground caribou of north-central Canada seem to prefer mature spruce-lichen forests as winter range. This is true even though studies have shown that only half (approximately) of winter food of this species is actually composed of lichens. It is known that caribou in Alaska and the northern Yukon adapt well to younger stages in succession, where grasses and sedges predominate; and it has been suggested that Canadian barren-ground caribou could similarly adapt if they were forced to do so.

Despite the fact that barren-ground caribou are one of the most thoroughly studied North American big game mammals, there are still areas where research is required. Their adaptability to sub-climax forests for winter use needs to be tested through study of herds that are wintering in such areas. Also in need of testing is the assertion that arboreal lichens provide a major source of food for barren-ground caribou in winter. Arboreal lichens are present in northern forests, but there is as yet no direct evidence to suggest that caribou browse them extensively. The widespread belief that caribou ranges have been subject to more severe burning than they can stand in recent years also needs testing. The best figures available, which are far from satisfactory, suggest that approximately 1% of the forests are burning per year. This figure does not represent an excessive rate of loss.

Black bears and grizzlies probably benefit through forest fires because berry-producing shrubs are more abundant and more productive in early seral stages. The fates of these large car-

nivores and of lynx, foxes and wolves are linked to that of their prey species. Wolves that depend on caribou are adversely affected by fire, but those that depend largely on moose may benefit. Coyotes and foxes benefit through increases in abundance of small mammals, which form their principal prey. Lynx live mostly on snowshoe hares, which require the sort of food and cover found in a mosaic of forests of various ages (including dense young growth).

In summary, the effects of fire on the Boreal Forest cannot be classified as either totally positive or negative. The precise effects, which reflect man's interests, depend much on the values that may be destroyed or created. There is an obvious need to zone northern forests in terms of the uses foreseen for them. Then, through research and planning, the extents to which fire suppression would be desirable in the various zones should be decided. Some key areas, such as principal caribou wintering ranges, may require absolute protection from fire, but there is a growing suspicion that absolute suppression would be desirable only in areas where logging would provide an alternative form of forest disturbance.

<sup>5</sup>Due to suppression efforts, it is possible that burned area has not increased proportionately.

# Topics for research

This review focuses on what is known and unknown concerning the effects of fire on the northern Boreal Forest. In order to adequately manage Boreal Forest, priorities must be set and measures must be carefully planned. Both the priorities and the planning will suffer in the absence of adequate baseline information.

In the planning of research programs and the application of the results, the variation between physiographic regions in the northern territories must be kept in mind. The impacts on the Canadian Shield are probably quite different from those on the deeper soils of the Great Plains to the west; furthermore, in the Cordilleran region effects will be localized. The important differences between the impacts on sites with a shallow active layer over permafrost and the impacts on those with a deep active layer must always be considered.

The following suggested research topics are designed to fill the most glaring gaps in the general field of knowledge.

## 1. Basic fire ecology in the north

1. Studies (beyond those cited) of the impacts of fire on permafrost areas having varied site characteristics are required. Such studies should concern the chemical and physical properties and moisture relationships of soils as affected by burning, the quantification of the extent of thawing caused by fire, and the net result of all effects on site productivity.

2. Estimates are required of the rate of burning in key areas in the past; these estimates would be based on studies of historical records and on analyses of existing vegetation and of pollen and charcoal accumulation. A knowledge of past situations will put present conditions in correct perspective. Rowe *et al.* (1975) have suggested that current rates of burning could be monitored by satellite imagery.

3. Studies are required as a basis of zoning of the northern forests for fire management purposes; for such zoning should proceed on a sound ecological basis (with local sub-strata for the protection of towns, villages and other high-value items of importance to man).

## 2. Effect of burning on aquatic resources

The following topics require investigation:

1. Changes in the chemistry of water bodies of various sorts and sizes following fire on adjacent uplands;
2. Effects (if any) of changed chemical environments on aquatic organisms (including fish and their food);
3. The extent to which riparian trees and shrubs are actually destroyed during wildfires;
4. Changes in water temperature resulting from fire-caused losses of riparian vegetation.

## 3. Effect of fire on terrestrial wildlife

1. Controlled studies are required of bird and mammal use of different sites burned at varying intensities of fire.
2. An intensive study to further elucidate the relationship between fire and the well-being of the barren-ground caribou should be conducted. The following questions appear to have overriding importance:
  - a) Can barren-ground caribou winter successfully as some Alaskan caribou do in early seral stages within their forested winter ranges?
  - b) Do wintering barren-ground caribou actually make significant use of the arboreal lichens that grow profusely on trees in some portions of their winter range?
  - c) On both range-wide and local bases, are the recent rates of destruction of caribou winter range by fire excessive?



# Appendix I

Journals and other serial publications searched systematically for literature relevant to the effects of fire on wildlife.

American Forestry  
Alaska Cooperative Wildlife Research Unit:  
    Quarterly Reports  
Alaska Department of Fish and Game: Pittman –  
    Robertson Project Reports  
Alaska Federal Aid in Wildlife Restoration:  
    Job Completion Reports  
The American Naturalist  
Arctic Bibliography  
Arctic  
The Auk  
Biological Abstracts  
British Columbia Forest Service: Annual Reports  
British Columbia Forest Service: Forest  
    Research Review  
British Columbia Forest Service: Research Notes  
Canada Forest Management Institute:  
    Information Reports  
The Canadian Field-Naturalist  
Canadian Geotechnical Journal  
Canadian Journal of Forest Research  
Canadian Society of Wildlife and Fishery  
    Biologists: Occasional Papers  
Canadian Wildlife Service: Wildlife Management  
    Bulletins and Report Series  
Citation Index  
Condor  
Dissertation Abstracts  
Ecological Monographs  
The Ecologist  
Ecology  
Fire Research Abstracts and Reviews  
Fire Technology  
Fisheries Council of Canada Bulletin  
Fisheries of Canada  
Fishery Bulletin  
Forest and Outdoors

Forest Science  
Forestry Abstracts  
Forestry Chronicle  
Forestry Quarterly  
The Journal of Animal Ecology  
The Journal of Ecology  
The Journal of Forestry  
The Journal of Mammalogy  
The Journal of Range Management  
The Journal of Soil and Water Conservation  
The Journal of Wildlife Management  
The Living Bird  
Mammal Review  
National Wildlife  
North American Wildlife Conference:  
    Annual Transactions  
Problems of the North  
Recent Literature of Mammalogy (Supplement  
    to J. Mammalogy)  
Riistatieteellisia Julkaisuja: Finnish Game  
    Research  
Soil Science Society of America: Proceedings  
Tall Timbers Fire Ecology Conference:  
    Annual Proceedings  
Vilttery: Swedish Wildlife  
Water Newsletter  
Water Research  
Water Resources Abstracts  
Water Resources Bulletin  
Water Resources Research  
Water Resources Review  
Wildlife Abstracts  
Wildlife Bulletins  
Wildlife Review  
The Wilson Bulletin  
Wisconsin Conservation Bulletin  
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