

CHAPTER 13

The Role of Fire in Lichen-dominated Tundra and Forest-tundra

A.N.D. AUCLAIR

Pacific Forest Research Centre, Canadian Forestry Service, British Columbia, Canada

ABSTRACT

Unique aspects of fire in lichen tundra and forest-tundra were enumerated. The very high inherent fire susceptibility is related to the presence of lichens and shrubs. Lichens are predisposed to burning by virtue of continuous distribution on the soil surface, high surface-volume ratio, and rapid dessication related to the absence of roots, vascular tissue, and tissue that resists moisture loss. In most fires, two-thirds of the organic matter in live biomass is not combusted and there is only minor loss of nutrients during burning. Decomposition rates are low and nitrogen limited.

Post-fire regeneration of vascular species is rapid. Shrubs sprout the same year of the fire and tree establishment peaks within 2–3 years. Lichen growth is slow by comparison and the lichen mat may require 50–80 years to develop a continuous cover.

13.1 INTRODUCTION

13.1.1 Predisposition to Fire

Forest-tundra and tundra are populated by inherently flammable plant species. Lichen woodlands, especially those dominated by *Picea mariana*, and lichen tundra, are highly susceptible to fire (Hardy and Franks, 1963; Viereck, 1973). The flammability of these ecosystems is due largely to the presence of dwarf shrubs and to the absence of vascular tissue in lichens that leads to rapid surface drying (Rowe *et al.*, 1975). In the forest-tundra, trees are not sufficiently dense to carry a fire. Rather, in both the forest-tundra and tundra the ground vegetation is the primary carrier of fire.

The low ericaceous shrub component is the most important vegetation component in terms of inherent fire susceptibility and flame propagation (Sylvester, 1975; Rowe *et al.*, 1975) for three reasons. First, low ericaceous shrubs, including *Empetrum*, *Ledum*, and *Vaccinium*, have a high percentage of ether extractives. Lipid content varies from 2.8% to 9.6% of dry weight

compared with 1.1% and 1.6% in *Stereocaulon paschale* and *Cladonia alpestris*, respectively (Bliss, 1962; Scotter, 1965). The lipid-free caloric values in the shrubs are also higher—5029 cal/gm compared with 4336 cal/gm in lichens (Rowe *et al.*, 1975). The result is relatively high flammability (i.e., low temperature for ignition) and high heats of combustion in shrub species. Second, the low shrub component often forms a continuous complex of fine fuels with an upright growth-form or vertical plane (Sylvester, 1975). Tall shrubs such as *Alnus* and *Salix* contribute little since they are clumped and have a large fraction of stems and branches over 1 cm in diameter. Third, shrub litter could be very important in community susceptibility to fire due to low moisture content during dry weather; however, the high moisture content of living shrubs can slow fire.

Lichens often serve as the initial point of ignition in woodlands and tundra and have an essential role in spreading the fire. They dry rapidly during periods of low atmospheric humidity (Mutch and Castineau, 1971; Larson and Kershaw, 1976) because of the absence of roots, water storage tissues, and a low resistance to water loss. Lichens resemble dead litter more than live tissue in their susceptibility to fire (Sylvester, 1975). Continuous mats of lichen of high standing crop present an uninterrupted surface along which fire spreads. Considerable site and geographic variation in this feature has been observed; however, lichen mats also typically accumulate tree and shrub litter. In *Picea mariana*-*Cladonia alpestris* woodland, litter (1927 kg/ha) suspended in the lichen mat (9392 kg/ha) added 20.5% dry weight to the total combustible material present above the soil (Rencz and Auclair, 1978). In addition, lichens are exceptionally fine textured. The area to volume ratio of *Alectoria jubata* lichen was 632 cm²/cm³ compared with 50–100 cm²/cm³ for needles of seven prevalent conifers of the Pacific northwest (Brown, 1970). The formation of polygons upon severe drying (personal observation, and K.A. Kershaw, 1977) results in a high air-fuel interface. Moreover, common fruticose lichens such as *Cladonia* species have relatively large vertical planes (Wein, 1975).

13.1.2 Fire Occurrence

There has been a growing awareness of the full extent of fire in tundra and forest-tundra, and recent emphasis has been given to documenting its occurrence, size, frequency, and causal agents (Barney, 1971). Evidence to date indicates clearly that fire is a natural phenomenon in these ecosystems. The presence of multiple fire scars on tree boles (Rowe *et al.*, 1974) and multiple charcoal layers in lake sediments (Rowe *et al.*, 1975) indicates that recurrent fire pre-dated industrial activities. Johnson and Rowe (1975), Requa (1964), and Scotter (1967) determined that 72–85% of all fires in northwestern Canada were caused by lightning. Barney (1969) reported that

about 30% of all fires during the 1940–1969 period in the Alaska interior were lightning-caused. From these observations, Rowe *et al.* (1975) inferred that since these systems have evolved in the presence of recurrent burning, they adapted to survive fire, and may even require periodic burning for their long-term maintenance. This has had enormous implications in the perceived need for fire suppression and in the formulation of management criteria.

The frequency and extent of fire has increased greatly with recent exploration and industrial development of northern areas. In interior Alaska, the number of fires doubled between the 1940s and the 1950s and remained high throughout the 1960s (Barney, 1971). In the vicinity of Whitehorse, Yukon, fire numbers increased from less than 0.5 fires/1000 km²/yr in the general landscape to over 20 fires/1000 km²/yr near the city, an increase of about forty-fold (Simard, 1975).

13.1.3 Vegetation Distribution

Tundra and forest-tundra occur in a circumpolar belt across North America, Scandinavia, and the Soviet Union (Shelford, 1963; Walter, 1973). Although the distinction is ecologically significant, graminoid tundras have not been mapped separately from lichen tundra. The composition and occurrence of forest-tundra is better known. Tree species typically include *Betula* (coastal climates), *Larix* (continental extremes), and *Picea*. Isolated individuals or small stands of these species occur in a matrix of dwarf shrub-tundra dominated by *Betula*, *Ledum*, *Vaccinium*, or *Salix* shrubs and lichens, including *Cladonia* and *Stereocaulon* spp. Detailed descriptions are given by Rowe *et al.* (1975), Wein (1975), Shelford (1963), Wielgolaski (1975a), and Walter (1973) for different regions of lichen-dominated communities.

13.2 VEGETATION FLAMMABILITY AND BEHAVIOUR OF FIRE

Fire is a normal, recurrent environmental event in lichen tundra and forest-tundra (Rowe *et al.*, 1974, 1975). Few vegetation areas are perceived to be fireproof and even wet meadows of sedge (*Carex* spp.) and cottongrass (*Eriophorum*) have been observed to burn (Wein, 1975). The question is not whether a particular vegetation tract will burn but rather how susceptible it is to fire (Sylvester, 1975).

13.2.1 Extrinsic Factors

13.2.1.1 Meteorology

Rowe *et al.* (1975) described a direct relation between intensive storm activity caused by air-mass movements and the incidence of lightning ignitions. In

fact, well-defined seasonal pulses along the Mackenzie Valley and Caribou Range, Canada, coincided with north-south air-mass movements during the summer. Other meteorological parameters such as rainfall, wind, and humidity are typically incorporated into indices of fire potential (Van Wagner, 1974; Rothermel, 1972).

In the Arctic and subarctic, weather conditions are conducive to fire as soon as the snow melts (Wein, 1975, 1976). The seasonal leafing-out of herbs and shrubs has little effect. In forest-tundra, Johnson and Rowe (1975) and Barney (1969) observed that the fire season was largely from the fourth week of May to the second week of August. Peaks of lightning-caused fires occurred in June and July. In contrast, man-caused fires occurred from early April to late September with a peak in late May (Barney, 1969).

13.2.1.2 Uniformity

Slope, topography, and vegetational discontinuities assume importance where fuel mass diminishes. Johnson and Rowe (1977) found a relation between a Weibull distribution of probability of fire and a measure of the complexity and roughness of the terrain. Fire size was less in Alaska than in northwest Canada due partly to less topographic variation in the latter (Viereck, 1973). Rowe *et al.* (1974) accounted for the increased size of burns (as distinct from percentage of area burned) northwards by the greater age and compositional uniformity of the vegetation.

13.2.2 Intrinsic Factors

Inherent properties of plants that influence the flammability, intensity, and spread of fire include four key parameters:

13.2.2.1 Tissue Content

High lipid and caloric contents of resinous evergreen shrub species are typical of forest-tundra and tundra vegetation (Bliss, 1962; Rowe *et al.*, 1975). In general, plants with high ash contents are less flammable (Mutch and Philpot, 1970). Sylvester (1975) observed differences in ash content among forest-tundra species and across the growing season suggesting vegetational and seasonal differences in fire susceptibility.

Only rarely have tissue moisture contents been measured in the process of evaluating fire susceptibility. Rowe and Scotter (1973) felt that the water deficits that develop during leafing-out of the vegetation at a time when soils are still frozen contribute strongly to fire susceptibility. Sylvester (1975) observed that seasonal moisture levels were generally similar among shrub species of forest-tundra, declining from July to August. A mid-August decline

was especially apparent in the graminoids (*Calamagrostis* and *Eriophorum*). While in most species moisture in early August ranged from 60% to 150% of tissue dry weight, mosses contained 550% water by dry weight. Lichen dwarf-shrub heath was two- to three-fold drier than other vegetation types (58% water of tissue dry weight versus 105% in *Picea mariana*, 106% in *Betula papyrifera*, and 143% in the *Eriophorum*-*Calamagrostis* vegetation type).

Lichens behave in marked contrast to vascular plants in both the absorption and retention of water. Most uptake is from atmospheric sources and resistances to water loss are very low. Mutch and Castineau (1971) determined that drying occurred 1.7 times faster than water absorption in *Cladonia* spp. Moreover, wetting and drying trends were curvilinear (i.e., rapid). No active metabolic or physiological control of water is apparent (Blum, 1973). Larson and Kershaw (1976), however, related variation in thallus morphology and mat structure to species differences in water loss resistances. Thick mats (up to 20 cm) typical of *Cladonia alpestris* had distinctly higher resistances than other lichens.

In its rapid drying behaviour lichen is more similar to dead litter than to live plants. Only recently have fire models been modified to include this characteristic of lichens (Fosberg and Schroeder, 1971; Van Wagner, 1974). The fact that most fuel is live is a complete reversal of the conditions assumed by fuel complex models (Sylvester, 1975).

13.2.2.2 Surface-volume Ratio

Once ignited, the rate of fire spread varies directly in proportion to surface-volume ratio (Rothermel and Anderson, 1966). Brown's (1970) analysis of the surface-volume ratio of different plant species indicated that lichen (*Alectoria jubata*) had a surface-volume ratio three to twelve times greater than common conifer trees in western North America.

13.2.2.3 Vertical Plane

Lichen mats are seldom more than 5-8 cm high. Exceptionally, *Cladonia* can attain heights of 10-12 cm. This increases the real air-fuel interface. In *Cladonia*-*Cetraria* mixtures the taller *Cladonia* sometimes burned while the thalloid *Cetraria* survived (Rowe *et al.*, 1975). The vertical stature is a significant feature of shrubs and trees. The fact that *Picea mariana* in forest-tundra typically has branches extending to the ground surface probably greatly increases the susceptibility of forest-tundra to creeping ground fires. Conversely, the low mat-like form of lichens sometimes results in the selective burning of shrubs and conifer litter but not the lichen mat (Hustich, 1954; Rowe *et al.*, 1975).

13.2.2.4 Fuel Mass

One of the important factors affecting flammability is the minimum mass required to carry a fire. Wein (1975) found that among five different vegetation types, the lowest mass that carried a fire at Inuvik, North west Territories, Canada, was 450 gm/m². The small biomass per unit area reduced the ability of fire to cross topographic discontinuities in tundra (Wein, 1975; Rowe *et al.*, 1975). The number of fires per unit area and annual percentage of area burned decreased from south to north in the Mackenzie Valley in part for this reason (Rowe *et al.*, 1975).

Biomass is strongly conditioned by the age of the stand. Rowe *et al.* (1975) found large differences between vegetation types in the recurrence of fire (e.g., 40-60 years in *Pinus banksiana* versus 100-200 years in *Picea mariana*), that are probably related to the time required for the buildup of essential fuel mass. They also noted that the probability of tree mortality (i.e., fire occurrence) increased with age. The mortality pattern best fits the Weibull distribution, with low mortality in the early years and an increasing risk of burning with age. In fact, Rowe *et al.* (1975) show that the risk or probability was not strictly exponential but increased dramatically from 0.2 to 0.8 between the 80- and 100-year periods. This strongly implicates the role of the lichen mat since it is in this time period that lichen forms a closed mat along which fire can spread (D.J. Hogan, unpublished data).

13.3 FIRE-INDUCED CHANGES

13.3.1 Combustion and Mineralization of Organic Material

13.3.1.1 Quantity of Organic Matter

In *Picea mariana*-*Cladonia alpestris* woodland, typically one-third of the biomass and two-thirds of the litter and fermentation (LF) layers combust (D.J. Hogan, unpublished data). Only 5% of the tree biomass is consumed during fire, whereas 97% combustion of the shrub layer (largely *Betula glandulosa*) occurs. In Hogan's study, a control area contained 6677 kg/ha of lichen biomass whereas 'burnt lichen' on a burned area had 9160 kg/ha. The increase may be partly attributed to particulate contamination of the 'burnt lichen' category, although site-to-site variation is likely. The large remnant fraction of charred lichen does serve to emphasize that this component is largely uncombusted.

Mass of the LF layer decreased from 603 kg/ha on the control to 183 kg/ha on the burn (D.J. Hogan, unpublished data). The depth of the LFH layer in

Table 13.1 Changes in *Betula glandulosa* root biomass, phosphorus concentration, and root phosphorus mass with burning of mature 140-year-old *Picea mariana* - *Cladonia alpestris* woodland at Schefferville, Quebec

Component	Units	Mature 140-yr-old	Burn 0-yr-old	Per- centage change	Reference
Root biomass	kg/ha	9159	8886	-4	D.J.Hogan
Root P concentration	% dry wt	0.047	0.133	283	unpublished
Root P mass	kg/ha	4.30	11.80	274	data
Lost by leaching	kg/ha	0.03	0.07	233	Moore (1980)
Absorbed by roots (Difference between burn and mature sites)	kg/ha		7.50	83	Auclair and Rencz (1982)
Mobilized by fire (Estimate)	kg/ha		9.01		

Picea mariana woodlands was reduced from 6.6 cm at maturity (200 years) to 2.2 cm after burning (Kershaw *et al.*, 1975). In a study of sixty-five stands, the LFH layer depth decreased from about 8 cm at maturity (215 yrs) to 0-0.5 cm after the burn (Kershaw and Rouse, 1976) suggesting that a considerable proportion of the mineral soil was exposed. In fact, Scotter (1964) observed that 35-40% of the mineral soil was exposed after woodland fires in northern Canada. Lutz (1956) found comparable exposure levels (30-40%) in Alaska. Obviously values depend on fire intensity and soil moisture conditions at the time of the burn.

13.3.1.2 Plant and Soil Nutrients

Fire has a fertilizing effect on soils in the tundra and forest-tundra (Rowe and Scotter, 1973; Viereck, 1973; Wein and Bliss, 1973). In *Picea mariana* woodland, Auclair and Rencz (1982) estimated mineralization in a natural fire would volatilize 131 kg/ha of nitrogen and release 31, 27, 10, and 9 kg/ha of Ca, K, Mg, and P, respectively. The data for P are presented in Table 13.1. Comparisons with the available or exchangeable soil element reserves indicated that the release of N and Ca exceeded the amount readily available in the soil.

With the exception of nitrogen, elements released by combustion of organic matter are deposited on the soil surface with resultant changes in the concentrations and mass of soil elements. Unfortunately, most workers have

typically included only comparisons of element concentrations before and after burning. Since 65–100% of the soil organic matter can be combusted, element concentration values alone cannot be meaningfully interpreted since the actual changes in the mass of elements varies greatly. Moreover, comparisons have typically been made between control areas and recent, adjacent burns. Our experience indicates that considerable caution is required in interpreting data of this type since large site-to-site variation exists within soils of these regions (Moore, 1980). Studies by Lutz (1956), Lotspeich *et al.* (1970), Lucarotti (1976), Scotter (1971), and Weber (1975) reported only soil element concentrations. All indicate an increase in pH and exchangeable soil P. The changes in soil phosphorus concentrations were often dramatic. On three out of four sites Scotter (1971) found one to two orders of magnitude increase in forest-tundra soil P concentrations after burning. In three out of four cases Ca concentration doubled whereas exchangeable K, Na, and Mg concentrations changed little and soil cation exchange capacity decreased slightly (Scotter, 1971). Changes in soil total nitrogen are variable. Scotter (1971) found that the concentration of total nitrogen increased in one case, did not change in another, and decreased in two other cases. Lutz (1956) found that whereas total nitrogen concentration decreased, the concentration of available nitrogen increased, a fact also noted by Viro (1955) in the Finnish boreal forest.

13.3.1.3 Allelopath and Burnt-litter Compounds

The destruction of lichen allelopath compounds (Brown and Mikola, 1974) by fire has not been examined but is suspected to occur on the basis of improved mycorrhizal establishment in burned soil (Mikola *et al.*, 1964). Widden and Parkinson (1975) observed a strong suppression effect of burnt-litter extracts on the growth rate, protein production, and spore germination of fungi in *Pinus contorta* forest soils. The occurrence and nature of organic compounds produced as the result of the destructive distillation of plant remains during a fire is considered important but has not been examined in lichen tundra and forest-tundra.

13.3.2 Changes in Surface and Soil Microclimate

13.3.2.1 Temperature and Radiation Flux

Burning lichen woodland in the Northwest Territories, Canada, created an immediate increase in mean soil temperature of 60–70% (Rouse, 1976). Even after a quarter of a century surface temperatures of the burn remained 30–40% warmer. Net radiation flux on a recent burn was 347 cal/cm²/day

Table 13.2 Comparison of soil temperatures ($^{\circ}\text{C}$) between unburned mature lichen woodland and recently burned woodlands at two geographic locations. Values at each 5-cm soil depth are averages for day-night recordings across the growing season (June to September). Means are arithmetic averages for the three depths, and differences is the change in soil temperature with burning

Soil depth (cm)	Abitau Lake, N.W.T. (Rouse, 1976)		Schefferville, Quebec (Lucarotti, 1976)	
	Mature	Burn	Mature	Burn
5	10.2	15.1	8.1	8.4
10	9.6	13.4	5.7	8.3
15	9.3	12.9	7.9	9.5
Mean	9.7	13.8	7.2	8.7
Difference	+4.1		+1.5	

compared with $333 \text{ cal/cm}^2/\text{day}$ in mature lichen woodland. Soil temperatures through 160 cm depth averaged 2.9°C warmer on the recent burn. Very large diurnal variations and extreme temperature maxima occurred on burned surfaces. Temperature maxima were as high as 65°C on 0-, 1-, and 2-year old burns compared with 28°C under mature lichen woodland (Rouse, 1976).

The large soil temperature increase noted by Rouse (1976) has not been observed universally. Comparisons with similar observations on *Picea mariana*-*Cladonia alpestris* woodland in Quebec (Lucarotti, 1976) are given in Table 13.2. Lucarotti (1976) attributed his more modest temperature increases in the upper soil to evaporative cooling. Where surface soils remain close to saturation following fire, latent heat loss may continue to suppress surface temperature changes well after the fire.

Regional differences in rainfall and evaporation may also account for differences noted in changes in depth of soil thaw. Typically the depth of the 'active layer' increases after fire but the range varies greatly. Viereck (1973) observed a 6% increase under a burned *Picea mariana* open woodland. Mackay (1970) reported a 42% increase two years after a burn in *Picea mariana* woodland near Inuvik, Canada. Lotspiech *et al.* (1970) found no changes in soil temperature or active layer depth after fire in Alaskan *Picea mariana* forest. Kryuchkov (1968) noted a decrease in active layer depth on a recent burn and attributed the change to an increase in water content from ice melt. Obviously there is a significant interaction between soil energy balance and soil moisture.

The seasonal dynamics of thaw depths can be important in judging the effects of fire on soil energy balance. Viereck (1973), for example, noted that the greater depth of thaw persisted longer in the autumn on burned woodland. Rouse (1976) observed that a thaw started eight days earlier on a burned woodland than on an unburned site. Unfortunately, seasonal changes have been measured only rarely.

13.3.2.2 Soil Moisture

Typically, soil moisture levels increase after fire in temperate forests due to a reduction of transpiration. However this generality cannot be applied universally in lichen-dominated systems because the presence of permafrost appears paramount. On permafrost soils, in particular where ice wedges prevail, soil moisture levels increase several-fold due to melting of soil ice, and this increase can last for 50 years or more (Kershaw *et al.*, 1975; Kryuchkov, 1968; Mackay, 1970; Rowe *et al.*, 1974). In lichen woodland on coarse-grained soils without permafrost, Rouse (1976) observed a decrease in soil moisture following fire. Compared with mature woodland, soil (to a depth of 160 cm) was 3.1% drier one year after burning. It must be emphasized that the studies of Rouse (1976) are specific to sandy-gravel soils in an extreme continental climate.

13.3.3 Alteration of Soil Stability and Hydrology

13.3.3.1 Thermokarst Subsidence

One of the most important and conspicuous effects of burning in tundra and forest-tundra is thawing of permafrost soils and resulting subsidence. Fine-textured soils, organic soils, and peat are typically extremely ice-rich. When thawed, the volume ratio of excess water to saturated thawed soil is often 5:1 to 10:1 (Mackay, 1970). The soil slurry that results has flow rates (for the top 15 cm) of 1.7 km per day on a slope of 5 m/km; the flow rate increases twenty-fold with depth.

On flat terrain thaw results in thermokarst formation and ponding. Viereck (1973) reported that thermokarst following fire on soil with ice wedges produced ditches 2–3m deep that remained active 40–50 years after fire. Rowe *et al.* (1974) noted that on frost-mounded lichen terrain (Northwest Territories, Canada) the active layer had deepened from 50–60 cm to over 100 cm after fire and soil slurry was moving from the centre to the mound edges. The central areas of the mound developed thermokarst.

On slopes, even of slight magnitude, soil flow and slumping often assume massive proportions (Zoltai and Pettapiece, 1973). Slumping can occur within a few days of the fire or may be delayed until the next year (Heginbottom, 1971). Widespread slumping in areas of the Northwest Territories, Canada (Mackay, 1970; Heginbottom, 1971; Rowe *et al.*, 1974; Wein, 1975) suggests it is a common occurrence on sloping terrain.

13.3.3.2 Hydrology and Erosion

There is considerable evidence that burning has little impact in increasing erosion runoff or element loss in lichen woodland and tundra. On extensive burns at Schefferville, Quebec, the author did not observe any soil erosion on recent burns. Scotter (1971) observed little surface runoff and no more than light sheet erosion during rainstorms in northern Saskatchewan. Lutz (1956) found the amount of erosion in the interior of Alaska surprisingly small despite the high erosion potential of the soils. From a review of the literature Viereck (1973) concluded that 'increased erosion and runoff as a result of fire seems to be at a minimum in northern areas in contrast to temperate regions where fire nearly always results in increased runoff and flashy stream flow (Ahlgren and Ahlgren, 1960)'.

The reasons for this unique quality of tundra and forest-tundra include at least seven different features of these systems:

- (1) A considerable fraction of the terrain is either flat or only slightly rolling and often poorly drained.
- (2) Rainfall is typically of low intensity.
- (3) Soils are frozen for 6–8 months of the year. Although snow-melt is rapid, soils remain frozen at the time of rapid runoff.
- (4) Surface layers are high in accumulated organic matter which confers high infiltration rates and high water retention capacity. Both soil infiltration rates (Scotter, 1964) and soil moisture capacity (Rouse, 1976) appear to be enhanced by burning and soils do not acquire hydrophobic organic coatings characteristic of some soils in temperate climates (Krammes and DeBano, 1965).
- (5) There is only partial combustion of the biomass, litter, and soil humus by the fire.
- (6) Root systems are very extensive and highly concentrated in the uppermost fraction of soil. Shrub roots typically survive those fires in which soil humus is not combusted. Shrub root biomass of a *Picea mariana* woodland was 3290 kg/ha (Rencz and Auclair, 1978).
- (7) Vegetation regenerates rapidly after burning. Liverworts (*Marchantia*) and mosses (*Ceratodon* and *Polytrichum*) reestablish rapidly on some burns (Scotter, 1971) and shrubs sprout rapidly.

There is very little empirical information on the hydrological effects of fire. Actual levels of erosion and siltation in streams remain to be determined under different climate, soil, and vegetation conditions.

13.3.3.3 Element Losses

In contrast to the pronounced post-fire increases in available nutrients in some temperate systems (Grier, 1975; Stark, 1977), most evidence indicates that nutrient elements are very largely retained on lichen woodland sites after burning. Nutrient concentration in streams and lakes which drain recently burnt woodlands do not appear to increase, based on the limited data available. Lotspeich *et al.* (1970) detected only slight increases in potassium and in O_2 demand and no changes in benthic organisms in streams draining burned forest in Alaska. Only slight increases were observed in phosphorus leaving a small watershed sprayed with fire-retardant chemicals (Lotspeich, 1972).

Elements leached below the rooting zone on a 1-year-old burn increased 1.2- to 2.8-fold over that in mature woodland (Moore, 1980). However, the very low base saturation and high phosphorus fixation capacity of the subsoil horizons resulted in little or no leaching losses. Also, integration of annual phosphorus flow to lysimeters (Moore, 1980) indicated that over the first 47 years after fire 1.34 kg/ha would be 'lost' over and above the losses occurring naturally in mature lichen woodland. This was 3.3% of the available phosphorus in the system, including that in the soil component to 30 cm depth. The author estimated that 83% of the phosphorus mineralized at the time of the burn was captured by shrub root systems (Table 13.1). The immobilization was achieved by a tripling of the tissue P concentration rather than additional root growth.

13.4 POST-FIRE REGENERATION

13.4.1 Plant Succession

To date, few in-depth studies are available on the post-fire dynamics of plant regrowth. Studies of Johnson and Rowe (1977), Kershaw and co-workers (Kershaw *et al.*, 1975; Kershaw and Rouse, 1976; Maikawa and Kershaw, 1976), and Scotter (1967) have been the most detailed but represent a relatively specific region (Caribou Range, Northwest Territories, Canada) in the continental interior. Although a comparison of available data indicates large differences between regions of tundra and forest-tundra (Maikawa and Kershaw, 1976), certain common patterns have been observed.

One of the most emphasized effects of fire on tundra and forest-tundra has

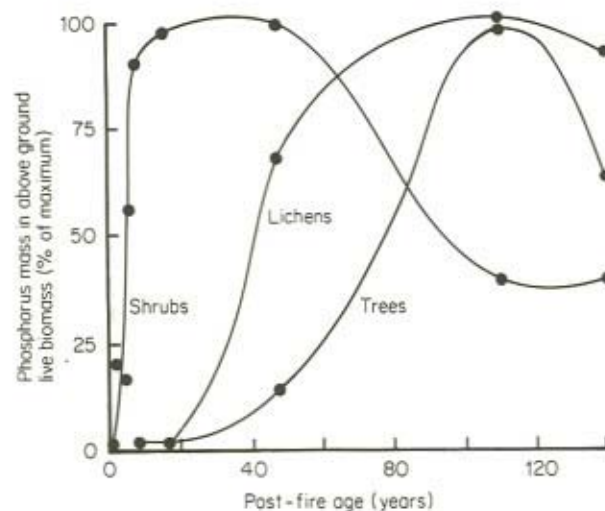


Figure 13.1 Post-fire change in the relative mass of phosphorus in aboveground live biomass of tree, shrub, and lichen components of a *Picea mariana*-*Cladonia alpestris* woodland at Schefferville, Quebec. Values are expressed relative to the maximum occurring during 140 years of post-fire regeneration and are based on actual biomass samples at nine sites (D.J. Hogan, unpublished data)

been the elimination of the lichens (Scotter, 1967). Whereas most plants are killed, shrub rhizomes and roots survive the fire in areas where soil humus has not been combusted. These shrubs are typically rooted at a depth of 2–5 cm, within the mineral soil–humus interface, and can sprout to heights of 40 cm or more the same summer as the fire (Vioreck, 1973). Johnson and Rowe (1977) identified three major forms of regrowth: vegetative reproduction (sprouting), seeds from serotinous cones, and invasion by propagules.

All common shrubs and deciduous tree species in forest-tundra including *Betula* and *Alnus* reproduce vegetatively after fire. *Picea* and *Pinus* do not (Johnson and Rowe, 1977). Among bryophytes, *Polytrichum* spp. and *Ceratodon purpureus* sprout readily from underground stem bases or protonema after fire (Leach, 1931; Marsh and Koerner, 1972). Feathermosses and lichens are not completely killed (Hustich, 1954). Tenuous evidence indicates some *Cladonia* species can produce new 'shoots' after fire (Sarvas, 1937) and Rowe *et al.* (1975) have suggested that this phenomenon be examined.

From the rapid regrowth of shrubs, one suspects that considerable incorporation of nutrients in biomass would occur. A large proportion of phosphorus was captured by roots of *Betula glandulosa* and subsequently incorporated in new stem and leaf tissue (Figure 13.1). Within seven years

after fire 91% of the maximum phosphorus mass in *B. glandulosa* had been incorporated in tissue (D.J. Hogan, unpublished data). Marks (1974) noted this rapid capture of nutrients by pin cherry (*Prunus pensylvanica*). *Prunus* had incorporated more than 90% of the maximum N, K, and Mg levels within six years.

Although buried seeds stored in the soil may assume importance (Viereck, 1973), Johnson (1975) found no viable seeds in three different (*Pinus banksiana*, *Picea glauca*, and *Picea mariana*) lichen woodlands. Seeds were present but were not viable. This is in contrast to temperate forests, where as many as 3000 viable seeds per square metre occur. Serotinous cones of *Picea mariana* and *Pinus banksiana*, however, provide an ideal mechanism for reinvasion of burned areas and few woodlands fail to regenerate these species within the first five years after fire. Peak establishment in *Picea mariana* occurred two to three years after fire and had ceased by the sixth year (Wein, 1975). In a burned *Picea mariana* stand of 909 dead trees per hectare, 8200 000 seeds remained, of which 3 400 000 were viable (Zasada, 1971). Obviously, the tree seed pools can be large. Some evidence indicates that high seed production in *Picea* and *Pinus* coincides with hot summers and therefore with years of high fire frequency (Uggla, 1958; Zasada and Gregory, 1969).

The post-fire colonization by invading species is of secondary importance to sprouting in forest-tundra and tundra. In general, seed invasion occurs rapidly and most species occupying mature stages are present within the first few years after fire (Johnson and Rowe, 1977). *Populus* and *Betula* are wind-dispersed and can invade across large distances. Reinvasion by *Picea* and *Pinus* from seeds of live trees tends to be localized. In the author's observations, shrubs such as *Betula*, *Ledum*, *Salix*, and *Vaccinium* can flower profusely from young sprouts soon after burning. This must be significant in their establishment on areas of woodland and tundra in which they have undergone natural mortality or have been killed in intense fires which consume soil humus.

Pioneering species of grass, sedge, and forbs such as *Agrostis*, *Calamagrostis*, *Poa*, *Carex*, *Corydalis*, and *Epilobium* produce large numbers of light seeds and are typically abundant immediately (within weeks) after fires (Johnson and Rowe, 1977). In eastern Canada, both short growing seasons and the marked infertility of soils prohibit the occurrence of these species (Broderick, 1979).

Most terrestrial lichens establish by small thallus fragments (Fink, 1917; Ridley, 1930) within the first several years following a burn. Their slow growth limits their abundance for the first 25–30 years. Reestablishment of feathermosses (*Dicranum*, *Hylocomium*, *Pleurozium*) occurs 30–50 years post-fire and may depend on the presence of tree canopy cover (Tamm, 1964; Weetman, 1968; Busby *et al.*, 1978).

Changes in vegetation composition and structure with age after fire are due largely to differences in growth rates and life spans. Most species establish at an early date but may not be abundant for a prolonged interval due to slow growth. Although three to five compositional 'phases' have been defined by various workers, Johnson and Rowe (1977) found little evidence of a real compositional series. The mature vegetation is actually a mixture of 'pioneer' and 'mature' lifeforms. Shrub species, some bryophytes, grasses, and forbs are typically pioneer. Trees, lichens, and feathermosses colonize early but dominate at a later age (Johnson and Rowe, 1977). There is often a post-fire shift from deciduous species early in the recovery to leaf-persistent species at maturity (D.J. Hogan, unpublished data).

In the long-term absence of fire there is evidence both of sustained equilibrium as open lichen woodland (Johnson and Rowe, 1977), and, depending on location, change to either open lichen tundra (Strang, 1973) or closed *Picea*-moss forest (Kershaw and Rouse, 1976; Maikawa and Kershaw, 1976). On the basis of decreasing depth of thaw layer with age of lichen heath, Strang (1973) argued that a continuation of the trend would lead to the elimination of trees and predominance of lichen. Maikawa and Kershaw (1976), on the other hand, observed an increase in depth of the peat layer and an increase in the density of trees when sites of increasing age were compared, and concluded that this resulted in the succession of open lichen woodland to closed moss forest.

A two-stage model was formulated to integrate these contrasting trends. The first stage involves lichen-tree interactions. Lichens presumably diminish tree establishment by reducing the soil energy budget and effective soil fertility, and by physical obstruction of seeds at the soil surface (Figure 13.2(a)). Countering this trend, opportunities for tree seedling establishment occur when disturbance (frost scars, tree tip-up mounds, desiccation of lichens) 'opens' the lichen mat. Layering of lower branches can also contribute to increasing tree density. The second stage of the model involves site factors. On highly oligotrophic and/or climatically severe sites, trees may be disadvantaged and possibly eliminated from the lichen-tree interaction, and open lichen heath results. On sites that are climatically and nutritionally favourable to trees, establishment of tree seedlings may continue, resulting eventually in closed forest. It is assumed that a wide spectrum of environmental conditions exist in which open lichen woodland persists as a stable vegetation type (Figure 13.2(b)).

13.4.2 Changes in Soil Decomposers

Studies on post-fire changes and recovery of the soil decomposers are few. In *Picea mariana* woodland at Schefferville, Quebec, a difference in the frequency of eleven fungal species was found to be correlated with post-fire

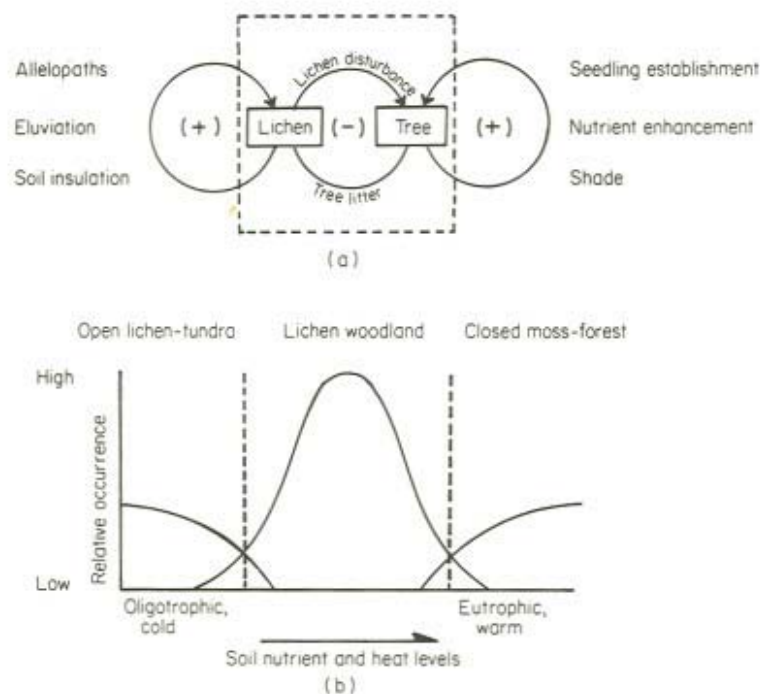


Figure 13.2 Hypothesized feedback relations between lichen and tree components and relative occurrence along environmental gradients. (a) In mature lichen woodland tree-lichen interaction is in a stable equilibrium. Factors enhancing lichen dominance and tree dominance are enumerated separately. (b) Site conditions influencing the dominance of each vegetation type

age (Lucarotti *et al.*, 1978). Mites were reduced from 31 240/m² in an old (137 years) stand to 16 280/m² the first year after a fire (Lucarotti, 1976), and collembola increased from 9010/m² on an unburned site to 11 690/m² on a recently burned area (Lucarotti, 1976).

Moore (1980) worked on the same woodland. Carbon losses from a complete organic soil profile incubated over a 21-day period at 12°C were about half (6.3 mgC/gm) on a 2-year-old burn compared with a mature (138-year-old) woodland. The difference was attributed to the relative absence of readily assimilated organic compounds on the recent burn. Moore (1980) also tested for the effect of lichen leachate, sucrose, urea, NH₄⁺, NO₃⁻, CaO, K, Mg, and P additions on soil respiration rate. Urea, NO₃⁻ and sucrose resulted in significant ($p < 0.05$) increases in CO₂ evolution compared to a control (H₂O) in both recently burned and mature woodland

soils. Obviously, low litter quality, especially with respect to nitrogen, limits decomposition in these lichen woodland soils. Measured Q_{10} with temperature was only 2.0–2.3 between the 1°C and 20°C range (Moore, 1980). The author infers from these observations that the small soil temperature differences (average 1.5°C in upper 15 cm of soil) between burned and unburned sites would not result in large increases in decomposition unless (a) temperature maxima on burned surfaces are high and (b) large nutrient supplements to the litter and humus occur as a result of the 'fertilizing effect' of the fire.

Wielgolaski (1975a,b) has summarized decomposition data on Fennoscandian lichen heaths. Soil respiration (carbon loss in litter horizon) in lichen heath had the lowest level, and the smallest rate of increase with temperature, of five different ecosystems (Svensson *et al.*, 1975). Lichen heath also showed the lowest rate of decomposition when compared with four other ecosystems. Weight loss in the L horizon was 94 gmC/m²/yr compared with 689 gmC/m²/yr in *Betula* forest. Cellulose and barley-straw decomposition rate, bacterial and fungal hyphae per gramme soil dry weight, and primary production were also the lowest in lichen heath (Rosswall *et al.*, 1975). Decomposition of leaf litter in *Cladonia alpestris* was 4.9–5.6% in the first year compared with 21–27% in *Betula* spp. leaves, 37% in *Eriophorum vaginatum*, and 42% in *Carex nigra* (Rosswall *et al.*, 1975). Graminoid species had the highest rates of decomposition of any vegetation type. These data suggest that undisturbed lichen-dominated systems have slow mineral cycling rates. In fact, soil respiration (94 gmC/m²/yr) was less than the primary production (114 gmC/m²/yr) in Norwegian lichen heath (Rosswall *et al.*, 1975). The accumulation of organic matter and nutrients in humus of northern ecosystems has been widely recognized. Whether fire is an essential agent of mineralization in the sense that in the absence of fire mineral cycling slows and severely limits primary production has not been studied (Rowe and Scotter, 1973). At Schefferville, Quebec, mature *Picea mariana* – *Cladonia alpestris* woodlands do exist in which there is no evidence of fire, yet trees appear healthy, suggesting that adequate decomposition and mineral cycling can occur in very old stands.

13.4.3 Changes in Insect, Bird, and Mammal Species

Several reviews of animal changes after fire in tundra and forest-tundra are available (Lutz, 1956; Rowe and Scotter, 1973; Viereck, 1973). Most studies have compared unburned and recently burned tundra and woodland. In general, insects, snowshoe hare, black bear, and moose increase on recently burned sites. However, grouse, small mammals (lemming, shrew, vole), 'fur bearers' (fisher, marten, wolverine), and caribou decrease on burned areas (Viereck, 1973). With the exception of Scotter's (1967) work on caribou–fire

interaction, changes in animal population size with post-fire vegetational changes have not been examined.

Species relations to fire are complex. Skoog (1968) cautioned that generalities based on the impact of fire on caribou in Canada may not be applicable in Alaska. Autumn-winter diet of Alaska caribou consist only of 30% lichen, and, despite fire, there appeared to be a large quantity of forage lichens relative to demands by existing herds. Also, Wein (1975) indicated that, despite the decline (60-85%) observed in vole, lemming, and shrew populations with burning in tundra, succession to predominantly graminoid communities may ultimately permit high density populations of these grazers. In turn, large populations of carnivores such as marten and fox could be expected.

13.5 FUTURE RESEARCH NEEDS

In the literature there are several cases noted where broad generalizations were unwarranted. There is an apparent need to recognize that the nature and impact of fire will not be uniform geographically. What is now required are studies on specific sites and/or vegetation types within lichen tundra and woodland such that management criteria can be applied on a local scale.

The question remains whether fire is essential in sustaining active mineral cycling and primary production (Rowe and Scotter, 1973). This question requires that comparisons be made between mature vegetation and various stages of regrowth after fire. This would also be expected to vary a great deal from site to site. Few studies are available on nutrients and none are available on any aspect of mineral cycling. Major aspects that could be studied include:

- (1) The fraction of biomass and soil organic matter combusted in a 'typical' fire and at differing fire intensities.
- (2) Changes in the mass and concentration of elements in live and dead biomass and soil organic pools with burning and with post-fire regeneration; quantity of nitrogen volatilized, elements lost in smoke, and soil organic matter oxidized.
- (3) The uptake of mineralized elements by post-fire vegetation regrowth and the role of various species in element uptake and retention.
- (4) The fraction of mineralized elements bound on cation exchange of different soil horizons, loss to depths beyond the rooting zone, and loss to streamflow.
- (5) The role of elements in limiting primary production.

There is a need to use prescribed burning to implement objective management treatments and as an experimental tool to answer ecological

questions. Little is known at this point of the autecology of species in relation to fire. It would also be useful to know in more detail what population changes in animal species (including insects) and what coincident changes in vegetation regrowth occur after fire. The effects of multiple burns and soil moisture content on combustion of soil organic matter appears to be a critical aspect on which no data are yet available.

13.6 REFERENCES

- Ahlgren, I.F., and Ahlgren, C.E. (1960) Ecological effects of forest fires, *Bot. Rev.*, **26**, 483-533.
- Auclair, A.N.D., and Rencz, A.N. (1982) Concentration, mass and distribution of nutrients in a subarctic *Picea mariana* - *Cladonia alpestris* ecosystem, *Can. J. For. Res.* **12**: (in press).
- Barney, R.J. (1969) Interior Alaska wildfires, 1956-1965, *US For. Serv., Pac. Northwest For. Range Exp. Stn., Misc. Publ.* 47 pp.
- Barney, R.J. (1971) Wildfires in Alaska — some historical and projected effects and aspects, in C.W. Slaughter, R.J. Barney, and G.M. Hansen (eds), *Fire in the Northern Environment — A Symposium*, US For. Serv., Portland, Oregon, pp. 51-59.
- Bliss, L.C. (1962) Caloric and lipid content in alpine tundra plants, *Ecology*, **43**, 753-757.
- Blum, O.B. (1973) Water relations, Ch. 11 in V. Ahmadian and M. Hale (eds), *The Lichens*, Academic Press, New York.
- Broderick, D. (1979) Establishment, maintenance and reproduction of fireweed (*Epilobium angustifolium* L.) on disturbed and undisturbed sites at Schefferville, Quebec, MSc Thesis, Geography Dep., McGill University, Montreal, Canada. 162 pp.
- Brown, J.K. (1970) Ratios of surface area to volume for common fuels, *For. Sci.*, **16**, 101-105.
- Brown, R.T., and Mikola, P. (1974) The influence of fruticose lichens upon the mycorrhizae and seedling growth of forest trees, *Acta For. Fenn.*, **141**, 1-22.
- Busby, J.R., Bliss, L.C., and Hamilton, C.D. (1978) Microclimate control of growth rates and habitats of boreal forest mosses, *Tomenthypium nitens* and *Hylocomium splendens*, *Ecol. Monogr.*, **48**, 95-110.
- Fink, B. (1917) The rate of growth and ecesis in lichens, *Mycologia*, **9**, 138-158.
- Fosberg, M.A., and Schroeder, M.J. (1971) Fine herbaceous fuels in fire-danger rating, *US For. Serv., Res. Note RM-185*. 7 pp.
- Grier, C.C. (1975) Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem, *Can. J. For. Res.*, **5**, 599-607.
- Hardy, C.E., and Franks, J.W. (1963) Forest fires in Alaska, *US For. Serv., Res. Pap. INT-5*. 163 pp.
- Heginbottom, J.A. (1971) Some effects of a forest fire on a permafrost active layer at Inuvik, N.W.T., in R.J.E. Brown (ed), *Proc. Seminar on Permafrost Active Layer*, *Can. Nat. Res. Council, Assoc. Comm. Geotech. Res., Tech. Mem.* 103, pp. 31-36.
- Hustich, I. (1954) On forests and tree growth in the Knob Lake area, Quebec-Labrador Peninsula, *Acta Geogr.*, **16**, 1-48.

- Johnson, E.A. (1975) The buried seed populations in the subarctic forest east of Great Slave Lake, N.W.T., *Can. J. Bot.*, **53**, 2933-2941.
- Johnson, E.A., and Rowe, J.S. (1975) Fire in the subarctic wintering grounds of the Beverley caribou herd, *Am. Midl. Nat.*, **94**, 1-14.
- Johnson, E.A., and Rowe, J.S. (1977) Fire and vegetation change in the western subarctic, *Can. Dep. Indian Aff. North. Develop., ALUR Rep. 75-76-61*, 58 pp.
- Kershaw, K.A. (1977) Studies on lichen-dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada, *Can. J. Bot.*, **55**, 393-410.
- Kershaw, K.A., and Rouse, W.R. (1976) The impact of fire on forest and tundra ecosystems, *Can. Dep. Indian Aff. North. Develop., ALUR Rep. 75-76-63*, 54 pp.
- Kershaw, K.A., Rouse, W.R., and Bunting, B.T. (1975) The impact of fire on forest and tundra ecosystems, *Can. Dep. Indian Aff. North. Develop., ALUR Rep. 74-75-63*, 81 pp.
- Krammes, J.S., and DeBano, L.F. (1965) Soil wettability: a neglected factor in watershed management, *Water Resour. Res.*, **1**, 283-286.
- Kryuchkov, V.V. (1968) Soils of the far north should be conserved, Museum of Soil Science, Moscow State University, *Priroda*, **12**, 72-74 (in Russian; translated in J. Brown, W. Rickard, and D. Vietor (eds) (1969) The effect of disturbance on permafrost terrain, *US Army, Cold Regions Res. Engin. Lab., Spec. Rep. 138*, Hanover, N.H. 13 pp.).
- Larson, D.W., and Kershaw, K.A. (1976) Studies on lichen-dominated systems. XVIII. Morphological control of evaporation in lichens, *Can. J. Bot.*, **54**, 2061-2073.
- Leach, W. (1931) On the importance of some mosses as pioneers on unstable soils, *J. Ecol.*, **19**, 98-102.
- Lotspeich, F.B. (1972) Effects of the Wickersham Dome fire on water quality of Washington Creek, *US Environ. Protect. Agency, Alaska Water Lab., College, Alaska, Working Pap. 14*, 17 pp.
- Lotspeich, F.B., Muller, E.W., and Frey, P.J. (1970) *Effects of Large Scale Forest Fires on Water Quality in Interior Alaska*, US Dep. Interior, Federal Water Pollution Control Admin., Alaska Water Lab., College, Alaska. 115 pp.
- Lucarotti, C. (1976) Post-fire change in mycofloral species and mesofauna populations in lichen woodland soils, Schefferville, Quebec, MSc Thesis, McGill University, Montreal, Quebec, Canada. 64 pp.
- Lucarotti, C.J., Kelsey, C.T., and Auclair, A.N.D. (1978) Microfungal variations relative to post-fire changes in soil environment, *Oecologia*, **37**, 1-12.
- Lutz, H.J. (1956) Ecological affects of forest fires in the interior of Alaska, *US Dep. Agric., Tech. Bull. 1133*, 121 pp.
- Marks, P.L. (1974) The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems, *Ecol. Monogr.*, **44**, 73-88.
- Marsh, W.M., and Koerner, J.M. (1972) Role of moss in slope formation, *Ecology*, **52**, 489-493.
- Mackay, J.R. (1970) Disturbances to the tundra and forest tundra environment of western Arctic, *Can. Geotech. J.*, **7**, 420-432.
- Maikawa, E., and Kershaw, K.A. (1976) Studies on lichen-dominated systems. XIX. The postfire recovery sequence of black spruce-lichen woodland in the Abitau Lake Region, N.W.T., *Can. J. Bot.*, **54**, 2679-2687.
- Mikola, P., Laiho, O., Erikainen, J., and Kuvaja, K. (1964). The effect of slash burning on the commencement of mycorrhizal association, *Acta For. Fenn.* **77**, No. 3.

- Moore, T.R. (1980) The nutrient status of subarctic woodland soils, *Arct. Alp. Res.*, **12**, 147-160.
- Mutch, R.W., and Castineau, O.W. (1971) Timelag and equilibrium moisture content of reindeer lichen, US For. Serv., Intermoun. For. Range Exp. Stn, Ogden, Utah (manuscript). 8 pp.
- Mutch, R.W., and Philpot, C.W. (1970) Relation of silica content to flammability in grasses, *For. Sci.*, **16**, 64-65.
- Rencz, A.N., and Auclair, A.N.D. (1978) Biomass distribution in subarctic *Picea mariana* - *Cladonia alpestris* woodland, *Can. J. For. Res.*, **8**, 168-176.
- Requa, L.E. (1964) Lightning behavior in the Yukon, *Proc. Tall Timbers Fire Ecol. Conf.*, **3**, 111-119.
- Ridley, H.N. (1930) *The Dispersal of Plants Throughout the World*, Reeve, Ashford, Kent. 744 pp.
- Rosswall, T., Veum, A.K., and Körenlampi, L. (1975) Plant litter decomposition at Fennoscandian tundra sites, in F.E. Wielgolaski (ed), *Fennoscandian Tundra Ecosystems. Part I. Plants and Microorganisms*, Ecological Studies 16, Springer, New York, pp. 268-278.
- Rothermel, R.C. (1972) A mathematical model for predicting fire spread in wildland fuels, *US For. Serv., Res. Pap. INT-115*, 40 pp.
- Rothermel, R.C., and Anderson, H.E. (1966) Firespread characteristics determined in the laboratory, *US For. Serv., Res. Pap. INT-30*, 30 pp.
- Rouse, W.R. (1976) Microclimatic changes accompanying burning in subarctic lichen woodland, *Arct. Alp. Res.*, **8**, 357-376.
- Rowe, J.S., Bergsteinsson, J.L., Padbury, G.A., and Hermesh, R. (1974) Fire studies in the Mackenzie Valley, *Can. Dep. Indian Aff. North. Develop., ALUR Rep. 73-74-61*, 121 pp.
- Rowe, J.S., and Scotter, G.W. (1973) Fire in the boreal forest, *Quat. Res.*, **3**, 444-464.
- Rowe, J.S., Spittlehouse, D., Johnson, E., and Jasieniuk, M. (1975) Fire studies in the upper Mackenzie Valley and adjacent Precambrian Uplands, *Can. Dep. Indian Aff. North. Develop., ALUR Rep. 74-75-61*, 128 pp.
- Sarvas, R. (1937) Referat: Beobachtungen über die entwicklung der vegetation auf den waldbrandflächen nord-Finnlands, *Silva Fenn.* **44**.
- Scotter, G.W. (1964) Effects of forest fires on the winter range of barren-ground caribou in northern Saskatchewan, *Can. Wildl. Serv., Wildl. Manage. Bull., Ser. 1, No. 18*, 111 pp.
- Scotter, G.W. (1965) Chemical composition of forage lichens from northern Saskatchewan as related to use by barren-ground caribou, *Can. J. Plant Sci.*, **45**, 246-250.
- Scotter, G.W. (1967) Effects of fire on barren-ground caribou and their forest habitat in northern Canada, *Trans. North Am. Wildl. Natural Resources Conf.*, **32**, 246-259.
- Scotter, G.W. (1971) Fire, vegetation, soil, and barren-ground caribou relations in northern Canada, in C.W. Slaughter, R.J. Barney, and G.M. Hansen (eds), *Fire in the Northern Environment - A Symposium*, US For. Serv., Portland, Oregon, pp. 209-230.
- Shelford, V.E. (1963) The tundra biome, in *The Ecology of North America*, University of Illinois Press, Urbana, Illinois, pp. 184-210.
- Simard, A.J. (1975) *Frequency of Forest Fires in Canada*, Can. For. Serv., Ottawa, Ontario. Map.
- Skoog, R.O. (1968) Ecology of the caribou (*Rangifer tarandus Granti*) in Alaska, PhD

- Thesis, University of California, Berkeley, California.
- Stark, N.M. (1977) Fire and nutrient cycling in a Douglas-fir/larch forest, *Ecology*, **58**, 16–30.
- Strang, R.M. (1973) Succession in unburned subarctic woodlands, *Can. J. For. Res.*, **3**, 140–143.
- Svensson, B.H., Veum, A.K., and Kjølvik, S. (1975) Carbon losses from tundra soils, in F.E. Wielgolaski (ed), *Fennoscandian Tundra Ecosystems. Part 1. Plants and microorganisms*, Ecological Studies 16, Springer, New York, pp. 279–286.
- Sylvester, T.W. (1975) Fuel characteristics of plant communities in the Mackenzie Delta Region, in R.W. Wein (ed), *Vegetation recovery in Arctic tundra and forest-tundra after fire*, *Can. Dep. Indian Aff. North. Develop., ALUR Rep. 74-75-62*, pp. 63–91.
- Tamm, C.O. (1964) Growth of *Hylocomium splendens* in relation to tree canopy, *Bryologist*, **67**, 423–426.
- Uggla, E. (1958) *Ecological Effects of Fire on North Swedish Forests*, Almqvist and Wiksells, Uppsala, Sweden. 18 pp.
- Van Wagner, C.E. (1974) Structure of the Canadian forest fire weather index, *Can. For. Serv., Publ. No. 1333*, 44 pp.
- Viereck, L.A. (1973) Wildfire in the taiga of Alaska, *Quat. Res.*, **3**, 465–495.
- Viro, P.J. (1955) Investigations on forest litter, *Commun. Inst. Forest Fenn.* **45**, No. 6.
- Walter, H. (1973) *Vegetation of the Earth in Relation to Climate and the Ecophysiological Conditions*, Springer, New York. 237 pp.
- Weber, M.G. (1975) Nutrient budget changes following fire in arctic plant communities, in R.W. Wein (ed), *Vegetation recovery in arctic tundra and forest tundra after fire*, *Can. Dep. Indian Aff. North. Develop., ALUR Rep. 74-75-62*, pp. 92–115.
- Weetman, G.F. (1968) The relationship between feather moss growth and the nutrition of black spruce, in *Proc. Third Inter. Peat Congress*, Quebec, Canada, pp. 366–370.
- Wein, R.W. (1975) Vegetation recovery in arctic tundra and forest-tundra after fire, *Can. Dep. Indian Aff. North. Develop., ALUR Rep. 74-75-62*, 115 pp.
- Wein, R.W. (1976) Frequency and characteristics of arctic tundra fires, *Arctic*, **29**, 213–222.
- Wein, R.W., and Bliss, L.C. (1973) Changes in arctic *Eriophorum* tussock communities following fire, *Ecology*, **54**, 845–852.
- Widden, P., and Parkinson, D. (1975) The effect of a forest fire on soil microfungi, *Soil Biol. Biochem.*, **7**, 125–138.
- Wielgolaski, F.E. (ed) (1975a) *Fennoscandian Tundra Ecosystems. Part 1. Plants and Microorganisms*, Ecological Studies 16, Springer, New York. 366 pp.
- Wielgolaski, F.E. (ed) (1975b) *Fennoscandian Tundra Ecosystems. Part 2. Animals and Systems Analysis*, Ecological Studies 17, Springer, New York. 337 pp.
- Zasada, J.C. (1971) Natural regeneration of interior Alaska forests — seed, seedbed, and vegetative reproduction considerations, in C.W. Slaughter, R.J. Barney, and G.M. Hansen (eds), *Fire in the Northern Environment — A Symposium*, US For. Serv., Portland, Oregon, pp. 231–246.
- Zasada, J.C., and Gregory, R.A. (1969) Regeneration of white spruce with reference to interior Alaska: a literature review, *US For. Serv., Res. Pap. PNW-79*, 37 pp.
- Zoltai, S.C., and Pettapiece, W.W. (1973) Studies of vegetation, landform and permafrost in the Mackenzie Valley, *Environ.-Social Committee North. Pipelines, Task Force on North. Oil Develop. Rep. No. 73-4*, 105 pp.