The Role of Fire in Northern Circumpolar Ecosystems
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CHAPTER 11

The Effects of Fire in Black Spruce Ecosystems of Alaska and Northern Canada

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ABSTRACT

Fire in the black spruce ecosystem of northern Canada and Alaska is characterized by large and frequent fires that usually kill the overstorey trees and most, if not all, of the vegetation aboveground. Most species within the black spruce ecosystem show adaptations to fire, and black spruce stands are usually perpetuated by fire. Depending on the site, revegetation follows one of two primary patterns, although under some conditions there may be intervening stages of birch, aspen, or lodgepole pine. In general, the succession on dry sites develops as open lichen woodland with a nearly continuous cover of fruticose lichens. On moist sites, the development is that of a closed forest with a forest floor dominated by dense feathermosses and with a buildup of an organic mat. The final or climax vegetation that develops depends on site and climate and may vary from treeless bogs through feathermoss types to open lichen woodlands. In some areas, balsam fir replaces the black spruce. Fire reduces the organic layer on the forest floor and causes higher soil temperatures, an increase in available nutrients, and an increase in productivity for a period following the fire.

11.1 INTRODUCTION

Within the northern parts of the North American taiga, black spruce (*Picea mariana* (Mill.) B.S.P.) is widely distributed, and it is black spruce types which burn the most frequently and cause the greatest problems in fire suppression. This chapter concentrates on the black spruce ecosystem in the northern part of the taiga. This includes all of the taiga of Alaska (Viereck, 1975) and the northern part of Canada defined by Rowe (1972) as the boreal forest, especially that subregion defined as 'forest and barren' and the northern portion of the 'predominantly forest' subregion. In this chapter we use 'taiga' in the broad sense to include all of the closed boreal forest, forest-tundra (forest and barren of Rowe (1972)), *lesotundra* of the Soviet Union (Tikhomirov, 1970), and the open boreal woodland zone (Hustich, 1966; Hare and Ritchie, 1972). In Scandinavia this would be equivalent to the northern, middle, and southern boreal of Ahti *et al.* (1968).

11.2 CLIMATE

The climate of the northern part of the taiga of North America is characterized by long, cold winters and short, hot summers. Precipitation is adequate for tree growth but periodic droughts are common. Long and clear days may result in June and July temperatures in excess of 33°C in many areas, and average daily July temperatures are rather uniformly between 15° and 18°C. Mean annual temperatures in the northern taiga are well below 0°C, with some stations near the tree line having mean annual temperatures as low as −10°C. This accounts for a permafrost distribution which is continuous under much of the forest-tundra area but is discontinuous, sporadic, or lacking in the southern regions (Brown, 1970).

Much of the precipitation in June and July results from lightning storms. These storms cause a high frequency of lightning fires over much of the taiga, even though the incidence of lightning is less than in southern regions. Annual precipitation in interior Alaska and the central part of Canada may be as little as 250 mm but it increases eastwards to more than 1000 mm in Newfoundland. According to Thornthwaite's (1948) climate types, the boreal forests of Alaska and Canada range from dry subhumid climate over most of Alaska and western Canada through moist climate to a perhumid (moderately wet) climate in eastern Quebec-Labrador and Newfoundland (Rowe, 1972). Fire frequencies and fire effects vary greatly across the range of these climatic types.

11.3 FIRE REGIME IN THE BLACK SPRUCE TYPE

Most fires in the black spruce type are either crown or ground fires of enough intensity to kill overstorey trees. Usually some of the organic layer of the forest floor remains, but fires in late summer following exceptionally dry periods or under dry, windy conditions may consume all of the organic layer, exposing mineral soil. The tendency of fires to crown is related to the distribution of fuels within the stands. In most black spruce stands there is an open, highly flammable ericaceous shrub layer that will carry the flame at 0.5 to 1 m above the surface. From that point, ignition into the black spruce crown is frequent because the spruce usually have dead lower branches that are lichen covered and will carry the flame directly into the crown. Layering of the lower branches of spruce also provides a nearly continuous fuel ladder from the forest floor to the tree crowns.

Size of individual fires is also important in characterizing the fire regime of any given vegetation type. Fires in the taiga tend to be large, often reaching 50 000 ha or larger. The ecologically significant fires usually occur during the exceptional fire years and may reach sizes of over 200 000 ha. Rowe *et al.* (1974) pointed out that in the southern area of the Mackenzie Valley, 42% of the fires studied occurred in five exceptional years and in the northern area four years accounted for 60% of the fires. In Alaska, during the 38 years for which there are fire records, six years (1940, 1941, 1950, 1957, 1969, and 1977) account for 63% of the total area burned.

One interesting question relates to the synchrony of these fire years over wide geographic areas. Rowe *et al.* (1974) found only two years where the fire record was similar for the northern and southern areas of Mackenzie Valley—1881 and 1863. The latter year has also been reported as a serious fire year in Jasper Park (Tande, 1979), in Montana (Arno, 1976), and in Minnesota (Frissell, 1973; Heinselman, 1973). A comparison of the short record for Alaska and some early major fire years listed by Lutz (1956) with the data provided by Rowe *et al.* (1974) indicate that 1893, 1915, 1937, 1941, 1950, and 1969 show a correlation between Alaska and the Mackenzie Valley. Several severe fire years in Alaska, such as 1940 and 1957, have no counterpart in the Mackenzie area.

There is also an apparent but unexplained periodicity in the occurrence of exceptional fire years. Fox (1978) has proposed that fire frequency is characterized by an 11-year cycle following that of the sun spots. Data from Alaska and Canada show a rough correlation of annual area burned to a 9- to 11-year time interval. Rowe *et al.* (1974) for the Mackenzie Valley and Heinselman (1973) for northern Minnesota have suggested that in one year out of every four there is a probability of some significant fire activity. Wilton and Evans (1974) showed that the area burned in Newfoundland between 1910 and 1970 followed a periodic but not cyclic pattern. They pointed out that the extreme fire years occur as pairs, with the first year less severe than the second. The question is unresolved as to whether there is a regular cyclic pattern for the whole circumboreal region, a cyclic pattern for small geographic areas, or whether there is only a random periodicity, but not a regular cyclic pattern in the occurrence of severe fire years.

The most important consideration in describing the fire regime of an area or vegetation type is the expected time interval between fires. This has been termed fire frequency, natural fire rotation (Heinselman, 1973), or fire cycle (Van Wagner, 1978). Heinselman (1973) accounted for the fact that many areas will be burned several times and others not at all with the definition: 'The fire rotation cycle is the long-term average number of years required under the prevailing fire regime to burn-over an area equivalent to the total area under consideration.'

There is limited information available on the natural fire rotation for the taiga regions because of its remoteness and lack of fire records. In the Mackenzie Valley, Rowe *et al.* (1974) showed a fire recurrence interval between 80 and 90 years for the black spruce type. Smith and Henderson (1970) showed approximately a 100-year fire rotation for spruce in northern British Columbia. In Alaska a fire rotation of about 200 years can be calculated by using the mean area burned since records have been kept and the estimated areas of vegetation types. Heinselman (1981) has modified this to an estimated 130 years for open spruce-lichen forests and 100 years for closed black spruce. These are general figures based on the whole Alaska taiga. Trigg (1971) published a map of 16 fire climatic zones of Alaska which range from hot and arid to cold and wet. One would expect fire frequency to correlate with these zones, and thus the shortest fire cycles would occur in interior Alaska and the Yukon Basin and longer fire cycles would be typical of western and southwestern Alaska. In corroboration of this, Yarie (1979) estimated the natural fire rotations for the Porcupine River area to be 49 years, based on stand ages of 375 randomly located stands in the 3.6 million ha area.

With increased precipitation from western to eastern Canada, one would expect the natural fire cycle to increase from west to east. Although no estimates of the fire cycle are available from the northern forested areas of eastern Canada, some information is available from Newfoundland and New Brunswick. Wein and Moore (1977) calculated a fire rotation of 230 years for the red spruce-hemlock-pine type and over 1000 years for the high elevation conifer types in New Brunswick. They also reported a fire rotation for Nova Scotia of 200 years prior to fire suppression activities beginning around 1900 and a rotation of 1000 years since 1915 (Wein and Moore, 1979). Wilton and Evans (1974) have carefully recorded the history of fires in Newfoundland. They found that over the past 60 years 15% of the commercial forest and 12.5% of the total land area had burned. This gives a fire rotation of approximately 400 years for the forested areas and 480 years for the total island. Wilton and Evans (1974) pointed out that this is not a natural fire regime but one established under much development and man-caused fires. These figures from eastern Canada indicate that the fire rotation or fire cycle is much greater in the wetter regions of the boreal forest than it is in the dryer areas of western Canada and central Alaska.

In summary, the natural fire regime of the boreal forest can be characterized as one of high-intensity crown or surface fires. The fires are usually large due to the types of forest, continuity of fuels, and the climatic conditions. The fire rotation time is relatively short, 50 to 100 years, in much of Alaska and western Canada but may increase to 500 years or more in the wetter section of eastern Canada.

11.4 ADAPTATION TO FIRE

One reason black spruce is so widespread in the northern taiga is its adaptation to fire. While most of the common species in the black spruce type show adaptation to fire through their regeneration capabilities (Zasada, 1971), only the adaptations of black spruce will be discussed here. The adaptation to fire of a number of northern species are discussed by Uggla (1958) and by Rowe in this volume (Chapter 8).

Black spruce is adapted to fire primarily through its semi-serotinous cones. Much of the information on cone and seed production in black spruce comes from the southern parts of the boreal forest, but some information is available from the Mackenzie Delta region of northern Canada (Black and Bliss, 1978; Wein, 1975) and from Alaska (Zasada, 1971). Black spruce may begin to produce cones as early as 10 to 15 years following fire (Fowells, 1965), but optimum seed production is usually not until 50 to 150 years later. Seed matures in late summer, and some seed is dispersed throughout the year. Fifty percent or more of the viable seed remains in the cones one year after ripening, and about 15% remains after five years (Wilton, 1963). Following fire in northern Canada, Wein (1975) found that the percentage germination of black spruce seed varied from 0% to 19% six years following fire and from only 0% to 1% 20 years after a fire. Little information is available on seed dispersal patterns following fire in black spruce. Seedfall continued for at least eight years following a fire in 70-year-old black spruce in Alaska. Wilton (1963), in monitoring seed dispersal following a relatively hot fire in Newfoundland, found that about half the seed fell during the first 60 days after the fire. He also found a rather quick drop in viability of the seed, from about 60% immediately after the fire to 20% in the spring of the following year. In Alaska, Zasada *et al.* (1979) measured a real germination percentage of 90 for an unburned black spruce stand, 65 for the year following a fire, and 32 for seeds the second year after the fire.

Establishment of seedlings usually begins the first year following fire and continues for several years. In Canada, Wein (1975) found that, six years following the 1968 Inuvik fire, 22% of the established black spruce seedlings were four years of age, and 35% were five years of age, indicating that the second and third summers following the fire were the greatest for seedling establishment. In Alaska a general increase in the number of seedlings through the first three summers following the 1971 Wickersham fire was found (Viereck and Foote, 1979). After the first three years of seedling establishment, we calculated that only 0.2% to 1.8% of the seeds that fell had actually produced seedlings three years after the fire (Zasada *et al.*, 1979). This was following a fire that burned about one-third of the organic layer but did not expose mineral soil over most of the burned area. The study illustrates the importance of a suitable seedbed for germination in addition to an adequate seed source.

Black spruce also reproduces abundantly by layering of the lower branches. This adaptation may be important for persistence of clones of black spruce north of the present tree line and in increasing the density of spruce stands following fire, but it does not seem to be important as an adaptation to recovery following fire. The layered branches are usually buried only in the surface moss layers and are easily destroyed by fire. The layering habit may be important in the susceptibility of black spruce stands to crown fires as they often form continuous fuel from the ground to the crowns of trees, especially in open spruce stands. The layering habit, shallow roots, thin bark, and the frequent occurrence of abundant lichens on its lower branches make the black spruce particularly susceptible to fire. It is usually only at the very edge of fires or where fires creep slowly through the moss mat that spruce may survive and leave a fire scar record. The persistence and abundance of black spruce in areas of high fire frequency is due primarily to its production of abundant seed in semi-serotinous cones at an early age.

11.5 EFFECT OF SEVERITY OF BURN

The amount of organic material in the forest floor that is removed by fire may determine the successional sequence following fire. Viereck *et al.* (1979) utilized five forest floor fire disturbance classes to quantify this effect: (1) heavily burned with a deep ash layer present, organic material in the soil consumed or nearly so to mineral soil, no discernable plant parts remaining; (2) moderately burned with the organic layer partially consumed, shallow ash layer present, parts of wood twigs remaining; (3) lightly burned, plants charred, but original form of mosses and twigs visible; (4) scorched, mosses and other plants brown or yellow, but species identifiable; and (5) unburned, plant parts green and unchanged.

Fire intensity is difficult to determine for a post-fire site and, as a result, few of the studies of succession in the taiga take intensity into account when discussing the sequence of revegetation following fire. It is obvious, however, that the severity of fire is important, especially in an ecosystem where much of the revegetation is from plant parts that remain on the site through the fire. A heavy burn which removes most of the organic layer usually will kill the underground parts of most shrubs. *Equisetum* and *Polytrichum* species, with rhizoids going into the mineral soil, may be the only species to survive on these sites. The mineral soil provides ideal conditions for the germination of spores and seeds of most invading species, and quickly becomes covered with *Marchantia polymorpha* L., *Ceratodon purpureus* (Hedw.) Brid., and *Epilobium angustifolium* L. Mineral soil sites are also good germination sites for black spruce seeds (Fowells, 1965).

On the other hand, a light fire that merely kills the aboveground plant parts and chars and kills the moss layer will leave the underground parts of the shrubs and many herbs intact. Revegetation will be rapid from rhizomes and root and stump sprouts. This type of burn encourages the proliferation of shrubs that reproduce from underground rhizomes, such as *Vaccinium uliginosum* L. and *Ledum groenlandicum* Oeder.

11.6 REVEGETATION FOLLOWING FIRE IN THE BLACK SPRUCE TYPE

The successional sequence following fire in the black spruce type is complex and related to a number of factors including the pre-burn vegetation type and age, the climate, severity and time of year of the burn, parent material, presence or absence of permafrost, and the weather patterns following the fire. Thus there is no general sequence of vegetation following fire in the black spruce type throughout Canada and Alaska. As pointed out by Maikawa and Kershaw (1976), a review of succession studies following fire in Canada indicates large differences between revegetation sequences with respect to rates of revegetation and the species involved. In spite of this variability, there seem to be two main patterns of succession following fire in the black spruce type in northern areas. The first develops as closed to open stands on sites that are mesic to wet and are dominated in most of the successional stages by mosses, either feathermosses or *Sphagnum*. The second black spruce type, with an entirely different successional sequence, is that of the open black spruce-lichen woodlands found on well-drained sites in Canada and occasionally in Alaska. Within each of these two types there are many variations related to some of the factors listed previously.

11.6.1 The Black Spruce-feathermoss type

Succession in the black spruce-feathermoss type has been described for Alaska by Lutz (1956), Viereck (1973), and Foote (1976) and for the Mackenzie District, Northwest Territories, by Wein (1975) and Black and Bliss (1978). Following is a synthesis and summary of their descriptions of the successional sequence.

The first stage of revegetation, the seedling-herb stage, usually lasts from one to four years depending on the site and fire conditions. Areas of bare mineral soil are covered with *Marchantia polymorpha, Ceratodon purpureus, Polytrichum commune* Hedw., *Epilobium angustifolium* and other light-seeded herbaceous species. Spruce seedlings usually become established during this stage, often in the *Marchantia* and *Ceratodon* mats. In the lightly to moderately burned areas regeneration is primarily by the continued sprouting of underground parts of the shrubs such as *Salix* spp., *Betula glandulosa* Michx., *Rosa acicularis* Lindl., *Vaccinium uliginosum, Ledum groenlandicum,* and herbs, primarily *Calamagrostis canadensis* (Michx.) Beauv., *Rubus chamaemorus* L., and *Equisetum silvaticum* L. Plant cover during this stage increases rapidly from 0% to as much as 40% or 50%. It is during this stage that most of the vascular species that will continue on through the successional sequence are established. Few of the mosses and lichens that are abundant in the mature stages become established until later.

In the shrub stage, the shrubs that have originated from sprouts and shoots continue their rapid growth and dominate the vegetation, but the herb layer also continues to increase, primarily through the expansion of rhizomes of *Epilobium angustifolium* and *Calamagrostis canadensis*. The mosses, again primarily *Ceratodon* and *Polytrichum*, also continue to increase in the early part of the shrub stage, although they may begin to decrease toward the end of this stage if the shrub canopy closes and leaf litter becomes abundant. The first lichens, usually the foliose lichens *Peltigera canina* (L.) Willd. and *P. aphthosa* (L.) Willd., become established during this stage. This stage usually occurs from six to 25 years following the fire.

The tree canopy begins to dominate from 25 to 30 years following the fire. Young stands 40 to 60 years old are dense, with as many as 4000 to 6000 trees and saplings per ha, and seedlings may be as dense as 12 000 per ha. The tall shrub layer of willows and alders begins to thin out as the spruce become taller, but the low shrub layer of *Vaccinium uliginosum*, *V. vitis-idaea* L., *Ledum groenlandicum*, *Betula glandulosa*, and *Rosa acicularis* continues to expand and increase in cover. The most significant event that occurs during this stage is the invasion and rapid development of the feathermosses, *Hylocomium splendens* (Hedw.) B.S.G. and *Pleurozium schreberi* (Brid.) Mitt., which, along with some *Sphagnum* species, may develop as much as 50% cover. With the establishment of these mosses, there begins the development of a thick organic layer which accumulates the available nutrients and creates colder soil temperatures; the permafrost layer then refreezes on many sites. Another significant invasion is by fruticose lichens, the *Cladonia* and *Cladina* species and additional foliose lichens such as *Nephroma arcticum* (L.) Torss., which together may account for at least 20% cover.

Once the tree canopy is well established, the changes in the vegetation sequence are slower and more subtle. During the older stages, the tree canopy is mostly closed although the density is less, averaging 2200 stems per ha. The moss layer remains about the same as in the younger tree stage except for an increase in both *Hylocomium splendens* and fruticose lichens, and a decline in foliose lichens.

In Alaska, the development of the black spruce type into a mature stand over 100 years old follows without any major changes. Tree densities are about the same, 1700/ha for black spruce, and a few paper birch may persist into the mature stage. The spruce tend to be in clumps produced by layered branches, and there are more openings in the canopy. Because of this, the shrub layers, especially the low shrubs, are better developed than during the 60- to 90-year period when the tree canopy is more closed. Moss cover in mature stands is dense and covers nearly 75% of the forest floor, but the lichen cover continues to decline on these mesic sites so that total lichen cover of both foliose and fruticose lichens averages only 2%.

11.6.2 The Black Spruce-lichen Woodland

The open black spruce-lichen type has been studied throughout the northern areas of Canada where it is widespread. Since this type is important as winter range for caribou, several of the studies of succession in the black spruce-lichen woodland have been carried out as part of larger studies of caribou range and populations (Scotter, 1964; Bergerud, 1971, 1974; Hustich, 1951; Ahti and Hepburn, 1967). Johnson and Rowe (1975) and Maikawa and Kershaw (1976) studied this type in the central part of the Canadian Shield, in the region southeast of the Great Slave Lake and in the Caribou Hills in central Northwest Territories. Ahti (1959) and Bergerud (1971) described succession in this type from eastern Canada. Although there is some variation in the sucessional patterns related to different substrates and different climate, general similarities in the succession patterns will be stressed in the following discussion.

The first stage of revegetation, which lasts from one to 20 years, is dominated by pioneer mosses, such as *Ceratodon purpureus*, *Polytrichum juniperinum* Hedw., *P. piliferum* Hedw., and the liverwort, *Marchantia polymorpha*. Crustose lichens, primarily *Lecidea* spp., may cover as much as 20% of the ground in this stage. In some areas, a number of vascular plants, especially *Epilobium angustifolium*, *Calamagrostis canadensis*, and several other grasses and sedges, are also important.

The second stage, which commonly occurs from 10 to 60 years following the fire, is characterized by the invasion and dominance of fruticose lichens of which several *Cladonia* species are the most prominant. Ahti (1959) and Bergerud (1971) both described this stage as the 'horn lichen stage' because of the dominance of *Cladonia crispata* (Ach.) Flat and other closely related species. On some sites, feathermosses may become established and spread during this period. There is also a development of low ericaceous shrubs, especially *Vaccinium vitis-idaea* and *Ledum groenlandicum*. An open tree canopy is established during this stage.

In stands about 100 years old there is a general shift in lichen species to domination by *Cladina alpestris* (L.) Harm. and *C. rangiferina* (L.) Harm. In the Drumlin area of the Northwest Territories, Maikawa and Kershaw (1976) reported an exception to this pattern in which 60 to 130-year-old stands are dominated by *Stereocaulon paschale* (L.) Hoffm. On some sites during this stage there is a general increase in the density of the tree cover resulting also in an increase in the feathermosses, *Hylocomium splendens* and *Pleurozium schreberi*. On other sites the lichen mat persists under an open spruce canopy.

11.7 RELATIONSHIP WITH OTHER VEGETATION TYPES

The most common occurrence after fire in black spruce stands is direct replacement by another stand with similar species. There are, however, many

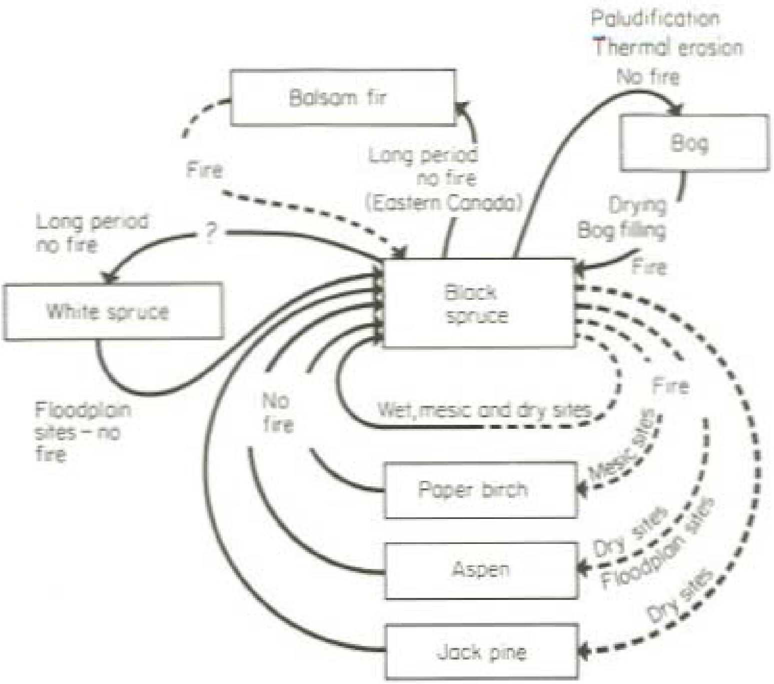

Figure 11.1 Successional relationship of black spruce to other forest types in Alaska and Canada (adapted from Lutz, 1956; Viereck, 1973; Johnson and Rowe, 1977)

examples of other tree species involved in the black spruce succession, as summarized in Figure 11.1. The invasion of black spruce burns by birch and aspen is more common in the southern areas of the boreal forest than in the north, due primarily to the decreased occurrence of these species in the northern areas. In northern Saskatchewan dense stands of *Betula papyrifera* Marsh. may develop following fire in the black spruce type and be eventually replaced by black spruce (Scotter, 1964). Farther north in the Mackenzie area, Black and Bliss (1978) mention *Betula papyrifera* as only an occasional component of the black spruce type.

Little information is available about the conditions required for conversion of black spruce to hardwood forest types following fire. Lutz (1956) and Viereck (1973) suggested that the conversion may result from either intense fires which destroy the black spruce cones in the tree tops and at the same time provide a good mineral soil surface for germination of the hardwood species, or a recurrence of fire in the black spruce type before the spruce have been able to produce a cone crop.

Of special interest are stands of aspen (*Populus tremuloides* Michx.) with an understorey of black spruce. Aspen usually occurs on dry warm slopes in interior Alaska and is replaced in time with white spruce. On old river terraces, usually underlain by coarse river alluvium, one occasionally finds aspen stands with an understorey of black spruce. It is speculated that in these cases a severe fire has removed the organic layer completely and allowed the seeding of aspen at the same time as the black spruce. The coarse river alluvium and the lack of an organic layer provides a temporary, warm, well-drained site for the aspen. Aspen, being relatively short lived, is eventually replaced by spruce and the associated moss and organic layer, and the site once again reverts to a cold, wet condition.

In the middle to southern taiga, black spruce is less frequently an invader of burned upland sites and is more commonly found as a shade-tolerant tree under other tree canopies, especially that of *Pinus banksiana* Lamb. (Carleton and Maycock, 1978). According to Scotter (1964) and Rowe and Scotter (1973), *Pinus banksiana* is better adapted to recovery from fire than black spruce because of its totally serotinous cones which it produces at an earlier age than black spruce.

In other areas of eastern Canada on many sites, succession passes from a black spruce stage to a balsam fir (*Abies balsamea* (L.) Mill.) climax (Damman, 1964). Carleton and Maycock (1978), however, pointed out that on many sites *A. balsamea* does not appear to be invading the older black spruce stands.

The relationship between *Picea glauca* (Moench) Voss and *P. mariana* is also an interesting one. Drury (1956) and Viereck (1970) described a situation in Alaska where alluvial white spruce stands are replaced by black spruce on the older river terraces because of the formation and rise of the permafrost table associated with the buildup of the insulating organic layer. In a permafrost-free situation, Ritchie (1959) reported that black spruce occupied some of the older river terraces in northern Manitoba, but did not suggest a succession from white to black spruce. On the other hand, Lutz (1956) and Scotter (1964) suggested that on some mesic upland sites white spruce should be considered the climax species which, in the absence of fire, would replace black spruce. Viereck (1970) suggested that even in the upland, black spruce may replace white spruce on sites underlain by permafrost. It is, of course, quite possible that on warm, dry sites white spruce may replace black spruce while on wetter and colder sites the opposite may occur. The difficulty in solving this problem relates to the high fire frequency in the most northern areas and the lack of many examples of the later stages of succession.

11.8 SUCCESSION AND CLIMAX

Some authors have avoided the term 'succession' in describing the sequence of revegetation following fire in the black spruce type. Johnson and Rowe (1977) used the term 'vegetation composition change' to describe the sequence of vegetation changes following fires in black spruce-lichen stands in the Caribou Hills of the Northwest Territories. Black and Bliss (1978) described the 'recovery sequence' in the *Picea mariana-Vaccinium uliginosum* type in the lower Mackenzie Valley area. They found an orderly post-fire succession of mosses and lichens but not of vascular plants.

The use of the term 'succession' is questioned (Johnson and Rowe, 1977) because, following fire in the black spruce type, most of the species that were on the site reinvade directly and there is no replacement of large numbers of species. Differential growth rates only make it appear that there are several different stages before a mature stand is reached. Whether or not the classical concept of succession is appropriate, most of the studies of revegetation following fire in the North describe a series of stages or phases from a recently burned area to a mature community.

The question of whether or not one can describe a climax community type in black spruce following fire relates primarily to the high frequency of fire. In many areas that have been studied it was difficult or impossible to find an old stand that had not been burned. Fire is a recurring phenomenon, and the species and communities have evolved with this disturbance. In many northern areas, fire rotation ages may not be more than 50 to 100 years, but it may be 300 or 400 years before a stable situation is reached. In many of the older stands there is no obvious self-perpetuation mechanism. This has also led to the questioning of the climax concept.

Drury (1956) and Viereck (1970) both suggested that on the floodplains in Alaska cycles of black spruce and bog may result if fire is absent for a long time. In the lower Mackenzie River Valley, Strang (1973) suggested that if fire were eliminated from the black spruce stands, the climax vegetation would be a treeless moss-lichen association. He based this conclusion on study of several older black spruce lichen communities, where he found little evidence of sufficient regeneration to continue the existing density of black spruce. In the same area, however, Black and Bliss (1978) found that understorey species tended to become 'more tundra-like' with prolonged absence of fire but that the *Picea mariana* was maintaining itself through layering, and, in fact, density of the tree species tended to increase with age. In the open lichen woodland type, Maikawa and Kershaw (1976) also found an increase in tree density with age and suggested that in the absence of fire, the open lichen woodland type was eventually replaced by closed stands dominated by feathermosses. Thus it was suggested that the climax vegetation on both the dry and moist sites is the black spruce-feathermoss type. On other sites, however, it was concluded that open lichen woodlands would persist as a climax type (Johnson and Rowe, 1977; Ahti, 1959).

11.9 EFFECTS OF FIRE ON ECOSYSTEM COMPONENTS AND PROCESSES

We need to think of fire as an ecosystem process rather than as an effect on particular organisms or plant and animal communities. Wright and Heinselman (1973) suggested that there are a number of general principles relating to fire effects in the conifer ecosystems, and Vitousek and Reiners (1975) and Odum (1969) discussed the changes in ecosystem components and processes that occur during succession.

There have been some attempts to look at ecosystem processes relating to the black spruce ecosystem—in the studies of the 1968 Inuvik fire by Wein and others, the studies of the 1971 Wickersham fire by scientists at the Institute of Northern Forestry (Viereck and Dyrness, 1979), the detailed studies of the lichen-dominated ecosystem by Kershaw and Rouse (1976) and Kershaw *et al.* (1975), and by Rencz and Auclair (1978) in eastern Canada. The latter is also reported in this volume (Chapter 13).

Figure 11.2 shows some hypothesized changes in five critical variables in a black spruce ecosystem following fire. This figure was developed as part of a study of the black spruce ecosystem in Alaska (Zasada *et al.*, 1977). The five variables are: (1) overstorey biomass and living forest floor, (2) dead and decaying forest floor biomass, (3) available pool of nitrogen and phosphorus, (4) soil temperature, and (5) soil moisture. The time axis represents the stages of succession through the mature black spruce-feathermoss forest to a more open black spruce-*Sphagnum* type, a time span of about 300 years.

Just prior to a fire in the black spruce type, which would usually occur during the third or fourth stage in the figure, the overstorey and forest floor biomass is high but the available nutrient pool is relatively low, because most of the available nutrients are tied up in the surface organic layers and overstorey. Decomposition is slow, with about 2% of the organic matter in the forest decaying each year (Van Cleve *et al.*, 1979). Soil temperatures during the growing season are low, about 3°C to 6°C at 10 cm (Viereck and Dyrness, 1979), and permafrost is as close as 30 cm below the surface and entirely within the organic layer. Because of the impervious permafrost layer, the continued slow melt of ice in the frozen layer during summer, and the high water-holding capacity of the mosses and organic layer, the moisture content is high throughout the summer at depths of 10 cm and deeper. In the organic layer, the percentage moisture by weight remains well above 100%.

Following fire, there is a drastic change in all of these components. The overstorey biomass is greatly reduced by the fire, although standing dead may persist for up to 50 to 60 years. The largest change is in the forest floor, which is partially or completely removed by fire. Burning of this material immediately releases large quantities of available nutrients (Grier, 1975;

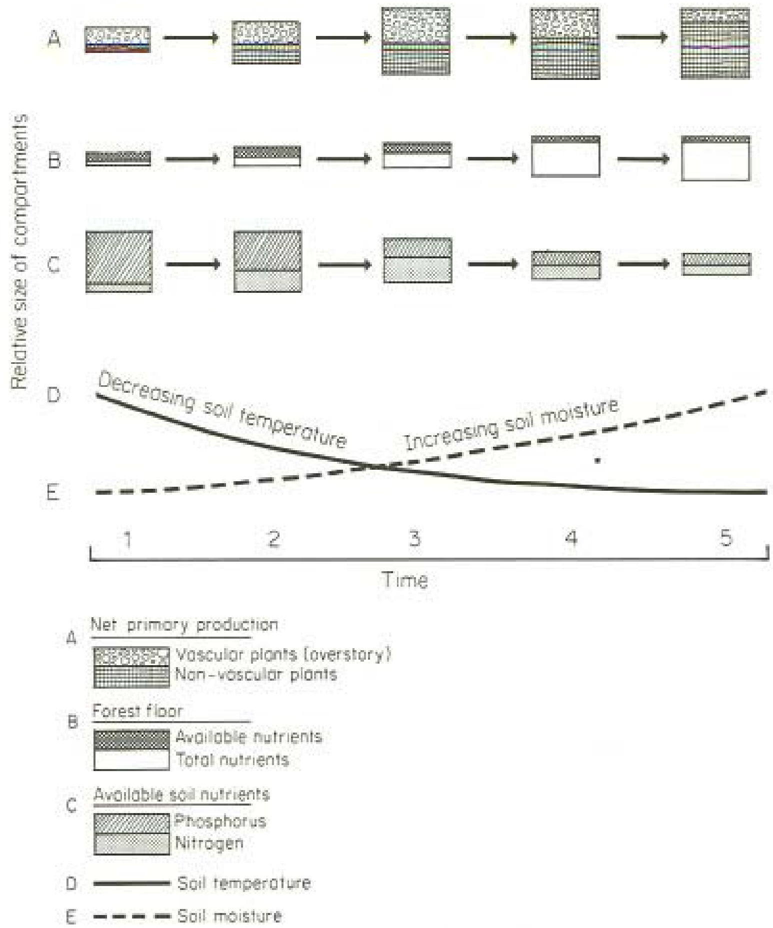

Figure 11.2 Hypothetical (and, in part, verified) successional changes in a burned black spruce stand being revegetated by more black spruce from early successional stages through mature 300-year-old stands (from Zasada *et al.*, 1977)

Stark, 1977). For example, the quantities of available phosphorus are greatly increased—as much as fifty times the mass of phosphorus was available following an experimental burn in a 70-year-old black spruce stand in Alaska (Viereck *et al.*, 1979). Nitrogen, on the other hand, may be volatilized by the fire, and quantities of available nitrogen may be reduced over what they were prior to the fire.

Soil temperatures increase and the permafrost layer recedes because of several factors, including removal of the overstorey, change in albedo, thinning of the organic layer, and death of the moss layer. Viereck and

Dyrness (1979) showed that summer soil temperatures were generally 5°C to 6°C warmer at depths from 10 to 50 cm the summer following the 1971 Wickersham fire than they were in an unburned 70-year-old black spruce control. Kershaw and Rouse (1976) have also shown a similar increase in soil temperature following fire in the black spruce-lichen woodland in central Canada. They found that the increase in surface soil temperatures could still be shown 25 years following the fire.

One of the most significant changes brought about by the increase in soil temperature is a thickening of the active layer. The depth of thaw may be two to three times greater following fire than it was before the burn. Seven years following a fire in the black spruce type in Alaska, the depth of thaw had increased from 40 cm in the unburned stand to 140 cm in the burned area (Viereck and Dyrness, 1979). Similar thaw has been shown for the Inuvik fire in Canada (Mackay, 1977). This increased thawing trend lasts for 10-15 years, followed by a gradual return to the pre-burn depth after about 50 years, when the insulating effect of the feathermoss mat has been completely reestablished (Viereck, 1973). The effect of fire on the underlying permafrost is reviewed in detail by Brown in this volume (Chapter 6).

For the first few years following fire the nutrient turnover is rapid and productivity high. Herbs and shrubs utilize the high availability of nutrients in the soil to grow rapidly (Ahlgren, 1960; Stark and Steele, 1977). The pioneering bryophytes, especially *Marchantia*, and the herbs, *Epilobium angustifolium* and *Calamagrostis canadensis*, take up the available nutrients immediately following the fire and recycle them quickly through their dead and decaying plant parts. Productivity is high because of the warmer soil and the increased nutrients. These species with high relative nutrient requirements and growth rates have an advantage in the early stages of succession but are less successful in the nutrient-poor later successional stages. Decomposition rates would also be relatively high during this period.

Few data are available comparing the productivity of burned and unburned black spruce stands in Alaska and northern Canada. Wolff and Zasada (1979) found that the amount of willow browse available to moose increased from 6.5 to 44.1 kg/ha, three to seven years following a fire, whereas in adjacent unburned stands, the available browse was less than 10 kg/ha. This study took into account only *Salix* spp. available to moose but gave an indication of the increased productivity of the shrub layer following fire. Total biomass accumulations for the first four years following the Wickersham fire in Alaska were approximately 160 gm/m^2, giving an average annual accumulation of 40 gm/m^2. Wein (1975) showed biomass accumulations of approximately 200 gm/m^2 five years following the Inuvik fire, for a mean annual accumulation of 40 gm/m^2. No comparable figures are available for a mature black spruce ecosystem, but, based on biomass measurements in a 130-year-old black spruce stand, annual foliage production was 24 gm/m^2, while the total annual aboveground tree production was 168 gm/m^2. In comparison the productivity of the moss layer was 125 gm/m^2, or about five times that of the tree foliage production (Van Cleve *et al.*, 1979). In young, recently burned stands, most of the productivity is in the herb and shrub species; in mature stands, most of the productivity is in the tree and moss layers.

As time passes following fire, the biomass and productivity of the mosses and lichens increase faster than those of the vascular plants. This is especially true once the feathermosses become widespread. On a unit area basis the productivity in the moss layer may be nearly as great as that of the tree layer.

Forest floor biomass increases greatly once the tree canopy is established and the feathermosses are abundant. Equilibrium may be reached between decomposition and accumulation in the forest floor on some sites, but on most of the cooler, moist sites, the forest floor continues to thicken and accumulate material. The criteria for a climax ecosystem—that net increment of biomass should equal zero—is not attained (Vitousek and Reiners, 1975). As the forest floor thickens, it accumulates nutrients that are no longer available to vegetation in the ecosystem. Mature black spruce stands are considered to be nutrient poor systems that conserve nutrients; one indication of this is that black spruce may retain its needles for up to 25 years (Van Cleve *et al.*, 1979).

In addition to acting as a nutrient sink, the thickening forest floor also acts as an increasingly efficient insulating layer. Soil temperatures decrease because of the moss layer and the increased shade from the tree and shrub canopy. Increases in soil moisture also occur as a result of the raising of the permafrost layer and the increased development of the water retaining organic layer. These conditions all tend to result in the typically less productive, nutrient poor, black spruce ecosystem with a thick organic layer closely underlain by permafrost. At this point, or earlier in the successional sequence, the forest usually burns, returning nutrients to the available form and increasing the productivity of the site. Thus fire in this type of ecosystem returns the site to a more productive condition and partially substitutes for the reduced decomposition rate.

In the long term absence of fire, it is hypothesized (Figure 11.2) that the forest floor would continue to thicken, further tying up nutrients. Moss and lichen productivity would continue to increase in comparison with the tree overstorey, which would become more open and less productive. Soil temperatures would continue to decrease and soil moisture would increase, creating conditions that encourage the development of the *Sphagnum* mosses over the feathermosses. This condition could eventually result in paludification of the site and the development of treeless bogs. Fire is thus an essential ecosystem process and maintains the permafrost dominated black spruce feathermoss ecosystem. The black spruce ecosystem supports the concept of Vitousek and Reiners (1975) that most forest ecosystems change in patches of various sizes controlled by intrinsic factors of the ecosystem or by extrinsic factors of the environment. In the case of black spruce, fire acts to recycle the vegetation before it reaches the steady state climax condition.

11.10 SUMMARY

The black spruce ecosystem is well adapted to the large and frequent fires that occur in northern Canada and Alaska. In some areas fire may be essential to maintain a certain level of productivity and to prevent the ecosystem from developing into bogs or treeless stands. Post fire revegetation is usually rapid and develops by vegetative reproduction from underground plant parts and from invasion by seeds and spores. Often most of the dominant vascular plant species of the entire revegetation sequence are present within a few years after the fire and resulting stages of revegetation develop primarily from different growth rates. Under some conditions, black spruce stands may be replaced by aspen, paper birch, or lodgepole pine, but the necessary conditions are not well documented. Although there are two main pathways of revegetation following fire, the feathermoss dominated sequence on moist sites and the lichen dominated sequence on dry sites, there is no one climax type that develops on all sites. Both lichen and moss sequences can result in a feathermoss type. Sequences that result in treeless bogs have been described for some of the colder sites, and on dry sites open lichen woodland can persist. Within its range, balsam fir can replace black spruce under some site conditions. The high incidence of fire, as frequent as 65 to 100 years, makes identification of the climax vegetation difficult.

As an ecosystem process in the black spruce feathermoss type, fire acts to remove the accumulated organic layer and make nutrients available. The warmer soils and increased available nutrients result in higher productivity levels for a number of decades following fire. Eventually, because of the slow decomposition rates, the organic layers again accumulate and productivity shifts from the overstorey to the forest floor. In some mature black spruce stands, the productivity of the moss layer may be twice that of the overstorey trees. When fire is absent for a long period on some cold sites, this process may result in the development of treeless stands dominated by *Sphagnum* and other mosses. On these sites, fire is essential to the rejuvenation of the site and the development and continuance of the black spruce ecosystem.

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