

A spruce-lichen woodland in northern Alaska : post-fire regeneration and community dynamics

by Janet S Christiansen

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CHAPTER 1: INTRODUCTION

Spruce-lichen woodlands are common on sandy glacial deposits in the boreal forest of North America. They are characterized by an open canopy of black spruce (*Picea mariana*) or white spruce (*Picea glauca*), a sparse shrub layer and a continuous carpet of "reindeer" lichens (*Cladina* or *Cladonia* species). Their distribution is controlled by temperature and substrate (Larsen, 1980). They occur in northern regions where low mean temperatures, short growing seasons and cold soils limit plant growth (Oechel and Lawrence, 1985). The droughty, nutrient-poor soils of these woodlands provide marginal sites for tree growth, resulting in open canopies of narrow-crowned trees that permit light-demanding lichens to dominate in the understory (Fraser, 1956). This is in contrast to other boreal forest types in which the slow-growing lichens are out-competed by shade-tolerant mosses (Kershaw, 1978).

Due to the continuous, flammable ground fuel provided by the lichen, these woodlands burn frequently (Auclair, 1983). Most are less than 150 years old and show evidence of previous fire. However, old stands (300+ years) without signs of fire are occasionally found (Zoltai, 1975; Payette, 1976). The status of these communities, as

edaphic climaxes or a long-term fire-dependent stage in succession toward closed spruce-moss forest, has been debated for many years (Auclair, 1983).

In Canada, spruce-lichen woodlands are extensive on deposits of the Laurentide glaciation. They occur in a wide belt from the Labrador Atlantic coast almost to the MacKenzie River delta (Hustich, 1957). Various aspects of their community dynamics have been described, such as the role of fire (Johnson and Rowe, 1977; Auclair, 1983), microclimatic changes after fire (Rouse, 1976), biomass (Rencz and Auclair, 1977), nutrient status (Moore, 1980), lichen succession (Maikawa and Kershaw, 1976; Johnson, 1981), and autecology of the major lichen species (Ahti, 1959; Kershaw, 1977).

Spruce-lichen woodlands are rare in Alaska compared to Canada. Because Alaska did not experience the continental glaciation, glacial deposits are confined to moraines of valley glaciers in mountainous areas. Also, the transition between boreal forest and tundra is narrow in Alaska, coinciding with the Brooks Range where the boreal forest abruptly meets alpine tundra. Therefore, the rarity of spruce-lichen woodlands is due to the combined effects of the lack of appropriate substrate and the abrupt transition from a boreal forest to tundra

climate. Alaskan woodlands have not been studied in detail (Viereck and Schandelmeier, 1980).

This study examined the community and age structure of a spruce-lichen woodland on a moraine at Walker Lake, on the south slopes of the Brooks Range, Alaska. The woodland had fairly dense stands of black spruce, more open stands of white spruce, and mixed stands of both species. Evidence of fire was abundant and no stand appeared to be over 100 years old, although older trees were scattered across the area. Seedlings and saplings were rare. These features raised questions about the fire history, the regeneration of the spruce after fire, and the future of these stands.

To address these questions, detailed community and age structure data were collected for seven stands in the woodland, representing two ages since fire. The specific objectives of the study were to:

- 1) Describe the vegetation of a spruce-lichen woodland;
- 2) Document the fire history; and
- 3) Document spruce regeneration after fire.

CHAPTER 2: LITERATURE REVIEW

2.1 DISTRIBUTION OF SPRUCE-LICHEN WOODLANDS

Spruce-lichen woodlands occur in the northern boreal forest and forest-tundra transition zone of North America. Spruce (*Picea* spp.) or pine (*Pinus* spp.)-lichen woodlands are reported from Scandinavia (Hustich, 1951; Ahti, Hamet-Ahti and Salas, 1968) and larch (*Larix* spp.) woodlands from the Soviet Union (Tikhomirov, 1970). Low temperature is the major factor limiting plant growth in these regions (Oechel and Lawrence, 1985).

Spruce-lichen woodlands are found on well-drained substrates, such as sandy glacial deposits, stabilized dunes, and old beach ridges (Hustich, 1951; Ahti, 1959; Kershaw, 1978). Atmospheric moisture is not a primary determinant of their distribution, as they occur in the continental climate of central Canada as well as the maritime region of eastern Canada (Rencz and Auclair, 1977). Climatic statistics reported for spruce-lichen woodlands have similar mean annual temperatures (about -5° to -1°C) but yearly precipitation varies greatly, from 30 cm to 110 cm (Maikawa and Kershaw, 1976; Foster, 1985).

Spruce-lichen woodland soils are typically Entisols or Spodosols. The major soil order is Spodosols, characterized by a bleached E horizon and a strong reddish brown B horizon (Rencz and Auclair, 1977). The soils are characteristically acidic and nutrient-poor (Moore, 1980). More fertile soils on well-drained sites are dominated by spruce-feathermoss forest (Rencz and Auclair, 1977).

Spruce-lichen woodlands are the most important forest type in the boreal forest-tundra transition of Canada (Rouse, 1976), where they comprise the winter range of the barren-ground caribou (Scotter, 1964). They also occur in the main boreal forest. Where woodlands occur within the ranges of other tree species, balsam fir (*Abies balsamea*), larch (*Larix laricina*), or jack pine (*Pinus banksiana*) may be mixed with the spruce. Jack pine-lichen woodlands occur on the poorest sites (Johnson and Rowe, 1977).

Spruce-lichen woodlands are mentioned as an uncommon community type in Alaska (Viereck and Schandelmeyer, 1980; Young and Racine, 1977). One large area is on stabilized sand dunes in Kobuk Valley National Park, 180 km west of Walker Lake (Young and Racine, 1977). Small patches of woodland occur on moraines in the river valleys draining the south slopes of the Brooks Range.

The woodland at Walker Lake may be the largest in the western Brooks Range.

2.2 VASCULAR PLANT COMMUNITY

Due to unfavorable site conditions, the productivity and biomass of spruce-lichen woodlands is much lower than that of other boreal forest types (Hustich, 1951; Fraser, 1956; Rencz and Auclair, 1977). For example, the total live biomass of 15 woodland stands in northern Quebec averaged 46,291 kg/ha-1, compared to 125,000 kg/ha-1 for spruce-moss woodlands on moist soils at similar latitudes and 150,000-300,000 kg/ha-1 for boreal conifer forests (Rencz and Auclair, 1977). The percent of biomass in the roots was high (34% for black spruce, 39% for shrubs) and 40% of the total community biomass was in the understory vegetation.

Black spruce is the dominant tree species in most spruce-lichen woodlands in Canada. White spruce may codominate on more productive sites, but rarely dominates (Rencz and Auclair, 1977). White spruce-lichen woodlands are reported more often on substrates other than glacial deposits, such as raised beaches (Savile, 1963; Hustich, 1957) or dunes (Young and Racine, 1977), and in regions with maritime climate influence (Savile, 1963; Hustich, 1957; Ahti, 1959).

Black spruce has the lowest nutrient requirements and lowest maximum growth rates of all the boreal forest

trees (Chapin, 1986). It is not fire resistant but is well adapted to fire, with terminally placed clumps of semi-serotinous cones. It can seed in rapidly after fire and maintains itself vegetatively by layering of lower branches later in succession (Viereck and Schandelmeier, 1980).

White spruce requires warmer, more well-drained, richer sites than black spruce. Its maximum potential growth rate is greater than that of black spruce but it is more limited by nutrients (Chapin, 1986). White spruce is not adapted to fire and the sites where it usually is found do not burn as frequently as black spruce sites (Viereck and Schandelmeier, 1980).

Aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*), occasional associates with spruce in lichen woodlands, have higher nutrient requirements than spruce (Chapin, 1986). They are adapted to regenerate after fire and can reestablish rapidly by profuse sprouting or seed germination (Zasada, 1971). Aspen stems deteriorate after 80 to 100 years, but paper birch can persist into later successional stages (Viereck and Little, 1972).

The sparse shrub layer in spruce-lichen woodlands is made up of the same common circumboreal species as other boreal forest types (e.g. shrub birch (*Betula glandulosa*), Labrador tea (*Ledum spp.*), and ericaceous shrubs, mainly *Vaccinium spp.*). Most species can

reproduce by sprouting after fires that do not consume the organic mat (Viereck and Schandelmeier, 1980).

Rowe (1983) classified common boreal forest species according to their functional adaptations to fire. The above-mentioned shrub species and aspen are classified as "endurers", which regenerate vegetatively. Paper birch and aspen are "invaders", which seed in rapidly after fire. Black spruce is an "evader", adapted to fire by storage of seed in the cones, while white spruce is an "avoider", with little adaptation to fire.

2.3 LICHEN

Lichens are physiologically adapted to tolerate stressful temperature or moisture regimes that are unfavorable for other plants, but they grow slowly and are poor competitors on more favorable sites (Larsen, 1980). For example, the "reindeer lichen" *Cladina stellaris* can survive high temperatures in an air-dried state and can have positive net photosynthesis at thallus saturation levels as low as 4% (Carstairs and Oechel, 1978), but often grows only a few mm per year (Kershaw, 1985).

Site conditions of spruce-lichen woodlands hinder tree and shrub growth and thus allow lichens to prevail (Fraser, 1956; Kershaw, 1978). The predominant lichen species, mainly in the genera *Cladonia* and *Cladina*, grow well in partial to open sunlight (Thomson, 1967). A

better-developed tree canopy allows shade-tolerant mosses to out-compete lichens (Kershaw, 1978).

The succession of lichen species has been documented by several authors (Scotter, 1964; Kershaw, 1977; Maikawa and Kershaw, 1976; Black and Bliss, 1978). In the first stage, lasting up to 20 years, pioneer mosses, such as *Polytrichum juniperinum* and *Ceratodon purpureus*, and crustose lichens, mainly *Trapeliopsis* (formerly *Lecidea*) species, colonize the bare ground and charred organic matter. From 10 to 60 years after fire, the horned and cupped *Cladonia* species dominate. After about 60 years the dominance gradually shifts to the "reindeer lichens", the *Cladinae*. *Cladina mitis* is more xerophytic than the other *Cladinae* and becomes abundant earlier, along with the shrubby *Cladonia uncialis* and the horned and cupped *Cladonias* (Ahti, 1959). *Cladina rangiferina* and *C. arbuscula* are mesophytic and prosper in shaded locations. *Cladina stellaris* is more of a generalist in habitat selection and, given the partial shade characteristic of a mature woodland, is capable of eventually out-competing the other species. Studies of mature spruce-lichen woodlands report a ground cover of nearly pure *Cladina stellaris* (Kershaw and Rouse, 1971; Rencz and Auclair, 1977), with low cover of other lichens.

The successional sequence results from the interaction of changing microclimate with the autecology

of the lichen species, rather than the facilitation of one species by previous ones (Johnson, 1981). All the lichen species invade soon after disturbance, but the later-successional species grow large enough to become apparent only after several decades (Johnson, 1981).

Authors disagree on the role of the lichen mat in the dynamics of spruce-lichen woodlands (Kershaw and Rouse, 1971). Fraser (1956) stated that interactions between lichen and trees may be in balance, resulting in self-perpetuating communities. While the trees control lichen growth by shading, the lichens may retard closure of the tree canopy by preventing successful establishment of seedlings and slowing the growth of adult trees. Lichens may provide a poor microenvironment for seedling germination and survival (Savile 1963; Smith 1952; Fraser 1956; Cowles 1982). They may slow growth of trees by insulating the soil and lowering the soil temperature (Kershaw, 1977), slowing nutrient cycling (Cowles, 1982), and by adverse chemical effects (Brown and Mikola, 1974). On the other hand, a mature lichen mat is an effective mulch and has been shown to maintain soil moisture levels at or near field capacity throughout dry periods (Rouse and Kershaw, 1971; Carroll and Bliss, 1982). The lichen mat may actually conserve sufficient soil moisture to stimulate tree growth (Carroll and Bliss, 1982), perhaps

even to allow trees in areas that would otherwise be too severe for their survival (Kershaw, 1978).

2.4 FIRE

The vegetation of spruce-lichen woodlands is highly flammable and the woodlands may burn more readily than other boreal forest types (Fraser, 1956). The lichen mat provides a continuous fuel along which fire can spread. The flammability of lichens is due to their high surface-volume ratio and rapid desiccation (Auclair, 1983). Their characteristics as a fuel are more similar to litter than to live plant material (Sylvester, 1975). On the Quebec-Labrador peninsula, the limits of recent burns corresponds to the margins of the spruce-lichen woodlands, with fires nearly always stopping when they encounter moss-floored forests or muskeg (Fraser, 1956). Similarly, I observed that a 700-hectare fire in a spruce-lichen woodland 13 km south of Walker Lake in 1985 burned to the edges of the woodland but did not enter the adjacent denser spruce-moss forest.

The natural fire regime for most spruce-lichen woodlands is one of fairly frequent fires of moderate severity, which kill all or most of the trees but do not consume most of the surface organic layer (Scotter, 1964). Almost all spruce-lichen woodlands have signs of fire. The fire frequency usually does not allow a stand to survive for more than one generation of trees

(Johnson, 1981). The length of fire cycles estimated for spruce-lichen woodlands with a continental climate range from 70 to 100 years (Maikawa and Kershaw, 1976; Johnson, 1979). In contrast, fire cycles may be about 500 years in maritime eastern Canada (Foster, 1985).

2.5 SUCCESSION

The successional status of spruce-lichen woodland has been discussed in the literature. It has been viewed as an edaphic climax community type (Fraser, 1956; Larsen, 1980; Viereck, 1983), or as successional to closed spruce-moss forest (Kershaw & Rouse, 1976; Maikawa & Kershaw, 1976) or to lichen tundra (Strang, 1973). Auclair (1983) formulated a model integrating the opposing trends of increasing tree canopy limiting lichens versus increasing lichen mat limiting trees. He stated that site factors control the balance between the two, with trees favored on better sites and lichens favored on sites that are more marginal for trees. He also stated that a wide range of environmental conditions may exist in which open lichen woodland persists as a stable vegetation type. The occurrence of some old (300+ years), open lichen woodlands with no signs of disturbance indicates that the maintenance of spruce-lichen woodlands is not necessarily dependent on fire (Zoltai, 1975; Payette, 1976).

The rarity of successional sequences of species replacement after disturbance has been noted from throughout the boreal forest (Larsen, 1980; Wein and El Bayoumi, 1982). While the moss and lichen flora appears to have an orderly sequence, the species composition of higher plants generally remains the same throughout community development (Black and Bliss, 1978; Viereck and Schandelmeier, 1980). Fire cycles are short in most vegetation types and theories of "climax vegetation" may not apply (Rowe, 1961). Long-term stability in this system comes from cycles of disturbance followed by the reestablishment of species present before disturbance (Cogbill, 1985).

2.6 TREE REGENERATION AFTER FIRE

Understanding of forest development and its relationship to disturbance has improved in recent years. Age distributions are useful for documenting tree population dynamics (Oliver, in prep.). However, population dynamics in the northern boreal forest are still poorly understood (Payette and Gagnon, 1979). Few age distributions have been determined for boreal forest trees. Age distributions, including the ages of all trees in a stand, have been described for spruce-lichen woodlands only in Quebec (Payette, 1976; Payette and Gagnon, 1979; Sirois and Payette, in prep.) and Labrador (Foster, 1985).

CHAPTER 3: STUDY AREA

3.1 LOCATION

The study area is a spruce-lichen woodland at Walker Lake, on the south slopes of the central Brooks Range (Figure 1). It is located at 67° 9' N and 154° 22' E, at an elevation of 235 meters, near the latitudinal and altitudinal treeline in northern Alaska. Walker Lake is in Gates of the Arctic National Park and is a designated National Natural Landmark.

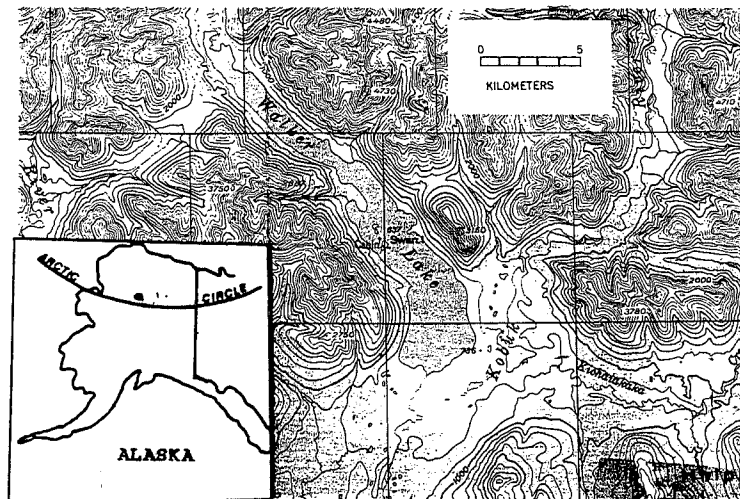


Figure 1. Location of study area. The woodland is the area shown in white along the south and southeast shores of Walker Lake.

3.2 CLIMATE

The area is in the Interior Basin Climatic Division of Alaska and has a continental climate. Winters are long, cold and dry, while the brief summers are relatively warm and moist. The mean annual temperature of Bettles, the nearest meteorological station, is -5.9°C . Mean monthly temperatures range from -25.1°C in January to 14.4°C in July. Annual precipitation averages 35.5 cm, but is highly variable (U.S. Environmental Data Service, 1977). Periodic droughts are common (Viereck, 1983). Precipitation is highest in August, 6.5 cm, and lowest in April, 0.8 cm. Annual snowfall ranges between 150 and 230 cm (U.S. Environmental Data Service, 1977). High temperatures in mid-summer, sometimes above 30°C at Walker Lake (Pat Anderson, per. comm.), are often accompanied by convective lightning storms. The continental climate of Walker Lake is probably modified by its proximity to the mountain zone and perhaps by occasional maritime influences from the west.

3.3 GEOLOGY AND SOILS

The Walker Lake area is underlain by paleozoic quartz-mica schists intermixed with older calcareous rock (Brosge and Pessel, 1977). It is mantled by drift from the Walker Lake Glaciation (Late Wisconsin), the last major valley glaciation in the Brooks Range (Hamilton,

1982), which retreated about 13,000 years ago, leaving distinctive terminal moraines within the valleys or at their mouths, often damming lakes (Hamilton, 1982).

The study area is on a terminal moraine damming the south end of Walker Lake, which is the type locality for the Walker Lake Glaciation. The moraine, about 10 km long and two to four km wide, rises 30 to 70 m above the lake level. It has an inner and an outer loop, formed by two pulses of the Walker Lake glaciation (Fernald, 1964). The terrain is characterized by broad rolling surfaces, arcuate ridges, and swales. The outlet river from the lake bisects the southern end of the moraine.

The glacial drift is a mixture of locally-derived metamorphics with granitics from the north (Ugolini, Reanier, Rau and Hedges, 1981). The soils, derived from sand and coarse rubble, are poorly-developed and underlain by permafrost. Soil profiles show thin organic layers and discontinuous leached horizons. Podzolization is the primary soil-forming process (Ugolini et al., 1981).

3.4 REGIONAL VEGETATION

The vegetation of the Walker Lake area is a complex mosaic of types. Plant distributions are controlled by topography through its effects on insolation, soil temperature, drainage, and depth of the active layer above permafrost (Viereck, 1973). Personal observations

indicate that black spruce-sphagnum and black spruce-feathermoss forests occur over vast expanses of poorly-drained, low-lying land and on northern exposures. White spruce-feathermoss forests occur on well-drained, warmer sites, such as south-facing slopes and along rivers. Balsam poplar (*Populus balsamifera*) grows along rivers and aspen and paper birch are found on south-facing sites in the uplands or as seral species in spruce stands. Sedge tussock tundra occurs in some lowland areas. Small isolated patches of spruce-lichen woodlands are found on glacial moraines in the valleys and on some summits in the foothills. Beyond treeline are alpine tundra and fellfields.

White spruce is the dominant tree species at altitudinal treeline, at 800 m elevation above Walker Lake, and forests of white spruce continue about 20 km further north in the valley. Walker Lake is located at or near the geographical limits of white spruce, black spruce, aspen and paper birch, the tree species present in the study area.

Wildfire, the major disturbance in the forested area, increases the complexity of vegetation distributions. Personal observations indicate that most black spruce sites have signs of fires. Large areas of the black spruce woodlands downstream from Walker Lake have burned in the past century. In contrast, little sign of fire is

found in the white spruce forests above the lake and in stands along the rivers.

3.5 STUDY AREA VEGETATION

The woodland at Walker Lake is characterized by open, slow-growing black and white spruce with a sparse shrub layer and almost continuous ground cover of fruticose lichens (Figure 2). The open appearance of the woodland contrasts strikingly with the surrounding denser forest vegetation.

The moraine is bounded by Walker Lake and rivers on most of its periphery. White spruce grows on the river alluvium and an old white spruce and paper birch forest grows above the lake shore west of the moraine. The valley downslope from the moraine is black spruce-moss forest.

The woodlands on the outer loop of the moraine are of relatively dense black spruce, with scattered white spruce and aspen and abundant aspen suckers in some areas. Some dominant canopy trees on the west side of the river are large, decadent individuals, while on the east side the woodlands are uniformly smaller black spruce.

The inner loop of the moraine has more open woodlands that are a mixture of black and white spruce, with predominantly white spruce in some areas. The density of the tree canopy varies greatly. Some large open areas are

Photo Page

dominated by shrub birch with few or no trees. Paper birch are found among the spruce on the west side, and the east side has groves of small aspen on southern exposures.

The vegetation is denser in the swales than on the high rolling surfaces. The many narrow swales have dense lichen woodland vegetation, with feathermosses intermixed with the lichens on the steeper north-facing slopes. Sink-hole depressions on the moraine surface are filled by herbaceous meadows, hummocks of moss (*Polytrichum* sp.) or lichen (*Stereocaulon* spp.), or lakes with aspen on the margins. The north-east section of the moraine is broken into smaller high areas of lichen woodlands surrounded by low, moist black spruce-moss woodlands and boggy areas.

Charred logs, charcoal, and scarred trees are evidence of past fires in the woodlands. However, logs and snags are widely scattered. They are more common in the moist depressions than on the high flat areas. No evidence of human disturbance was found in the woodlands, except for intermittent paths along the river and campsites on the lake shore. Four cabins are located further north on the lake. The woodlands are not a major wintering area for caribou nor are they on a main migration route, so disturbance by grazing may be minimal.

CHAPTER 4: METHODS

4.1 FIELD METHODS4.1.1 Fire History

The fire history of the woodlands was assessed by walking all parts of the moraine and noting evidence of fire, such as firescars and charred snags, logs, and stumps. Thirteen fire-scarred trees were cut for field counts of annual rings (Figure 3). These counts identified fire dates, which were used to select plots to examine patterns of post-fire tree establishment. Two fire dates were found and the dates of the fire scars agreed to the exact year. Disks from trees were taken back to the laboratory to verify dates. Cores were taken of the largest trees in stands throughout the woodland to support the stand-initiation dates indicated by the firescars.

4.1.2 Intensive Vegetation Plots

Plots were selected for intensive vegetation and age structure sampling according to three criteria: 1) similar topographical positions, 2) a range of stand densities, and 3) stands in each fire age class as defined during field reconnaissance. Seven plots were chosen on high, relatively flat surfaces of the moraine (Figure 3).

All were representative of surrounding vegetation. None were located in the extremely variable open areas on the inner loop of the moraine or in the swales.

All plots are 20 m X 30 m, except for Plot B1, which is smaller (15 m X 30 m) due to greater tree density. In each plot all spruce with basal diameters greater than 4 cm were cored with an increment borer. Cores were taken at a downward angle at the base of the stem to hit the pith at ground level. Trees less than 4 cm diameter were sectioned at the base. For each tree, diameter-at-breast-height, height, and visible condition (e.g. form, dead branches, fire-scars) were noted. Black spruce produced vegetatively by layering of lower branches were distinguished in the counts from non-clonal stems. The only exception to this procedure was in Plot W3, where two black spruce had a total of 49 densely-crowded layers. Thirty-two of these were cored and the ages of the remaining layers were estimated by a least squares regression of layer age on size.

The entire area of each plot was visually searched for seedlings. Two subplots (1 m X 30 m) through the center of each plot were more intensively searched, but no further seedlings were found in any plot.

Aspen and paper birch that were over 1 m in height and were upright were also cored. Aspen suckers were

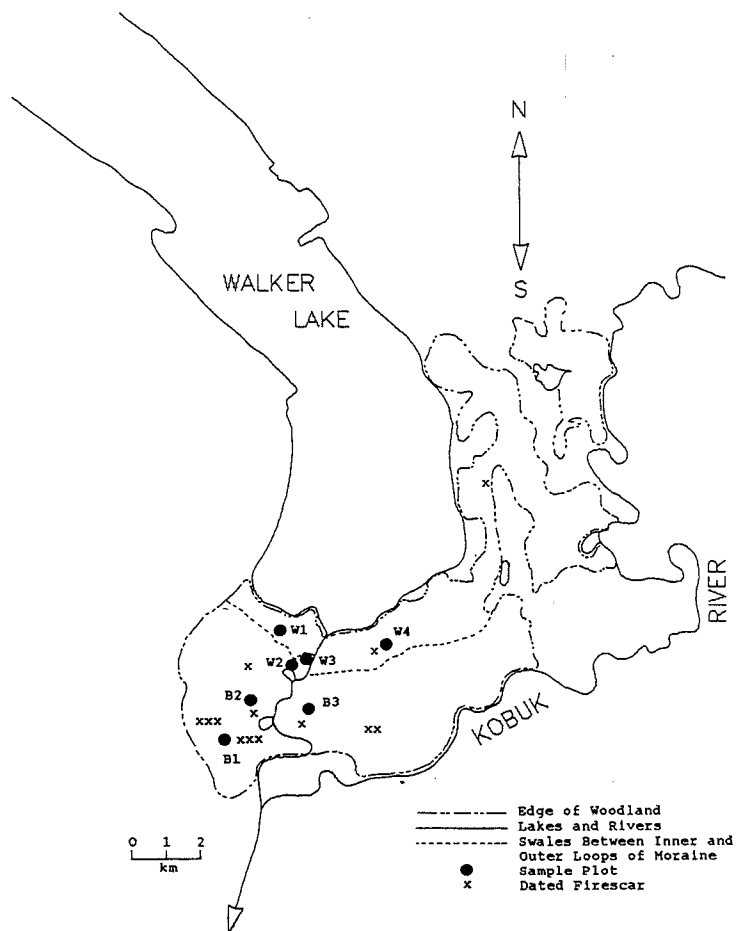


Figure 3. Map of study area.

counted. In one plot with many aspen suckers, those less than 0.3 m in height were estimated by counting in a representative one quarter of the plot.

Signs of fire and the sizes of all snags, logs, and stumps were recorded. For further information on the ages of the canopy dominants, several large trees near each plot were cored.

Percent cover of all understory vascular plants and cryptogams was recorded for 30 0.1 m² microplots laid out every 2 m along two parallel transects running lengthwise across each plot. Species present in the plot but not encountered in the microplots were also noted. Clumps of shrub birch and willow were counted. Samples of all lichens and mosses were collected. In 20 microplots, the depths of the living lichen mat and the organic layer (from the base of the live lichen to mineral soil) were also measured.

4.1.3 Soils

A 0.5 m-deep soil pit was dug in each plot, after five small pits were dug to identify a representative location within the plot. The depth and thickness of visible soil horizons, estimated percent of soil fractions larger than 2 mm, and presence of roots were recorded. A sample from each soil horizon was collected.

4.2 LABORATORY METHODS

4.2.1 Tree Ages

Cores and cross-sections were mounted and sanded and annual rings counted under a binocular dissecting microscope. The number of rings to the pith was considered the age of the tree.

There are two sources of error in the age determinations: annual rings may be missing due to poor growth years (Fritts, 1976), or the tree may not be cored to the pith at the base. Cross-dating was not feasible, since there was little year-to-year variation in ring-width. Thus, no adjustments in age estimations were made for the first possibility. The second source of error included trees that were cored 10 to 40 cm above the base because of basal heart rot and cores that missed the pith. In these cases the age of the tree was estimated by adding an adjustment factor to the innermost ring.

The following methods were used to choose the adjustment factors. For cores taken above the base, adjustment factors were calculated by sectioning three trees of each species at 10 cm intervals along the stem to determine rates of height growth. Because only dominant trees required coring above the base, open-grown saplings were sectioned, as they were most likely to have early growth rates similar to the stand dominants.

Adjustment factors were determined by hand-fitting a line to the age versus height plots and interpolating values for intermediate core heights. Adjustment factors are listed in Appendix A.

When a core missed the pith, the adjustment factor depended on the number of millimeters missing, the basal radius, and the species. The distance missed from the pith was estimated using a clear plastic template of concentric rings. Adjustment factors were derived by counting the number of annual rings within 2, 5, and 10 mm of the centers of 57 intact cores and plotting the data for each of these increment categories against the basal radius of the tree, as estimated by the length of the core (Appendix A). Radius proved to be better related to number of rings than height. Widths of other rings on the same core were not used because the innermost rings on intact cores were usually narrower than later rings.

For both black and white spruce, the mean number of rings in each increment category was greater for trees with radii less than 6 cm than for those greater than 6 cm. Therefore, two sets of adjustment factors were derived for each species (Appendix A). The trees with radii over 6 cm probably had greater early radial growth because they were established within 35 years after fire and therefore presumably had more favorable conditions for growth than those available to the smaller trees,

which either established later or established early but were suppressed.

Trees were grouped in five-year age classes for age distributions. In all, age adjustments were made for 23% of the trees sampled. For each tree this represents an average of 18% of its estimated age. The average number of years added is 14. The error of the final age estimates cannot be determined. The adjustment factors for missed piths were derived from the mean numbers of rings in given increment categories, which had standard deviations ranging from 2 to 9 years. Even if the number of years added was in error by a value equal to one standard deviation, the resulting error would not be great enough to shift the estimated age of a tree by more than one age class in most cases (Appendix A). Thus the possible errors in age estimations should not greatly affect the interpretation of the age distributions.

4.2.2 Tree Age-size Relationships

Age, height, and diameter-at-breast-height frequency distributions were constructed for each plot. The age distributions reflect both recruitment and mortality. Recruitment is assumed to be most important in these plots, because of the rarity of logs and snags, despite the cold, dry environment that causes slow decomposition (Larsen, 1980). Most logs and snags are less than 0.3 m long. Mortality is apparently high for young saplings,

but low after they reach this height. The risk of mortality probably decreases when a sapling develops an extensive root system. If a tree is not considered to be successfully established until it reaches 0.3 m in height, the age distributions can generally be interpreted as patterns of establishment.

Size-age relationships were analyzed using least squares regression. Trees with estimated ages were excluded from these regressions. However, R^2 s using both exact and estimated ages were within .05 of those using only exact ages in all cases. Survivors were also excluded, as they were often outliers (Appendix F), with excessive influence on the regressions.

Average height growth rates were calculated by dividing tree height by age. Diameter growth rates were not calculated, since diameter data were not collected on the 33% of all trees that were shorter than breast-height.

4.2.3 Understory

Microplot data were used to compute the frequency and average percent cover for understory species in each plot. Vascular plant nomenclature follows Viereck and Little (1972) for trees and shrubs and Hulthen (1968) for herbs. Lichens were identified using morphological and chemical characters according to Thomson (1984). Lichen

identifications were verified by John W. Thomson of the University of Wisconsin.

Lichens growing on trees or rocks and some crustose soil lichens were not identified. Only mosses with greater than one percent cover in any one plot were identified, according to Crum et al. (1973).

Scientific names of all plants, including their authorities, are listed in Appendix D.

4.2.4 Soils

Soil type was determined by David Marrett, based on field criteria such as visible soil horizons, and results of a previous study of soils on the lateral moraine east of Walker Lake (Ugolini et al., 1981; Stoner, Ugolini, and Marrett, 1983). Particle size distributions were determined for soil samples by the hydrometer method and by sieving. These analyses were conducted on samples from the B horizon. Soil pH of all horizons was determined with a PHM 62 Standard pH Meter.

CHAPTER 5: RESULTS

5.1 FIRE HISTORY

The dates of all fire scars found west of the outlet river were 1891, and all those east of the river were 1913 (Figure 3). These dates are supported by the ages of post-fire trees cored in and near the plots, and in other stands throughout the area. The absence of double fire scars indicates that neither fire burned both sides of the moraine.

Reconnaissance of the woodlands revealed many fire-scarred and unscarred survivors within stands of younger trees. The number of survivors varied greatly in different areas of the woodlands west of the river (Table 1). They were more common on the outer loop of the moraine than on the inner loop. In some stands, represented by Plots B2 and W3, many pre-fire trees survived and are currently the dominant trees in the stands. Survivors were less common on the east than on the west side of the river.

The oldest survivor trees cored were established in the 1840s, with many established in the 1850s. The small basal diameters of fire-scarred trees at the time of fire (2.4 to 5.5 cm in 1891, 3.5 to 7 cm in 1913), also

suggest that the dominant trees in the woodlands in those years were smaller than the current dominants. The stumps and logs were also small (Table 1). The evidence that the trees were young and small when the fires occurred suggests that the woodlands probably burned previously around the 1840s.

5.2 SOILS

Soils on the moraine were mainly Inceptisols (Pergelic Cryochrepts), with the possible inclusion of some Spodosols (Pergelic Cryorthods)(Marrett, per. comm.). Soils were very acidic, with pH ranging from 3.1 to 5.1 (Appendix C). The organic horizon was the most acidic, with pH of 3.1 to 3.8, while only the C horizon reached pH above 4.9. The pH did not vary significantly between plots. Organic horizons were sharply differentiated from the underlying soil and were usually thin (1 to 2.4 cm; Table 2). All of the plots had intermittent patches of leached soil (E horizons) below the organic layer, indicating discontinuous podzolization.

The soils in six of the plots were sandy (49 to 88% sand-size soil fractions). Classified by particle size distribution, they ranged from sand to loam (Table 2). Most were sandy loam to loamy sand, with less than 10% particles over 2 mm. The sandiest plot (Plot W2) was on a

Table 1. Plot Characteristics.

Plot #	B1	B2	B3	W1	W2	W3	W4
Trees in Plot	163	108	75	64	71	144	75
% PIMA ¹	87	100	100	15	34	47	37
% PIGL ²	13	0	0	85	66	53	63
PIMA layers	2	7	0	0	1	49	1
Fire date	1891	1891	1913	1891	1891	1891	1913
Survivors	2	14	0	0	4	15	3
Yrs after fire to est. 75% of trees	30	50	35	80	60	50	25
Yrs since last seedling est.	15	0	30	0	0	20	25
Average height growth/yr (cm):							
PIMA	3.0	2.1	4.8	1.7	2.6	4.3	5.1
PIGL	1.9	n/a	n/a	3.5	2.7	2.2	2.2
% trees <1m tall	30	45	8	62	49	23	36
Logs & stumps:							
Number	2	2	10	0	4	1	6
Basal diam. range (cm)	3-10	11-15	3-13	n/a	8-17	3	2-12
Spruce snags:							
<.5 m tall	3	1	0	0	4	3	8
>.5 m tall	2	0	0	1	0	0	0
Aspen snags (>1 m tall)	3	6	1	0	0	0	0
Regression R2:							
PIMA log ht/age	.45	.33	.63	n/a	.71	.32	.91
PIGL log ht/age	.61	n/a	n/a	.91	.78	.40	.54

¹ PIMA=Black spruce

² PIGL=White spruce

Table 2. Plot characteristics in relation to soil texture. Plots burned in 1891 are listed in order of increasing sandiness of soil.

Plot #	W3	B2	B1	W1	W2	B3	W4
Fire Date	1891	1891	1891	1891	1891	1913	1913
Soil % Sand	25	49	65	85	88	69	59
Soil % Silt	49	36	1	7	7	11	32
Soil % Clay	26	15	1	8	5	20	9
Soil Texture ²	Loam	Loam	S.L.	L.S.	Sand	S.L.	S.L.
Tree Basal Area (m ² /ha)	4.8	4.5	3.9	3.0	4.4	2.4	2.5
Tree Stems/ha	2400	1800	3621	1066	1183	1250	1250
# Survivors	15	14	2	0	4	0	3
Dominant Tree Species ³	PIGL	PIMA	PIMA	PIGL	PIGL	PIMA	PIMA
Lichen Depth	7.1	6.8	5.9	2.8	5.0	2.8	1.7
Organic Layer Depth	6.4	2.2	2.4	2.0	1.7	1.1	1.7
% Cover Fruticose Lichens	84	84	90	76	90	69	59
% Cover Late Succession Lichens ⁴	67	43	44	24	53	26	18
% Shrub Cover	71	49	38	28	36	44	24

¹ Silt and clay were not separated for Plot B1. They totaled 35%.

² S.L.=sandy loam. L.S.= loamy sand.

³ PIGL=White spruce. PIMA=Black spruce.

⁴ *Cladina stellaris* and *C. rangiferina*.

terrace above an oxbow of the river and had 45 cm of sand overlying a base with 25% rounded cobbles, indicating that the area had been reworked by the river.

The soil of Plot W3 was distinct from other plots. It was loam with 50% rounded cobbles and had a relatively thick organic layer (6.4 cm). This plot was located near the top of the river bank and was evidently deposited by the river.

5.3 VEGETATION

5.3.1 Tree Canopy

All plots had open canopies of narrow-crowned trees (Figure 4). Basal areas ranged from 2.5 to 4.8 m²/ha and stems/ha ranged from 1066 to 3621 (Table 1). Each plot had 5 to 15 widely-spaced trees over 5 m in height surrounded by many smaller trees (Appendix E). One third of the trees were less than 1 m in height. Both height and diameter-at-breast-height distributions are strongly skewed towards small sizes (Appendix E).

Logs and stumps were rare (0 to 10 per plot; Table 1). They ranged from 2 to 17 cm basal diameter, and were very rotten and sometimes charred. The only signs of recent mortality were 0 to 8 small (usually less than 0.3 m tall) spruce snags in each plot (Table 1). No snags or sound logs were greater than 1.5 m in length.

Three plots (B1, B2, and B3) were dominated by black spruce. They had relatively high tree densities and were

Photo Page

located on sandy loam soil on the outer loop of the moraine (Table 1, Figure 3). Plots B1 and B2 were burned in 1891, and Plot B3, directly across the river, was burned in 1913.

Aspen was important only in the plots dominated by black spruce (Table 1). Plots B1 and B2 had a few aspen over 1 m tall and about 50 small shoots from root suckers each. Plot B3 had 21 aspen over 1 m and a profusion of root suckers (about 800).

Four plots, W1-W4, had a majority of white spruce. They were generally less dense than the black spruce plots, and were located on the inner loop of the moraine or on river deposits (Table 1, Figure 3). Plots W1, W2, and W3 burned in 1891 and Plot W4 burned in 1913. The characteristics of these plots varied more than those of the black spruce plots. Important differences are summarized below.

Plot W1 was on loamy sand on the inner loop of the moraine and Plot W2 was on river-deposited sand. These were the least-dense plots and more than half of the trees were less than 1 meter in height (Appendix E). White spruce was dominant in these plots.

Plot W3 was on silt loam and cobbles. The overstory was made up of both white and black spruce, with two paper birch trees. 81% of the individual trees were white spruce but two black spruce were layering abundantly and,

including layers, black spruce made up 50% of the stems in the plot (Table 1). The understory vegetation was lush, with high shrub cover and a thick layer of lichen and organic matter, averaging 13.5 cm (Table 2).

Plot W4 was located on the inner moraine on sandy loam soil. Although it was 64% white spruce, the largest post-fire trees were black spruce. All post-fire white spruce were less than 3 m in height (Appendix E).

5.3.2 Understory

5.3.2.1 Vascular Plants

Shrub cover in the plots ranged from 26% to 71% and was generally greatest in the plots with the highest tree densities (Table 2). The shrub layer was mainly less than .3 m high, with a sparse, open canopy. The most common shrub, the low evergreen Labrador tea (*Ledum decumbens*), had 6% to 37% cover, with greater cover in the denser stands. Clumps of shrub birch were up to 1.5 m high and widely-spaced. The cover of shrub birch, as well as *Loiseleuria procumbens*, tended to be greater in the plots with fewer trees. Low-bush cranberry (*Vaccinium vitis-idaea*) and crowberry (*Empetrum nigrum*) had fairly uniformly low cover, while blueberry (*Vaccinium uliginosum*) occurred in the denser stands.

Herbaceous plants were rare, with only trace amounts of grass (*Festuca altaica*). The hemiparasite *Geocaulon lividum* and clubmosses (*Lycopodium* spp.) occurred in some

plots. *Polytrichum* (*P. juniperinum* and *P. piliferum*) was the only common moss, averaging 4% cover. Litter accumulations were low, averaging 12% cover.

5.3.2.2 Lichens

Lichen mats averaged 1.7 to 7.1 cm in depth (Table 2). Fruticose ("shrubby") lichens covered from 71 to 90% of the plot areas. The remaining area was covered by crustose lichens, primary squamules of fruticose lichens, dead lichen mat, litter accumulations under shrubs, or other plants. Bare ground was rare. The lichen mat was thickest in plots with the most trees and finest-textured soils (Table 2).

The lichen flora was diverse. Forty species of ground lichens, 22 in the genera *Cladina* and *Cladonia*, were identified (Appendix D). *Cladina stellaris*, *C. rangiferina*, *C. mitis*, *C. arbuscula*, *Cladonia uncialis*, and *Stereocaulon paschale* had cover of 10% or more in at least one plot (Appendix B). Species with lower cover but over 50% frequency in at least one plot included *Cetraria cucullata*, *C. islandica*, *Cladonia coccifera*, *C. cornuta*, *C. crispata*, *C. fimbriata*, *C. gracilis*, and *C. subfurcata*.

Cover of the "climax" species *Cladina stellaris* varied from 12% to 39%, while cover of another late-succession species *Cladina rangiferina* varied from 4% to 28% (Appendix B). Cover of these two species was greatest

in the plots that burned in 1891. Plots burned in 1914 had thinner, less-continuous lichen mats, with higher cover of mid-successional species, such as *Cladina mitis*, *Cladonia uncialis*, and the horned and cupped *Cladonia* species (e.g. *Cladonia coccifera*, *C. cornuta*, *C. fimbriata*, *C. gracilis*). These species occurred in open areas in all plots, while the later-successional species *Cladina rangiferina* and *C. arbuscula* occurred more in shaded areas. *Cladina stellaris* occurred throughout the plots, but was deeper in shaded areas. The mosaic of lichens suggests that the distribution of the lichen species is determined by different temperature and moisture regimes in the lichen mat, resulting mainly from canopy shading.

5.4 AGE DISTRIBUTIONS

5.4.1 General Features

The age distributions reveal a broad range of tree ages (Figures 5-7). Most plots had individuals that survived the fire and were dominant trees in the current stands. All had survivors nearby. Most survivors were established between 1840 and 1870.

Regeneration was relatively low in the first decade after fire, but increased greatly thereafter. The length of time required for 75% of the trees to establish varied between black and white spruce plots (Table 1).

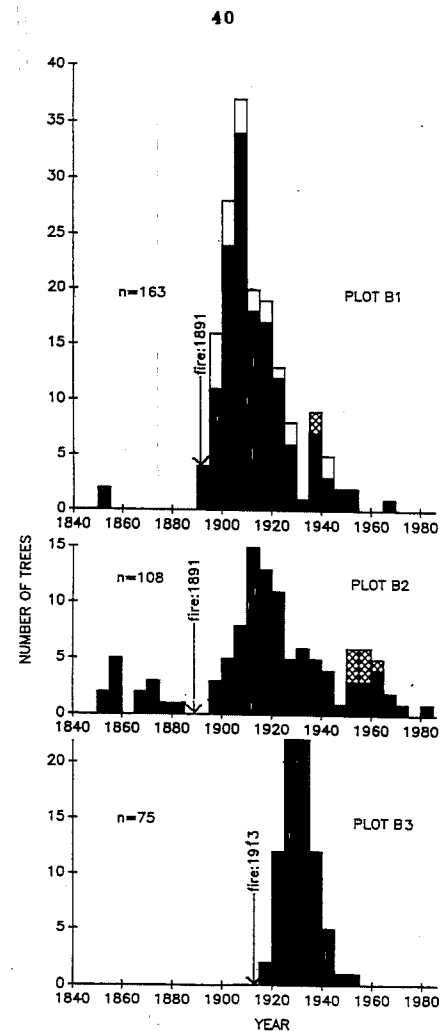


Figure 5. Age distributions of Plots B1, B2, and B3. ■ = Black spruce. □ = White spruce. ▨ = Black spruce layer.

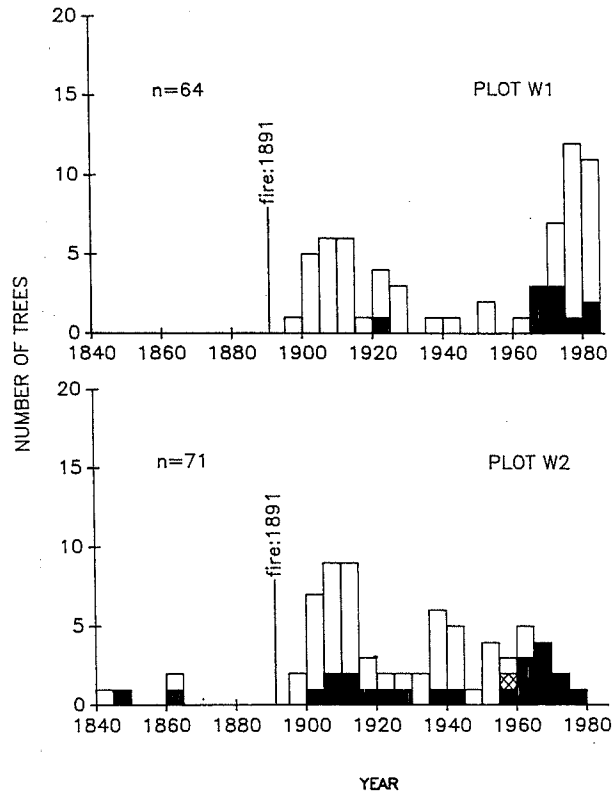


Figure 6. Age distributions of Plots W1 and W2.
 ■ = Black spruce. □ = White spruce. ▨ = Black spruce layer.

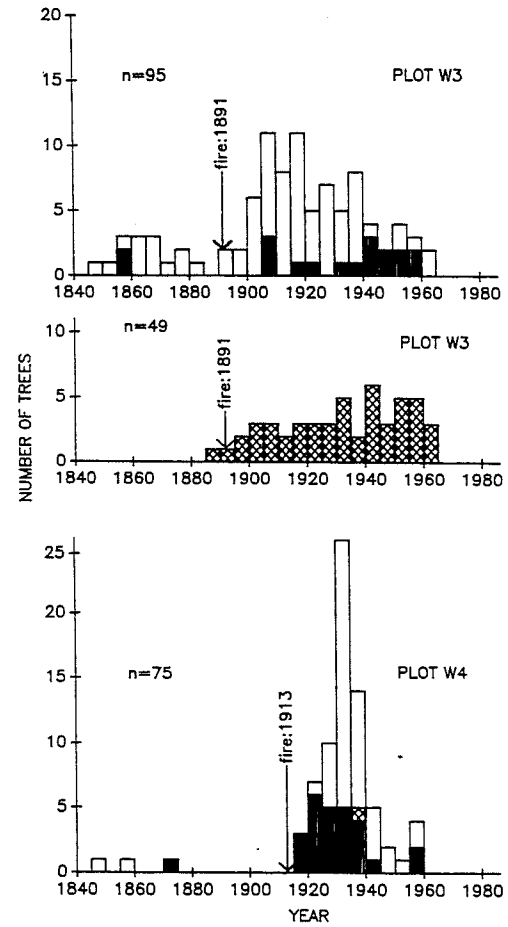


Figure 7. Age distributions of Plots W3 and W4.
 ■ = Black spruce. □ = White spruce. ▨ = Black spruce layer.

Regeneration then dropped off and little tree establishment occurred in recent years. Almost no trees established in the past 25 years in four of the plots.

5.4.2 Black Spruce Plots

Age distributions of these three stands show distinct peaks of regeneration soon after fire (Figure 5). Plots B1 and B3 show strong peaks 10 to 15 years after fire, which then drop off steeply. Over 75% of the regeneration occurred in the first 35 years after fire and there was no current tree establishment (Table 1). Plot B2 was dominated by 14 survivors. The regeneration peak was 20 years after the fire, but was less distinct than in the other stands. Fifty years were required for 75% of the regeneration to occur and establishment of small trees has continued to the present. Little regeneration of black spruce by layering was found in these plots.

5.4.3 White Spruce Plots

With the exception of Plot W4, the plots with a majority of white spruce had broad establishment periods without prominent peaks (Figures 6 & 7). Fifty to 80 years were required for 75% of the trees to become established. Trees were still establishing by seed in Plots W1 and W2, and current establishment was particularly high in Plot W1. Current establishment in Plot W3 was by layering of black spruce.

The age distribution of Plot W4 is more similar to those of black spruce than the other white spruce plots (Figures 5-7). Seventy-five percent of the trees were established in the first 25 years after fire and none have established in the last 25 years. Regeneration in the first decade after fire was predominately black spruce. Thereafter white spruce established at a higher rate.

5.4.4 Tree Growth and Age-size Relationships

Tree growth in the woodlands was slow. Average height growth for post-fire trees ranged from 1.9 cm/year, for white spruce in Plot B1, to 5.1 cm/year, for black spruce in Plot W4 (Table 1). The average height growth rate of black spruce, 3.3 cm/year, was slightly higher than that of white spruce, 2.6 cm/year. Trees established soon after fire had higher average growth rates than those established later, as ninety-five percent of all trees established more than 35 years after fire were less than 1 m in height and all trees less than 30 years old were under 0.3 m in height (Appendix F).

Tree age was poorly correlated with height and diameter-at-breast-height (Table 1). Least squares regressions of age on height gave R^2 greater than .70 only for Plots W1, W2, and W4 (Table 1). The R^2 was between .33 and .63 for black spruce plots and was also low (.32 and .40) for Plot W3, the densest white spruce-

dominated plot. Regressions with diameter-at-breast-height gave lower R² than height in all cases and are not reported.

CHAPTER 6: DISCUSSION

6.1 FIRE HISTORY

6.1.1 Fire Effects

The variability among the sample plots in number of surviving trees and thickness of the lichen and organic layers indicates that the stands burned with different severities. A fire regime of fairly frequent, moderately severe fires, such as that of most spruce-lichen woodlands, is characterized by a wide range of fire effects (Agee, in review). Individual fires are often patchy, with areas of high, moderate, and low severity.

The number of trees surviving the 1981 fire was relatively high, but variable among plots. They occurred on flat areas as well as in depressions. Fewer survivors were found in areas burned in 1913 and they were generally restricted to swales. The outer loop of the moraine burned in 1913 had fairly uniform stands of small black spruce, while tree cover on the inner loop was poorly-developed, with groves of small aspen on south-facing slopes and large areas of shrub birch with few trees. These observations indicate that the fire in 1913 was generally more severe than the fire in 1891.

Drier meteorological conditions may have caused the 1913 fire to be more severe than the 1891 fire. Another

reason for the severity of the 1913 fire may have been related to stand development. Assuming that the entire area burned in the mid-1800s and that the 1891 fire did not extend east of the river, by 1913 the woodlands east of the river were 22 years older than those burned in 1891. Increased fuel accumulations over this period may have contributed to a more intense fire. The stand ages at the time of burning in 1913 were similar to the current stand ages on that side of the moraine, since the oldest post-fire trees are now about the same age (60 to 70 years) as the oldest survivors were in 1913 (Figures 5-7). At present, the lichen and organic mat in these stands is thin (3.5-3.8 cm) and not yet continuous (71-72% cover; Table 2). The mat was probably even less well-developed at the time of the 1891 burn, hindering the spread of fire. The likelihood of fire in an area of lichen woodlands in the Northwest Territories of Canada increased from 20% to 80% between 80 and 100 years (Rowe et al., 1975). The lichen mat is implicated in the increased probability of fire, as during this time period lichen forms a closed mat along which fire can spread (Auclair, 1983).

6.1.2 Pre-fire Conditions

Trees at the time of the 1891 fire were young and small (Table 1). This agrees with a report by John C.

Cantwell, who mapped the Kobuk River area for the U.S. government and visited Walker Lake in 1886, only 5 years before the 1891 fire. He described the moraine as a "high rolling tundra plain", contrasting strongly with the surrounding forested areas (Cantwell, 1887). The trees were evidently so small and widely-spaced at that time that the area did not appear to be forested. This would have been the case if in fact the moraine had burned about 40 years before his visit.

Tree cover may also have been sparser on the moraine in the past because of climatic differences between the 19th and 20th centuries. Dendroclimatological reconstructions from white spruce in the Walker Lake area indicate that the climate was cooler in the nineteenth century than in this century (Garfinkel and Brubaker, 1980). Establishment of white spruce at treeline above Walker Lake increased in this century (Goldstein, 1981). Not only did trees establish above the former treeline, but the stands below treeline became more dense. Although this spruce-lichen woodland is located 300 meters below treeline, the substrate is marginal for tree growth and seedling establishment may be sensitive to slight climatic changes.

6.1.3 Fire Frequency

Fire is the most important disturbance in interior Alaska (Viereck, 1973) and in spruce-lichen woodlands in

general (Fraser, 1956). The woodlands at Walker Lake have probably been burned repeatedly, as fire cycles 70 to 100 years in length have been suggested for spruce-lichen woodland areas of Canada with similar temperature and precipitation to Walker Lake (Maikawa and Kershaw, 1976; Johnson, 1979).

Because of the isolated location, the woodlands at Walker Lake may burn less frequently than areas of continuous woodlands with comparable climate. Walker Lake is located in an area of great topographic variation and vegetation discontinuity, factors which decrease the extent of fires (Viereck, 1973). According to Means (1981), the fire frequency in "islands" of dry conifer forest surrounded by more mesic forest in the central Oregon Cascades is decreased by the surrounding forest, which ignites less often and retards fire spread. This may also be the case at Walker Lake.

Spruce-lichen woodlands with high rainfall in eastern Canada have longer fire cycles (up to 500 years) than the drier interior provinces (Foster, 1985). The continental climate of interior Alaska is probably modified by Walker Lake's proximity to the Maritime Climatic Division (U.S. Environmental Data Service, 1977) and location at the edge of the Brooks Range. Orographic precipitation may increase the annual totals above those recorded for the nearest weather station, Bettles, which

is 30 km south of the mountains and 110 km further inland. Thus, annual precipitation at Walker Lake may be higher than the recorded 35.5 cm, causing a lower fire frequency than would be expected. The evidence indicates that each section of the moraine burned twice in the past 150 years. Sufficient evidence is not available to estimate the average interval between fires.

6.2 VEGETATION IN RELATION TO SOILS

6.2.1 Distribution of White and Black Spruce

The distribution of white and black spruce in the woodlands appeared to be determined primarily by soil texture, with white spruce dominating on soils with at least 85% sand (sand and loamy sand in Plots W1 and W2) or on river deposits (cobble silt-loam in Plot W3). Black spruce dominated on sandy loam soil with 49 to 69% sand.

Soil texture is the most important factor determining water and nutrient properties of a soil, with moisture and nutrient levels increasing as soil texture becomes finer (Brady, 1986). Fine-textured soils also tend to be colder, due to higher water content. White spruce requires better-drained, warmer soils, with higher nutrient status than does black spruce (Chapin, 1986). The sandy soils of Plots W1 and W2 may favor white spruce by being excessively well-drained and relatively warm. Reasons for the dominance by white spruce on Plot W3 are

not clear, but the silty river deposits may have more available nutrients than the glacial deposits.

6.2.2 Other Plot Characteristics

Soil texture was related to several other characteristics of the vegetation (Table 2). This may have been due to the effects of soil texture on the moisture stress experienced by vegetation through its control of soil water-holding capacity (Brady, 1986).

These relationships are illustrated by data from the five plots that burned in 1891 (Table 2). Plots with finer-textured soils tended to have greater tree basal area, which generally indicates greater canopy cover. The stems per hectare showed a similar pattern, except for Plot B1, which had many small trees. The number of trees that survived the fire also increased with increasingly fine-textured soils, perhaps because on soils with higher water-holding capacity the understory vegetation had higher water content at the time of the fire, resulting in less complete burns.

The understory vegetation of these plots also varied in relation to soil texture. Finer texture was associated with thicker lichen and organic layers and higher shrub cover. Percent cover of the lichen mat did not vary enough to show a clear trend, but percent cover increased for *Cladina stellaris* and *C. rangiferina*, which require more mesic conditions than the other lichens. In the

above comparisons, values for Plot W2 were consistently higher than the trend shown by the other plots. The substrate of this plot was unusual, being 45 cm of sand deposited over a cobbly base, so soil moisture conditions may have been anomalous compared to other soils of similar surface texture.

Plots B3 and W4, which burned in 1913, were on sandy loam soil. Despite their moderately fine soil texture, they had low tree basal areas, thin lichen and organic layers, low cover of the lichen mat, and low cover of late succession lichens. The low values for these variables, compared to the other stands, were probably due to their younger age.

The most important environmental gradient operating in this community is probably available soil moisture. It is determined primarily by soil texture, but may be then reinforced by changes in the vegetation. The relationships between soil texture and other plot characteristics suggest a complex interaction between soil moisture, vegetation cover, and fire severity. The effects are carried over from one fire interval to the next, due to the importance of the moisture regime before fire in determining the extent of damage to the vegetation (Oechel and Lawrence, 1985).

Greater soil moisture apparently favors growth of all layers of the vegetation. Better tree growth provides

partial shade to the understory, which reduces surface temperatures and evaporation, allowing the lichen to remain hydrated and therefore to photosynthesize for longer periods (Kershaw, 1972). The resulting thicker lichen cover acts as a mulch that maintains higher soil moisture (Rouse and Kershaw, 1971), reinforcing the initially better moisture conditions. In Plots B2 and W3 this may have increased the moisture content of the fuel, decreasing fire intensity and allowing many trees to survive. This effect may be balanced against the fact that a thick lichen mat has higher fuel mass than a thin one and thus may increase fire intensity. Perhaps the lichen mat can reduce fire intensity when a fire occurs during weather that is not dry enough to desiccate the entire mat.

6.3 AGE DISTRIBUTIONS

The notable features of the age distributions are the variation among plots in the patterns of post-fire tree establishment, and the low levels of current establishment. These features will be discussed separately.

6.3.1 Tree Establishment Patterns After Fire

Reestablishment periods after disturbance can be long where harsh environmental conditions cause high seedling mortality, seed sources are unreliable, or tree growth is slow so that the first invaders do not increase in size

rapidly enough to exclude further regeneration (Oliver and Larson, in prep.). The age and size distributions of the sample plots suggest that the openness of the tree canopy in these woodlands is due to low levels of seedling establishment, slow tree growth, and an eventual termination of successful seedling establishment. As discussed below, variation among the sample plots suggests that tree species and fire severity are important factors controlling these processes.

6.3.1.1 Tree Species

Differences in patterns of regeneration among plots may be related to the tree species dominating the stand at the time of fire. Plots having large numbers of black spruce (Plots B1, B2, B3, and W4) had the sharpest peaks and narrowest periods of regeneration (Figures 5-7).

Black spruce is adapted to fire by having semi-serotinous cones, with seed released from dead trees for at least eight years after a fire (Black and Bliss, 1980). The ability to store and release seed slowly and the numerous survivors may have allowed the black spruce to reoccupy sites soon after fire, resulting in narrow regeneration periods.

Lack of seed source may have been a factor causing the broad establishment periods of white spruce, as white spruce survivors were rare. However, Plot W3 had 13 white spruce survivors and still had a broad establishment

period (Figure 7). There were fewer white spruce and they were mainly on the inner loop of the moraine, which bordered the lake and was far from seed-sources off of the moraine. Seed supplies in white spruce are variable, since good seed years are episodic, with abundant seed produced as seldom as once every 12 years, and no seed stored from year to year (Viereck, 1973). Therefore, establishment of white spruce seedlings may occur infrequently, resulting in broader establishment periods than for black spruce.

6.3.1.2 Fire Severity

The variation among age distributions of plots dominated by the same species may be attributed to different severity of burn or related factors such as number of survivors, soil moisture-holding capacity, and depth of organic mat (Table 2). Plots B2 and W3 presumably were established after less severe fires than the other plots, as indicated by their many surviving trees and thick lichen and organic layers. The age distributions of these two plots are different from other plots with similar species composition (Figures 5-7). In Plot B2, fewer trees were established in the peak of regeneration and establishment has continued to the present, unlike the other two black spruce plots (B1 and B3). In Plot W3, more trees were established than in the other two plots dominated by white spruce (W1 and W2),

but they generally grew slower and establishment (other than by layering) ceased after about 70 years. Less-severe burning in plots B2 and W3 may have moderated the differences otherwise seen between age distributions of black spruce and white spruce, by shortening the establishment period of white spruce and extending that of black spruce.

6.3.1.3 Seedbed

6.3.1.3.1 Importance of Microsite Temperature and Moisture Conditions

The regeneration patterns shown by the age distributions may be explained in terms of the changing surface environment over the course of stand development and its effects on seedling establishment. Slow development of the stands after fire may be due to poor site conditions and the lack of available microsites for seedling establishment and survival.

Tree seedlings mortality from temperature stress and drought is high on boreal forest seedbeds (Black and Bliss, 1980). Black and Bliss (1980) found that reproduction of black spruce is limited by the interaction of temperature and soil moisture within 40 km of treeline on the MacKenzie River. Microsite temperatures averaging above 150C are required for germination. These conditions must occur early in the short growing season, in order for the seedling radical

to elongate before the onset of drought, since slight reductions in soil moisture cause high seedling mortality. This requirement may not be met, even during years with normal temperature and precipitation, resulting in no successful establishment (Black and Bliss, 1980). Dry substrates near northern treeline may provide marginal, unstable conditions for tree establishment and result in failure of establishment, except in the most favorable years.

6.3.1.3.2 Charred Lichen Mat

The physical characteristics of the lichen mat after fire may be important to seedling establishment. Scotter (1964) reports that only about one third of the ground surface is exposed mineral soil after most fires in lichen woodlands. This agrees with my observation that, one year after a 1985 fire, charred organic matter covered 99% of the ground of a spruce-lichen woodland near Walker Lake.

Charred organic matter is an unfavorable environment for seedling establishment because it is subject to rapid fluctuations in temperature and moisture (Vincent, 1965). It has low water-holding capacity and the blackened surface has low albedo, which causes it to become hot during clear days. In the first season after germination the black spruce seedling radical may elongate as little as 2 cm or less (Foster, 1985). A thick organic layer may

thus prevent new seedlings from reaching mineral soil and a stable moisture supply (Ahlgren, 1959; Vincent, 1965).

6.3.1.3.3 Dry Mineral Soil

Fire aids seedling survival by removing the organic layer, but seedling mortality may also be high on exposed mineral soil. Although moist mineral soil is optimal for seedling establishment, dry mineral soil is poor (Smith, 1951; Vincent, 1965). Because of the droughtiness of the typically sandy soil and lack of shade, surface conditions after fire in lichen woodlands are analogous to a "hot desert" (Kershaw, 1976). Maximum soil surface temperatures can reach 65°C after fire, with a diurnal range of up to 46°C (Kershaw, 1978). Mid-day temperatures during the summer are commonly above 45°C, while under the open canopy of a mature lichen woodland they rarely exceed 30°C (MacFarlane and Kershaw, 1979).

The soil moisture regime after fire is also severe. Kershaw and Rouse (1971) found that soil moisture was 40% lower and fluctuated more on burned spruce-lichen woodlands than under the lichen mat on unburned sites. The poor soil moisture conditions may limit seedling establishment.

6.3.1.3.4 Improvement of Microsites Through Time

Stand regeneration may be delayed until the surface conditions are ameliorated by increases in vegetative cover and its effects on the surface temperature and

moisture regime (Kershaw and Rouse, 1971). Only a few moss and lichen species can grow well under the extreme post-fire conditions, and initial colonization is typically slow. The crust that pioneering species form on the bare mineral soil begins to modify the harsh microclimate. Two common pioneers, both found at Walker Lake, have been shown to be more favorable seedbeds than dry mineral soil: *Polytrichum* spp. moss (Smith, 1951; Vincent, 1965), and the lichen *Trapeliopsis granulosa* (Gagnon, 1966).

Increasing seedling establishment in the sample plots over the first two decades (Figures 5-7) may be related to improving soil moisture as lichen succession progresses (Kershaw & Rouse, 1971). The microsites available for seedling establishment after the fires at Walker Lake were probably a mosaic of dry mineral soil and dry, charred organic matter, both unshaded. The delayed establishment after fire may be caused by the unfavorable seedbed conditions immediately after fire. The improvement of conditions as pioneer mosses and lichens invaded and modified the microenvironment may have permitted increased establishment.

6.3.2 Lack of Current Establishment

Current establishment rates are low (Figures 5-7). Most plots have few or no seedlings established in the past 25 years. This section discusses possible reasons

for a change in conditions that could cause seedling establishment to cease.

6.3.2.1 Tree Competition

Steep declines in seedling establishment, as seen in age distributions of shade-intolerant temperate forest trees, are usually attributed to shading by a closed canopy of overstory trees (Oliver and Larson, in prep.). Goldstein (1981) states that at this northern latitude, shade may be important even in open stands, due to the low sun angle. However, in the woodlands at Walker Lake the canopy is so open, due to the small, narrow-crowned trees, that shading would not seem to be a factor except in the densest stands. In support of this, current seedling establishment on relatively moist places on the moraine indicates that the lack of successful seedling establishment is due not to overstory interactions, but rather to microsite conditions determined by the substrate. For example, 11 black spruce seedlings less than 20 years old were found on 4 m² of *Sphagnum* spp. moss in a shallow depression on the edge of Plot W3, while in the entire plot there were no trees younger than 25 years old.

Root competition may be more important than crown competition in these stands. Root-shoot ratios were high for spruce-lichen woodlands in Quebec, with 34% of the black spruce dry weight and 39% of the shrub dry weight

in the roots (Rencz and Auclair, 1977). On poor sites most roots are in the top few centimeters of the soil (Cowles, 1982), so competition for both water and nutrients may be intense in this zone.

6.3.2.2 Effects of the Lichen Mat

Another reason for the decline in seedling establishment may be that seedbed quality deteriorates as the lichen mat becomes thicker and more continuous (Kershaw, 1976; Cowles, 1982). A lichen mat provides an unstable temperature and moisture environment because lichens dehydrate rapidly, due to their high surface-to-volume ratio and lack of water conducting system (Kershaw, 1985). Lichens proved to be the worst of all seedbeds tested in germination trials with eastern white pine (*Pinus strobus* L.) on loamy sand soils in Connecticut (Smith, 1951). Mortality was due mainly to heat injury. In seedling surveys in Quebec, spruce seedlings were found along edges of the lichen mat, but never in centers of mats (Cowles, 1982), suggesting that the mat impeded establishment.

Thick lichen mats may present an effective physical barrier to seedling establishment, by preventing seeds from reaching contact with mineral soil and a reliable source of moisture. Penetration of the lichen mat by seeds probably becomes progressively more difficult as the mat thickens and the dying basal parts accumulate.

Without unusually moist weather, seedlings that germinate in the lichen mat will die before their roots can reach the soil (Allen, 1929).

As well as physical effects, lichens may have adverse chemical effects on tree establishment and growth (Brown and Mikola, 1974). Lichens produce a variety of water-soluble, biologically-active compounds that have antibiotic properties (Vartia, 1973). Applications of aqueous lichen extracts to tree seedlings in laboratory and field experiments have inhibited mycorrhizal infection of roots (Brown and Mikola, 1974), inhibited uptake of nutrients (independent of mycorrhizal interaction) (Fisher, 1979), and decreased growth (Arsenault, 1979; Brown and Mikola, 1974; Cowles, 1982; Fisher, 1979). Inhibition of germination by lichens is not reported for spruce, but has been shown in laboratory experiments for other plants, such as moss (Lawrey, 1977). The "climax" species *Cladina stellaris* was found to be the most effective inhibitor of mycorrhizal infection (Brown and Mikola, 1974), suggesting that these effects could increase as lichen succession progresses. Although studies with aqueous-extracts are not conclusive evidence (Kershaw, 1977), allelopathy may play a role in inhibiting tree establishment in these woodlands.

The influence of the lichen mat on adult trees is not known. Adverse effects, such as lowered soil temperatures

(Kershaw, 1977) and possible growth inhibition, are offset by the benefits of retention of soil moisture under the lichen mat (Cowles, 1982). This may explain why little evidence of adult tree mortality was found at Walker Lake. Figure 8 summarizes the possible interactions between the trees and the lichen mat.

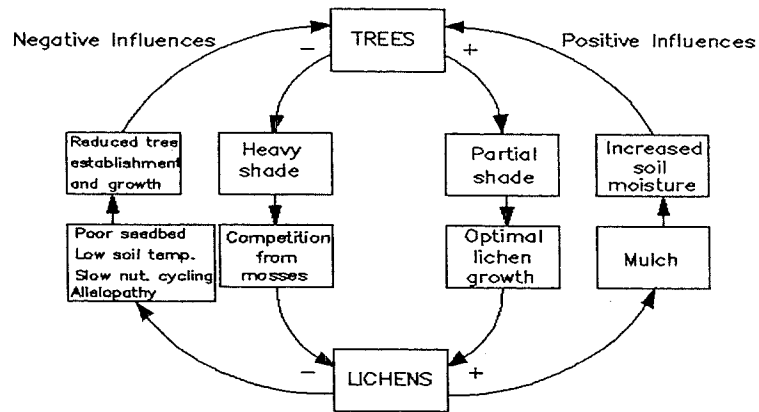


Figure 8. Interactions between trees and lichens.

6.4 TREE GROWTH AND AGE-SIZE RELATIONSHIPS

The low growth rates of the woodland trees, averaging 3 cm of height growth per year (Table 1), were probably as important as low seedling establishment rates in maintaining the open canopies of the stands. The small sizes and narrow crowns of the trees gave the stands an open appearance, even in Plot B1, which had high stem density (3621 stems/ha).

The slow growth is probably due to adverse climate and soil conditions. The fact that the average growth rate of white spruce, 2.6 cm/year, was lower than that of black spruce, 3.3 cm/year, despite the higher maximum potential growth rate of white spruce (Chapin, 1987), suggests that the growth of white spruce was more limited by the poor site conditions on the moraine than that of black spruce.

Examination of age-size relationships (Appendix F) provides a more accurate picture of the stand development than the age distributions alone. Although establishment had continued to the present in some plots (Figure 6), over 95% of the trees established more than 35 years after fire were less than 1 m in height and were slower growing than those established previously (Appendix F). In Plot W1, the only plot with high establishment in recent years, all trees established during the past 60 years were less than 0.3 m in height. Thus, the

continuing establishment in that plot was not increasing canopy cover.

Regression of age on size gave low R^2 in most plots (Table 1) because of the variability in tree size within age classes, particularly for those established soon after fire (Appendix F). An extreme example is Plot B1, where trees in the 80 to 85 year old class ranged from 1 to 7 m tall (Appendix F).

6.5 AGE DISTRIBUTIONS OF BOREAL FOREST TREES

6.5.1 General Patterns for Boreal Forest Trees

Black spruce can rapidly reoccupy sites after fire. Post-fire black spruce stands on moist sites in interior Alaska are typically dense, with narrow age ranges (Viereck, 1973). In contrast, white spruce does not commonly seed in directly after fire, but may follow earlier successional stages of poplar, aspen or birch (Viereck, 1975). This results in wider age ranges for white spruce, although the occurrence of some white spruce stands with narrow age ranges indicates that white spruce can invade rapidly under favorable conditions (Viereck, 1975; Payette and Fillion, 1985).

A variety of age distributions was found by Zoltai (1975) in black spruce stands in the MacKenzie River drainage in the Yukon territories. Young stands (60 to 100 years since fire) usually had narrow establishment

periods (10 to 20 years), while older stands (200+ years) had establishment periods spanning over 100 years.

Age distributions for stands near northern treeline often show long establishment periods. Continuous establishment of black spruce since fires 200 to 250 years ago was documented in northern Quebec (Payette and Gagnon, 1979). The slow regeneration of these stands was attributed to insufficient seed production and germination under unfavorable conditions. Long establishment periods were also documented for white spruce stands of undetermined origin near treeline in northern Quebec (Payette, 1976), Manitoba (Scott, Hansell and Fayle, 1987) and above Walker Lake (Goldstein, 1981). Establishment increased in this century in these age distributions and the authors suggested that improving climate allowed the increased establishment. In contrast, most regeneration occurred within 20 years after a fire about 1890 in a white spruce stand at treeline in Quebec, perhaps because of favorable climatic conditions (Payette and Fillion, 1985).

Age distributions for white spruce near treeline above Walker Lake (Goldstein, 1981) are different than those from this study. The high current levels of seedling establishment in treeline stands indicate that the macroclimate of the area has been favorable for seedling establishment in this century, suggesting that

the low rates of establishment on the moraine are due to microclimatic conditions particular to the unusual substrate.

6.5.2 Age Distributions of Other Spruce-lichen Woodlands

Spruce-lichen woodlands may be more severe sites for tree establishment and growth than other boreal forest types. However, tree regeneration after fire is typically rapid in black spruce- and jack pine-lichen woodlands in areas of central Canada with 50 to 100 year fire cycles (Larsen, 1980). Age distributions from eastern Canada have shown both narrow and wide age ranges. Sirois and Payette (in prep.) found that black spruce establishment periods after 20th century fires in northern Quebec usually lasted for about 20 years, but ranged from 10 to 55 years in length. The peak in establishment occurred 10 years or more after fire in half of the stands. In the first years after fire, a Labrador woodland was nearly barren of seedlings and only scattered regeneration was present 20 to 30 years after fire (Foster, 1985). An age distribution of a 36-year-old stand in Labrador showed continuous establishment of black spruce (Foster, 1985).

Foster (1985) hypothesized that establishment periods would be longer in eastern Canada than in the main boreal forest in interior Canada because of longer fire cycles. Longer intervals between fires allow the accumulation of

a thick organic mat, and cooler summers in this area would cause less severe fires that would not completely remove the organic mat. Foster (1985) also suggested that regeneration periods may be longer in the sub-arctic than in central Canada for similar reasons.

6.6 SUCCESSION IN THE WALKER LAKE WOODLANDS

Results of this study suggest that the spruce-lichen woodland at Walker Lake has remained open due to frequent fires, slow post-fire tree regeneration, slow growth of the trees, and lack of on-going seedling establishment. These woodlands will probably remain open for centuries, even in the absence of fire. They may slowly change towards closed spruce-moss forest by the infrequent establishment of seedlings and increasing importance of layering of the black spruce as the organic layer becomes thicker and mosses replace lichens in shaded areas. This process is probably occurring on sites with less sandy soils. In Plots B2 and W3 trees are now fairly dense, black spruce is beginning to layer, shrub cover is high, the organic layer and litter are accumulating, and some feather-mosses are established around the bases of trees. On the more open and sandier sites, increases in density will be slow but may occur as a few seedlings successfully establish.

The balance between tree and lichen dominance in a spruce-lichen woodland, and thus the direction and rate

of succession, is determined by climatic and site conditions that control tree growth (Auclair, 1983). Figure 9 is a graphical depiction of two different paths of stand development after fire, emphasizing the influence of soil texture on site productivity. The variation among plots in this study suggests that the rate of development towards closed forest varies with the favorableness of the substrate for higher plant growth.

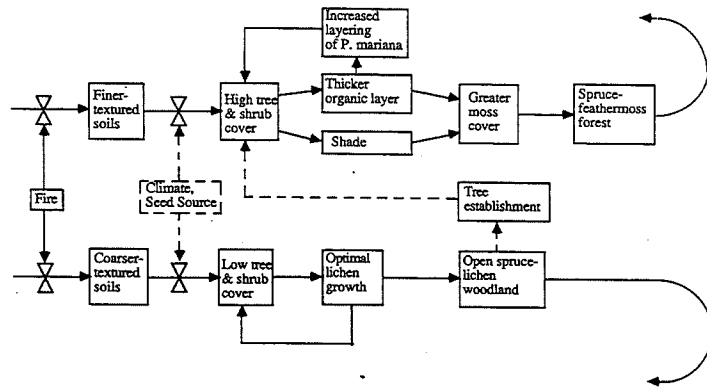


Figure 9. Successional processes in relation to soil texture.

CHAPTER 7: CONCLUSIONS

The conclusions of this study are the following:

- 1.) Wildfires burned the spruce-lichen woodlands at Walker Lake in 1891 and 1913. Trees that survived these fires are scattered among younger trees and are numerous in some areas.
- 2.) Patterns of tree regeneration after fire were different for black spruce than for white spruce. Age distributions for black spruce stands show strong peaks of establishment within the first two decades after fire, with establishment dropping off to low levels within 35 years of the fire. Regeneration in the white spruce stands was more continuous, without strong peaks.
- 3.) Few trees have established in the past 25 years. The lack of current tree regeneration may be due to the poor seedbed provided by the lichen mat.
- 4.) The soil moisture regime is probably a major factor determining the vegetation composition of the woodlands. Black spruce dominates on finer textured soils, while white spruce occurs mainly on sandier soils. The stands on finer textured soils are also generally denser, with thicker lichen mats and higher shrub cover.

5.) Tree growth is slow on all plots. Because of the slow tree growth and narrow crown form and the eventual termination of seedling establishment, these stands develop slowly. Stand canopies would probably remain open for several centuries, even in the absence of fire, allowing the continued dominance of the understory by lichens.

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APPENDIX A: TREE AGE ADJUSTMENT FACTORS

A. Adjustment factors for cores above stem base

<u>Black Spruce</u>		<u>White Spruce</u>	
Cm above base	Years added	Cm above base	Years added
10	6	10	6
20	10	20	11
30	13	30	15
40	16	40	18

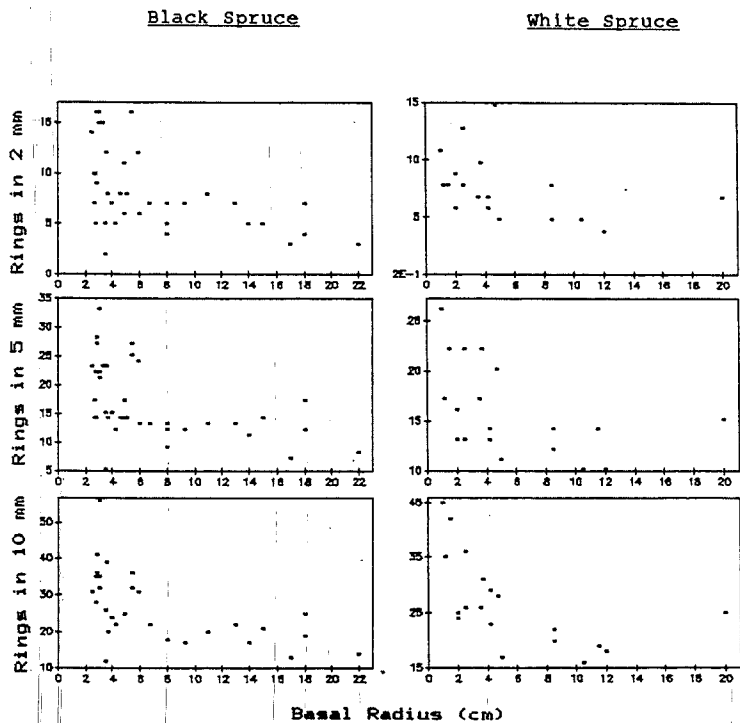
B. Adjustment factors for missed piths.

The mean numbers of annual rings within 2, 5, and 10 mm of the centers of cores of 38 black spruce and 19 white spruce were used as adjustment factors for missed piths. Trees with less than 6 cm basal radius had higher mean numbers of rings than trees with more than 6 cm basal radius, so two sets of adjustment factors were used. Values were interpolated for trees with radii of 5.5 to 6.5 cm.

<u>Black Spruce</u>			
Basal radius	mm	Mean # of rings	S.D.
>6 cm	2	6	2
	5	12	3
	10	19	4
<6 cm	2	10	4
	5	19	6
	10	30	9

<u>White Spruce</u>			
Basal radius	mm	Mean # of rings	S.D.
>6 cm	2	6	2
	5	13	2
	10	20	3
<6 cm	2	9	3
	5	17	5
	10	29	8

C. Scatter plots of the number of annual rings in the inner 2, 5, and 10 mm vs. basal radius of the tree.



APPENDIX F. TREE HEIGHT/AGE AND DIAMETER-AT-BREAST-HIGHT/AGE PLOTS

