7

Trees

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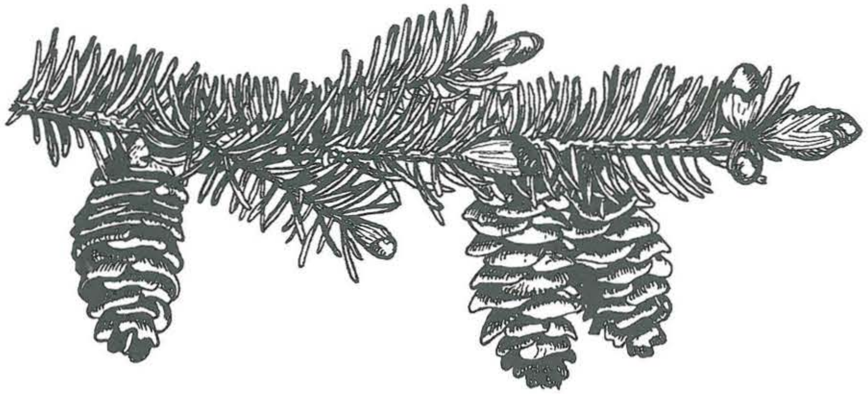

7.1 Tree Community at Kluane

The tree flora of the Kluane Valley is remarkably depauperate, even for the boreal forest, which is not known for high diversity of tree species. Three species of trees are present. The only species of conifer is the white spruce, *Picea glauca* (Moench) Voss. The absence of its congener, the black spruce, *Picea mariana* (Mill.) BSP, which is widespread and common in other parts of the boreal forest, is surprising, particularly since black spruce occur to the north and to the east of Kluane. The other two tree species in the valley are angiosperms of the genus *Populus:* trembling aspen, *Populus tremuloides* Michx., and balsam poplar, *Populus balsamifera* L. In spite of their ability to spead clonally, the two species of *Populus* are comparatively rare in the valley, making spruce the dominant tree in area, cover, and biomass. This chapter is therefore primarily about white spruce. Although some herbivores feed on parts of the spruce trees (e.g., red squirrels eat the seeds), these trees are more important to the other organisms in the ecosystem because of the physical structure they create. The second way in which spruce are important is as primary producers because they are responsible for a large portion of the net primary productivity in the valley. Although this production does not benefit all the herbivores directly, it affects them indirectly through the accumulation of litter, which provides cover and in turn affects their food plants through its physical and chemical properties.

An obvious feature of the tree vegetation of the study area is its heterogeneity. Much of the valley is covered by spruce forest, but it varies from open stands to closed canopy and has a range of ages due to the disturbance regime, of which fire is the dominant feature. Fire initiates forest succession and maintains the heterogeneous character of the boreal forest vegetation mosaic. In general, the North American boreal forest fire regime is characterized by large, high-intensity, stand-replacing wildfires with short return intervals (Wein and MacLean 1983, Johnson 1992). Few other natural disturbance mechanisms control vegetation dynamics on such large scales in this region. To assess the vegetation of the valley and its spatial heterogeneity, we undertook several studies, including a fire history of the valley.

Some historical climate information is available for the region in the form of a dendroclimatic study by Allen (1982). Like most areas in northwestern North America, our region has experienced a warming trend since the end of the Little Ice Age in about 1820. The current climate is, however, still cold and dry because of the rain shadow of the adjacent St. Elias Mountains. It has a mean annual temperature of −3°C and mean annual precipitation of about 230 mm, most falling as rain during the summer.

The predominant wind direction during summer is from the southwest, but local wind patterns are influenced by glacial effects, topography, and valley orientation. The large side valleys, which enter perpendicular to the main trench (the Alsek, Slims, and Jarvis rivers), can funnel katabatic and glacial winds into the trench, creating brief wind storms and spectacular dust clouds along loess-filled stream beds. These wind characteristics may be important during forest fires.

The frequency of lightning storms can strongly influence the frequency and spatial pattern of fires on a landscape (Johnson 1992). Lightning, however, is rare in the study area compared with neighboring systems because the Kluane region lies outside the major "lightning belt" of central Yukon Territory (Hawkes 1983). This low frequency of lightning may also be an orographic effect of the St. Elias Mountains.

Table 7.1 Tree abundance on the study grids estimated from T-square sampling.

	White Spruce		*Trembling Aspen*		*Balsam Poplar*	
Grid	Small Trees	Large Trees	Small Trees	Large Trees	Small Trees	Large Trees
Control 1		421 ± 80		0		0
Control 2						
Control 3	907 ± 104	544 ± 92	0	0	0	0
Food 1	768 ± 122	414 ± 76	545 ± 256	0	137 ± 131	48 ± 123
Food 2						
Fertilizer 1	985 ± 142	109 ± 38				
Fertilizer 2						
Fence	685 ± 204	164 ± 28	611 ± 282	44 ± 15	0	0
Fence + food						

Small trees are >10 cm height and <10 cm dbh. Large trees are >10 cm dbh. Estimates are stems per hectare (± 1 SE).

7.1.1 *Tree Abundance on the Study Area*

Tree abundance was estimated on each of the control and treatment areas by T-square sampling (Krebs 1999). Stems were estimated separately for small and large trees, with 10 cm diameter at breast height (dbh) as the point of separation. Small trees shorter than 10 cm were not measured in these samples. Because the vegetation of the valley is so patchy (see CD-ROM frame 12), we attempted to cover the entire area of each grid to provide an average value for tree density.

Table 7.1 gives the estimates of tree abundance for five of the three control areas and the six experimental areas, and table 7.2 gives the overall habitat classification for each of these nine areas from the airphoto (see 2.3, table 2.2). The tree component of the vegetation differs substantially among these nine areas. The most dense closed spruce forest occurs on control 2, control 3, food 2, fertilizer 2, and fence; the most open forest types occur on fertilizer 1, food + fence, food 1, and control 1.

7.1.2 *Tree Growth*

We estimated tree growth only for white spruce. Spruce twigs grow from the distal end, and each year of growth is marked by a growth ring that circles the stem. The most recent year of growth may have lateral buds, but these buds do not grow into branches until the next year. The length of each year's growth provides a measure of the tree's vigor. We can measure growth in branch length for the last 3–4 years and thus quantify year-to-year variation in growth rates as well as fertilizer effects. We used relative growth within each tree to control somewhat for variation among individual trees. We adopted 1986 as the base year and expressed all growth as relative to growth in that year; for example,

$$\text{Relative growth for 1990} = \frac{\text{Length of branch growth in 1990}}{\text{Length of same branch growth for 1986}}$$

In 1989 two observers measured 120 branches in duplicate to calculate repeatability of the measurements on growth. Repeatability was 0.98, so there seemed to be no need to mea-

Table 7.2 Percentage of vegetation classes of the nine major study sites in the Kluane study area.

Vegetation Type	Control 1	Control 2	Control 3	Food 1	Food 2	Fertilizer 1	Fertilizer 2	Fence	Fence + Food
Closed spruce (50–100% cover)	18.87	61.45	55.28	7.26	48.03	11.73	46.34	32.91	0.57
Open spruce (25–50% cover)	34.37	18.43	15.66	54.91	28.07	44.26	20.59	28.81	30.99
Poplar–aspen	2.16	3.09	0.00	7.97	0.29	5.77	0.25	1.74	5.88
Willow shrub	21.00	11.05	18.28	27.27	11.66	32.68	27.56	26.08	51.09
Grass-open	22.96	5.98	10.01	2.59	11.89	5.56	5.26	10.45	11.47
Water	0.64	0.00	0.77	0.00	0.05	0.00	0.00	0.00	0.00
Totals	100	100	100	100	100	100	100	100	100

Estimates were obtained from airphoto analysis as described in Chapter 2. Each study site is a 1-km^2 block centered on the snowshoe hare study grid. Percentages are given for the five main habitat types and water.

Table 7.3 White spruce branch extension growth on two control areas at Kluane, 1986–1995.

	Control 1		*Control 2*	
Year	Mean Growth	SE	Mean Growth	SE
1987	0.936	0.030	0.882	0.030
1988	0.949	0.036	0.823	0.027
1989	1.069	0.048	0.881	0.031
1990	1.080	0.063	0.900	0.042
1991	1.030	0.056	0.881	0.045
1992	0.973	0.058	0.876	0.045
1993	0.903	0.037	1.190	0.128
1994	0.870	0.043	1.285	0.143
1995	0.658	0.045	1.058	0.090

Growth rates are expressed as ratios relative to 1986 = 1.00, the year the study began. We measured 75 trees on each area in each year.

sure everything twice. We also sampled three branches on each tree to measure variation within one tree as well as variation between different trees. These two sources of variation were nearly equal, and the optimal sampling design was thus to measure only one branch per tree.

Table 7.3 gives the estimated white spruce growth ratios for two control areas for 1987–1995. Spruce growth varied markedly from year to year; 1987 and 1988 were years of relatively poor growth, and 1990 and 1991 were years of good growth. During the last 2 years of the study, some growth rates deteriorated because of spruce bark beetle attacks (see 12.3).

7.1.3 *White Spruce Cone and Seed Production*

Spruce trees tend to produce some cones each year, but there are certain years, called *mast years,* in which all of the trees produce huge numbers of seeds. This occurs at irregular intervals but over large geographic areas. Spruce seeds are an important food source for red squirrels, chipmunks, mice, voles, and passerine birds. We sampled seed production by spruce in two ways: by counting cones and by collecting seeds in buckets. We used both methods because red squirrels tend to harvest many cones before they open each year. As a consequence, counting cones on the trees in August tells us how much is produced by the trees, and counting seeds falling to the ground over the next 8 months tells us how much is available to other small mammals and birds after the red squirrels have finished harvesting.

We collected seeds in buckets 28 cm in diameter, placed at 86 hare-trapping stations on control 1, food 1, fertilizer 1, fence, and fence + food grids. The buckets were set out in late August and collected the following May. The buckets were covered with wire to prevent animal access over winter. Only intact spruce seeds were counted.

We estimated cone production in the first week of August of each year on all the seed grids listed above as well as on control 2 and fertilizer 2 grids. On each grid, 86 spruce

Table 7.4 White spruce cone crop index and seed production on control areas, Kluane Lake, 1986–1995.

	Cone Index per Tree			*Number of Seeds per m²*		
Year	Mean Count	Lower 95% CL	Upper 95% CL	Mean Count	Lower 95% CL	Upper 95% CL
1986	77	70	85	194[a]	80[a]	376[a]
1987	39	36	43	68[a]	33[a]	145[a]
1988	57	50	63	31	16	68
1989	0	0	0	0	0	0
1990	35	28	42	34	5	150
1991	2	1	3	2	0	3
1992	72	62	83	129	67	223
1993	164	146	183	675	416	1090
1994	2	1	3	20	7	36
1995	102	90	115	460	256	696

Control 1 and Control 2 were counted for cones, but only Control 1 was used for seed production estimates. Year is the year of seed production; $N = 86$ for all counts.

[a] Estimated from regression of seed counts on cone counts from 1988 to 1995.

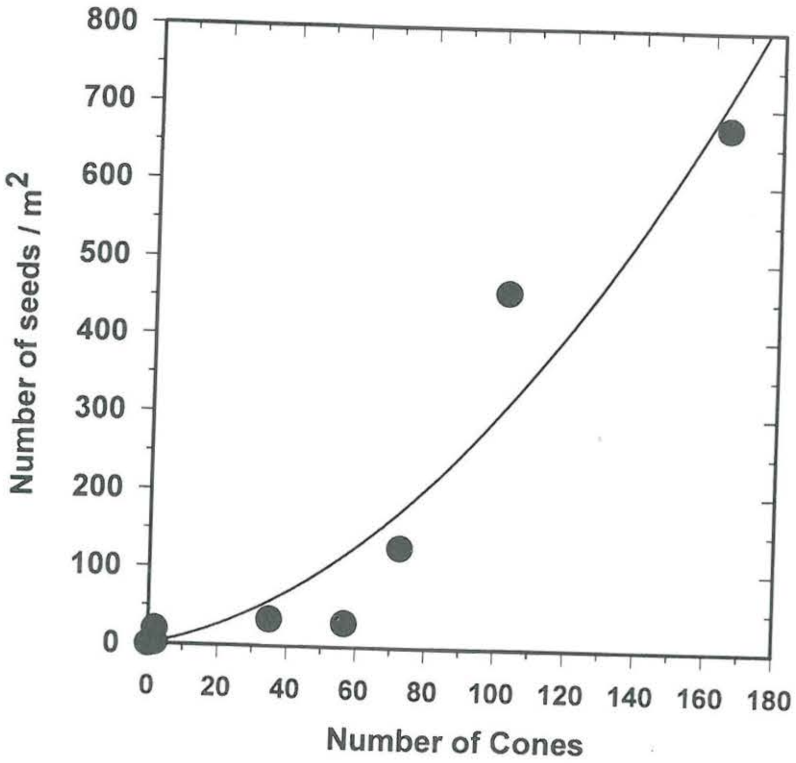

Figure 7.1 Relationship between cone counts for white spruce and seed production per square meter for 8 years, 1988–1995, on control 1 grid. Cones were counted in August while still maturing, and seeds were counted as an accumulation falling to the ground over the following winter months. Squirrels harvest cones before they release seeds, and for low cone crop years the seeds that fall to the ground are less than one would predict from cone production counts. Regression line is a second-degree polynomial, $y = 0.9210\,x + 0.02080\,x^2$ with $R^2 = .93$.

trees that were 5 cm dbh or larger were counted, and the same trees were recounted each year. The number of new cones in the top 3 m of the tree was counted using binoculars. If the total number of cones exceeded 100, we took a photograph of the top of the tree using a telephoto lens and, using a magnifying glass, counted cones on the photographs.

Table 7.4 gives the white spruce cone counts and the seed production for control areas from 1986 to 1995. High cone counts occurred in 1986, 1993, and 1995. Complete cone failure occurred in 1989, 1991, and 1994. Figure 7.1 shows the relationship between cone counts and seed production for white spruce on the control areas. Seed production from small cone crop years is less than one would predict from the regression. This could result from red squirrels harvesting a high fraction of the cones in low cone crop years or could result from measurement error.

7.2 Vegetation Mapping

The vegetation can be divided into three ecological zones based on elevation (Douglas 1980): montane valley bottom forests (760–1080 m), subalpine forests (1080–1370 m), and alpine tundra (above 1370 m). The two lower zones are complex mosaics of forests of white spruce, stands of aspen and balsam poplar, and shrub-dominated areas of willow (*Salix* spp.) and dwarf birch (*Betula glandulosa* Michx.). The subalpine vegetation, consisting of open-canopy spruce mixed with tall willow shrubs, grades into the low shrub–dwarf plant communities of the alpine.

To assess the processes leading to the heterogeneous vegetation of the valley, we mapped the vegetation and developed a fire history of the area. Based on three bands of LANDSAT image, we created both supervised and unsupervised classification maps of the vegetation (see Dale 1990). Based on this classification, closed and open spruce account for 32% and 30% of the area, with shrubland covering another 26% and *Populus*-dominated stands only 3%. A revised version of a supervised classification (Kenney and Krebs unpublished data) was imported into the SPANS Geographic Information System, (GIS) which was then used to make comparisons of individual animal's home ranges and other areal characteristics. A digital elevation model of the valley was also produced for use in the GIS environment. Useful as these images were, they did not provide sufficient detail to serve as a precise map of vegetation types, and their resolution was not appropriate to serve as a base for a fire history study. We decided, therefore, to use airphoto interpretation for these purposes. The valley was flown for airphotos in July 1992 and the 317 1:10,000 black-and-white photos provide complete coverage of the study area (see 2.3, table 2.2).

7.2.1 Fire History of the Study Area

In addition to providing the information for a 1:32,000 vegetation map (Hucal and Dale 1993), the airphotos were used as the basis for the valley's fire history. To begin the fire history analysis, a 1:50,000 universal transverse mercator (UTM) grid was set out on acetate airphoto overlays using a transfer scope. Based on interpretation of canopy-height differences on these airphotos, distinct stand margins were identified and sample sites chosen.

The field sampling for the fire history took place during the summers of 1994 and 1995. Along distinct fire margins, fire-scarred trees were found and their locations recorded on the airphotos. At these locations, we collected the following: (1) disks from fire-scarred trees, (b) two or more increment cores (at 30 cm height) from large canopy trees in the post-fire regenerating stand and in the adjacent unburned stand, (3) height and diameter at breast height from all trees cored or cut, (4) physical site description, and (5) general stand information. The cores from unburned trees were collected to provide an estimate of the regeneration lag following fire. Obtaining complete tree cores in stands greater than 200 years old was difficult because of heart rot.

We dated all fire-scarred tree disks (362) and tree increment cores (more than 1500) using the techniques of Yamaguchi (1991) and McBride (1983). Relative ring-width patterns were noted, and a tree marker-year chronology was developed to cross-date samples using the method of Yamaguchi (1991). This method allows the detection of missing and false rings and creates an accurate tree chronology.

We reconstructed individual fires by transferring fire scar and tree increment core dates to acetate overlays using the 1:32,000 scale vegetation map as a base layer. Individual fires were reconstructed back to 1800; the reconstruction of earlier fires is inaccurate due to a shortage of fire scar evidence and spatial resolution. In the absence of fire scar evidence for stands originating before 1800, the time since fire was estimated as 25 years more than the age of the oldest tree found. The increment of 25 years was based on the average post-fire regeneration lag we determined from regenerating stands, and it agrees well with the value reported by Hawkes (1983) for the neighboring Kluane National Park.

Acetate fire boundary overlays were digitized in the "v.digit" module of the GRASS 4.1 (U.S. Army Corps of Engineers 1993) geographic information system. A separate data layer was constructed for each fire year back to 1800, and the annual area burned was calculated with the GIS. We then converted these vector maps to raster maps and combined with the "r.patch" command to produce a time-since-fire map for the period 1800–present. In this map, the most recent fires have definite boundaries and overlie earlier events. Areas of overlap can then be calculated and displayed to produce a fire frequency map for this time period. For areas originating before 1800, with no fire scar evidence and unknown fire boundaries, a single stand origin data layer was digitized and patched with the area burned from 1800–present. This combination of stand origin dating methods provided a complete time-since-fire map for all areas below treeline.

Fire history statistics for 1800–1994 are summarized in table 7.5 (CD-ROM frame 50). There has not been a wildfire in the study area since 1956. The last fire event to burn more than 200 ha occurred in 1929 near Kloo Lake, and this was the only fire with written documentation. Glover (1929), on a routine Royal Canadian Mounted Police patrol, noted "A forest fire was burning in the vicinity of Kloo Lake and considerable timber had fallen across the government road." Figure 7.2 displays the location of all areas burned since 1800.

Table 7.5 gives the area burned annually in the valley from 1800 to 1994. Some of the larger fire years were synchronous with large fire events (late 1840s and 1880s) across western North America, as indicated by fire history studies performed at Jasper National Park (Tande 1979), the Boundary Waters Canoe Area (Heinselman 1973), and the Bitterroot National Forest (Arno 1976). These fire years may be characterized by particular weather conditions (Johnson and Wowchuck 1993). Some of the large fire years in the Shakwak Trench, however, are not synchronous with the rest of the continent, indicating that small-scale, localized weather systems may also be important. Similarly, large fire years in the Kluane National Park are not all synchronous with those in the Shakwak Trench (Hawkes 1983). The extreme topography of the Kluane region may be responsible for highly variable conditions over small distances.

Fire sizes are highly variable, with a few large fires being responsible for most of the area burned. This fire regime is characteristic of conditions throughout the boreal forest of North America (Johnson 1992). The largest individual fire event during the past 200 years affected 12.46% of the forested area within the study site. Large areas of very old, contiguous subalpine and upper-montane forest along the south study boundary may have arisen from a single fire that affected more than 6000 ha. Generally, individual fires appear to be smaller than in other areas of the boreal forest with more subdued topography. Individual fire events larger than 10000 ha are relatively common in other parts of the boreal forest.

Individual burn patterns are complex and variable. Some recent burns with easily detectable margins display classic elliptical shapes (Anderson 1983, Alexander 1985). Other burns have irregular, complex margins and do not display patterns associated with strong

Table 7.5 Fire history of the 350-km² main study area at Kluane from 1800 to 1994 (fires are listed in reverse chronological order).

Year of Fire	Area Burned (km²)	Percent of Total Study Area	Interval between Fires	No. of Spatially Discrete Fires
1956	<0.01	<0.01	39	1
1953	0.01	<0.01	3	1
1951	0.01	<0.01	2	1
1943	0.04	0.01	8	3
1939	0.11	0.03	4	1
1937	0.16	0.05	2	1
1936	1.22	0.35	1	3
1934	1.10	0.31	2	3
1932	0.51	0.14	2	2
1930	0.04	0.01	2	1
1929	7.38	2.09	1	2
1928	1.47	0.42	1	2
1925	0.07	0.02	3	1
1924	2.60	0.74	1	5
1923	0.77	0.22	1	2
1921	4.21	1.19	2	2
1920	9.03	2.56	1	7
1919	3.72	1.05	1	1
1918	0.23	0.07	1	1
1916	0.19	0.05	2	2
1915	1.18	0.33	1	2
1914	0.16	0.05	2	1
1913	1.56	0.44	1	2
1912	0.10	0.03	1	1
1908	2.66	0.75	4	1
1907	0.57	0.16	1	2
1906	8.46	2.40	1	2
1904	0.10	0.03	2	1
1903	1.80	0.51	1	2
1902	0.01	<0.01	1	1
1898	0.15	0.04	4	2
1893	0.61	0.17	5	3
1892	8.64	2.45	1	2
1891	0.43	0.12	1	1
1888	10.74	3.04	3	3
1885	2.75	0.78	3	3
1883	1.06	0.30	2	1
1881	0.51	0.14	2	2
1878	32.13	9.10	3	2
1877	14.18	4.02	1	3
1875	3.17	0.90	2	2
1872	9.92	2.81	3	4
1871	2.36	0.67	1	1
1865	21.09	5.97	6	1
1861	0.03	0.01	4	1
1858	2.57	0.73	3	1
1855	0.09	0.02	3	1
1853	0.04	0.01	2	1

(continued)

Table 7.5 *(Continued)*

Year of Fire	Area Burned (km²)	Percent of Total Study Area	Interval between Fires	No. of Spatially Discrete Fires
1849	3.62	1.03	4	1
1848	0.05	0.02	1	1
1847	15.98	4.53	2	2
1845	43.97	12.46	1	1
1844	6.22	1.76	1	1
1836	23.10	6.55	8	2
1822	3.76	1.07	14	1
1820	2.97	0.84	2	1
1818	0.27	0.08	2	1
1815	0.55	0.16	4	1
1814	0.48	0.14	1	1
1806	14.07	3.99	8	1
Totals	274.99	77.92	—	105

wind-driven fires. Irregularities in burn patterns appear to be partly associated with terrain complexity. The Jenny Lake area has a network of eskers and associated glacial features that may have dramatically influenced burn patterns in this area. In the Jarvis River area, the orientation of some fires is perpendicular to the main valley orientation and may be associated with strong winds funneling out of the Jarvis River valley.

Fire behavior in our valley cannot be fully reconstructed due to the long time periods involved, but the following observations can be made. Fires are generally stand replacing, with the exception of meadow areas, where individual trees were found to have survived several low-intensity events with little direct evidence of the fire on the ground. One other interesting feature was the existence of *permanent residuals* or unburned patches within the fire margins. Many of these residuals were found in the Sulphur Lake-Sulphur Creek area, which is quite wet. Many residuals have survived several fires as indicated by differently aged fire scars along their margins. This evidence suggests that many small fires have followed the same boundaries and were contained by the same topographic features.

There has been extensive overlap of fires since 1800. Based on forest age-class information from the Shakwak Trench, the total area burned since 1800 is 16874 ha, or 47.80% of the forested area. Based on individual fire reconstruction the total area burned is much greater—27,499 ha or 77.90% of the forested area—because this calculation takes into account the extensive overlap. This difference is due primarily to the spatial distribution of fires on the landscape: some areas burn frequently, while others burn rarely. More recent fires thus mask regeneration from older events. Large fires occurred in the 1840s, 1860s, and 1870s but are responsible for little of the current forest age-class composition because most of these areas have reburned since.

The fire regime appears to have changed over the past 200 years from large, infrequent events during the 1800s to small, relatively frequent fires during the early 1900s (CD-ROM frame 49). It is possible that smaller fires occurred during the 1800s but that more recent fires have erased the evidence of these events. Fires of the magnitude experienced in the 1800s did not occur in the 1900s. This change in fire frequency and size around 1900 cannot be directly attributed to human intervention: active fire suppression did not begin until the 1950s.

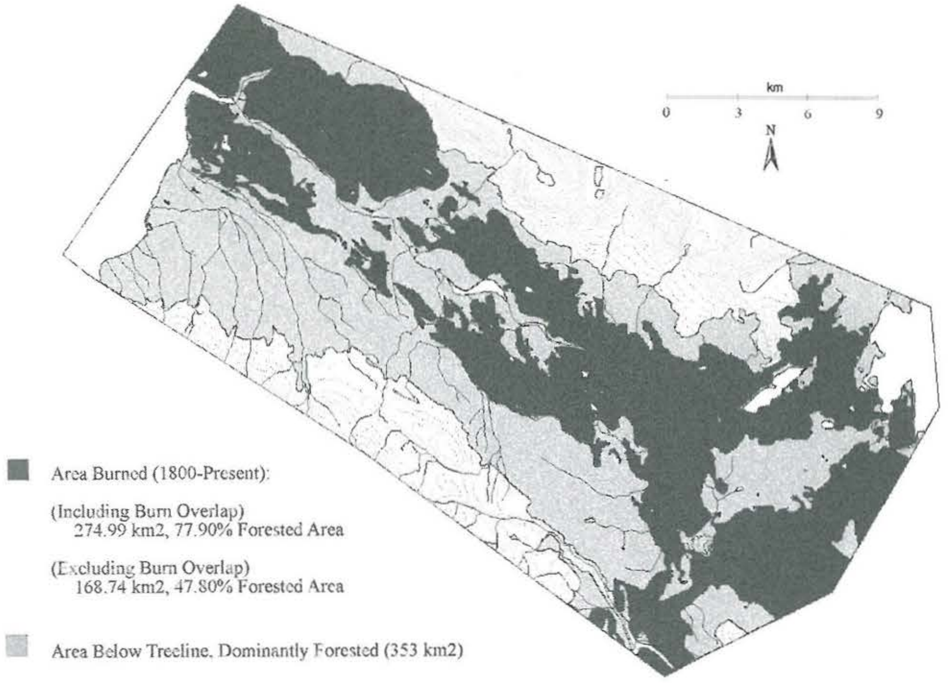

Figure 7.2 Location of all areas in the main study area that were burned since 1800 (after Francis 1996).

The building of the Alaska Highway in 1942–1943 appears to have had little effect on the fire regime. Small fires adjacent to the Old Alaska Highway (1–4 ha in size) were dated to 1943 and 1953, suggesting some human association. These fire events and a small fire (1–2 ha in size) on the shore of Sulphur Lake in 1956 were the most recent fires detected. Our evidence does not suggest that human land-use patterns directly caused the shift in fire regime between the 1800s and 1900s. Instead, dendroclimatic data, glacial geomorphological evidence, and older burn patterns suggest a natural change in the fire regime.

Unlike the recent fire history, the reconstruction of older individual fires is nearly impossible due to the loss of evidence over time. Only seven fire scars were found to date pre-1800 events accurately, and, of these, five date a large 1767 fire that probably burned about 4000 ha in the valley bottom. All forest stands sampled displayed some evidence of fire and are therefore assumed to be of fire origin.

Figure 7.3 displays the current forest age-class distribution of the entire study site, grouped into 20-year age classes. Two age classes, the 1870s and 1650s, dominate the distribution of forest ages and give a bimodal appearance to the graph. Nearly 40% of the forested area is made up of these two age classes, possibly indicating that large areas

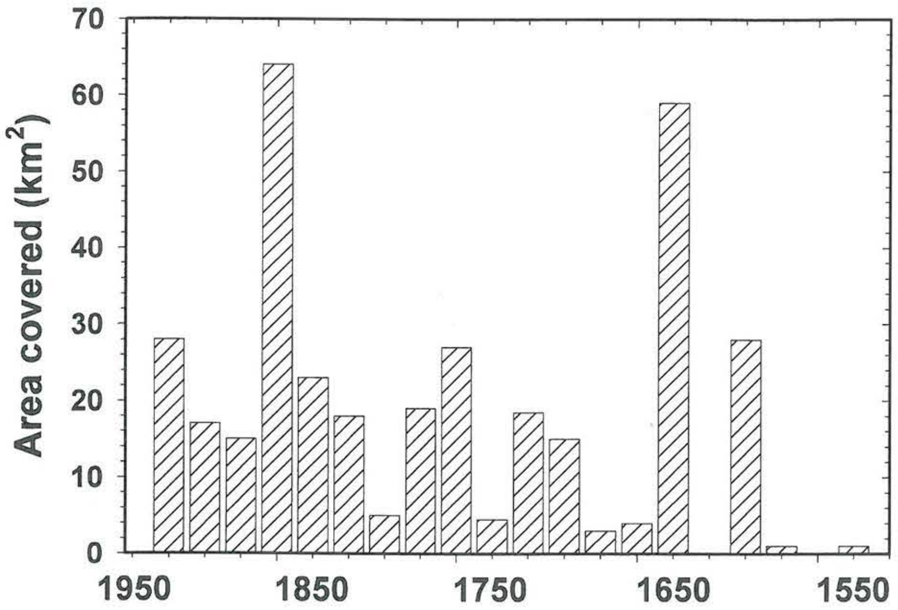

Figure 7.3 The current forest age-class distribution of the entire study site, grouped into 20-year age-classes (after Francis 1996).

burned during these periods. Twenty-seven percent (9508 ha) of the forested area has been fire-free for more than 300 years.

The map in figure 7.4 (CD-ROM frame 49) shows the geographic distribution of 100-year forest age-class elements throughout the study area. The entire south side of the valley is dominated by forests more than 300 years old, while the valley bottom and north boundary are dominated by younger age classes and a more heterogeneous pattern of stand ages. The spatial difference in age-class distribution between the north and south sides of the valley gives rise to the bimodal appearance of figure 7.3, where the south boundary is dominated by old forests and the valley bottom is dominated by younger forests.

7.2.2 *Other Forms of Disturbance*

In addition to wildfire, flooding, landslides, wind throw, soil movements, people, and insects are all disturbance agents in this forested landscape. Each operates at different scales and has different effects on the forest. During the last 200 years, these agents appear to have played relatively minor roles in shaping the current vegetation mosaic within the study area.

Flooding and landslide hazards near Kluane Lake have been reviewed by Clague (1979, 1981). High gradient streams flowing from the mountains across alluvial fans and aprons at the edge of the Shakwak Trench can cause localized flooding. The only area in the valley that has been largely affected by these events is near the southeast shore of Kluane Lake. Silver Creek and associated streams have caused washouts on the Alaska Highway many times in the past, which have also disturbed the surrounding forests. Also, the

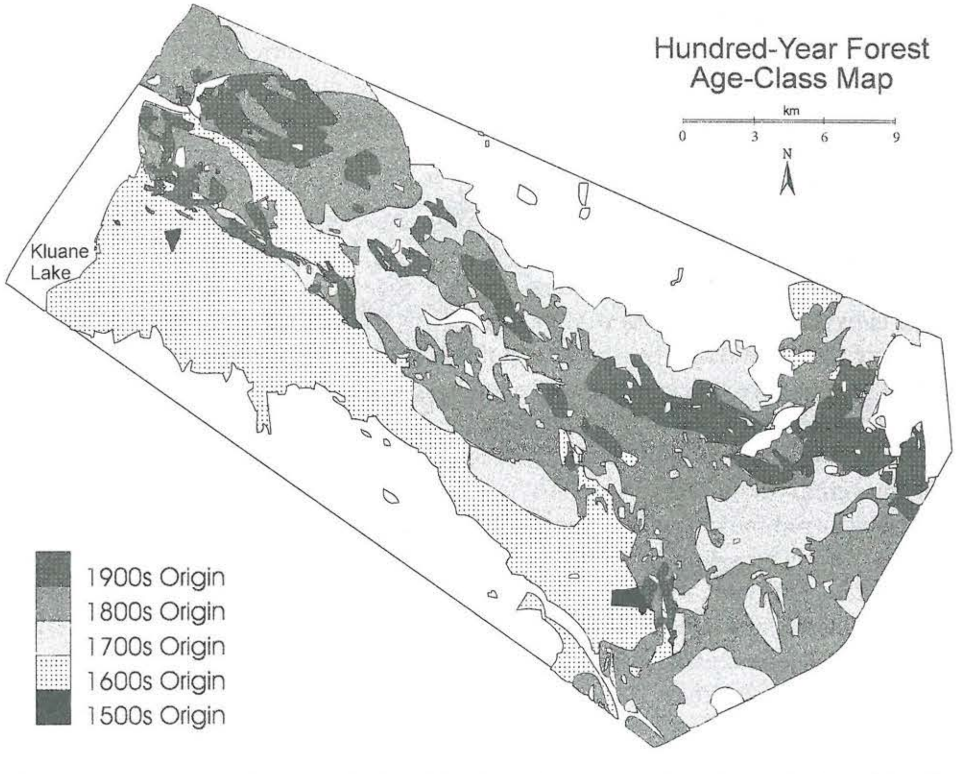

Figure 7.4 The geographic distribution of 100-year forest age-class elements throughout the study area (after Francis 1996).

entire shoreline area on which the KRS is situated is underlain by alluvial deposits and dissected by numerous abandoned river channels. This area has been stabilized for a long time; the stand origin for this alluvial fan was dated to approximately 1650.

Large patches of wind throw damage were not found in the study area. Only localized patches along stand margins and exposed ridges displayed effects of this kind of disturbance, which in some forests can be extensive, if infrequent (Hemstrom and Franklin 1982, Baker and Veblen 1990). Associated with wind throw are low-gradient soil movements. These were detected in many locations throughout the valley but primarily along slopes of the Kluane hills and the Kluane range. It appears that through some mechanism of permafrost melt or simple colluvial processes, soil cohesion is lost and downhill creep begins. Waterlogging may also be a factor. The net effect is that shallow root systems of spruce become displaced and trees become more disposed to wind throw.

Human impacts on the valley have historically been small. Besides the few transportation corridors which run through the valley bottom and some minor fuel wood harvesting and lumbering around Jenny and Kloo Lakes, the study area remains little altered by direct human impact.

From 1994 to 1997 much of the valley and southern portions of neighboring Kluane National Park Reserve experienced a major spruce beetle (*Dendroctonus rufipennis*

Kirby) outbreak, affecting an area orders of magnitude larger than any single fire event in recent history. Although an event similar to this may have occurred in the past, little evidence for a major historical forest insect outbreak of this magnitude was detected. Large numbers of dead, unburned boles are not present as would remain after such major canopy mortality. Hawkes (1983) provides a picture of a spruce stand thinned by spruce beetles in the 1940s when only some of the trees in the stand were killed.

Although spruce beetle outbreaks and forest fires may operate on similar temporal and spatial scales, they can have very different ecological consequences. As a forest disturbance agent, spruce beetles differ from wildfire in four major aspects: (1) spruce beetles select individual trees, whereas wildfire is more nonselective, (2) spruce beetles create a more heterogeneous stand age-structure through host tree selection, (3) spruce beetle mortality results in a greater abundance of large-diameter, coarse woody material carry-over than fire, which creates structurally complex forest stands, and (4) spruce beetles can cause massive canopy mortality without removing forest floor duff, an important factor in spruce seedling germination.

The history of interaction between spruce beetles and fire can only be speculated, but large, infrequent fires or large, infrequent spruce beetle outbreaks will both result in rapid shifts from old to young forests. Spruce beetles and fires may therefore operate at similar spatial and temporal scales in this system. Recently burned areas less than 100 years old are generally not susceptible to spruce beetle damage, because the trees are still young and vigorous (Baker and Veblen 1990, Veblen et al. 1991). In this sense, spruce beetle damage and recently burned areas display a spatially non-overlapping distribution. This is visible in the study area, with stands of damaged and healthy green conifers forming a patchwork on the landscape. We do not know whether this spatially non-overlapping pattern of disturbance perpetuates itself through time. There is no direct evidence that beetle damage in spruce forests leads to large conflagrations.

7.3 Succession in the Boreal Forest

The Kluane region is a harsh growing environment, and recovery from disturbance events is a lengthy process. Post-fire regeneration lag time, particularly for spruce, can be very long and highly variable. Drier sites are able to regenerate relatively quickly and densely in less than 25 years, but low-lying, hydric sites can take 50–75 years to recover even sparsely from fire and thus remain shrub dominated for most of this time. Possible reasons for this include decreased transpiration rates due to vegetation removal, which results in an elevated water table and melting permafrost caused by forest duff consumption, again resulting in periodically saturated soils. Depending on the intensity of the fire, *Populus* and *Salix* may resprout from surviving below-ground parts immediately after fire (Hawkes 1983, Rowe 1983). Sites dominated by these deciduous species may be undergoing a slow succession toward spruce forest.

White spruce establishes only from seed and not by vegetative means. Seed production begins when the trees are 40 years or more in age (Rowe 1955), but cone and seed production is highly variable between years and locations. There may be 2–6 years between years of good seed production or even 10–12 years in some locations (Zasada et al. 1992). The timing of fires relative to good seed years is important for reestablishment, particularly because white spruce seeds have limited longevity and dormancy (Putman and Zasada 1986). Seed availability may be an important limiting factor that contributes to the long lags observed. It is often suggested that exposed mineral soil is necessary for seedling establishment, but there is evidence that downed woody material such as rotting logs will also support seedlings (Rowe 1955, Putman and Zasada 1986).

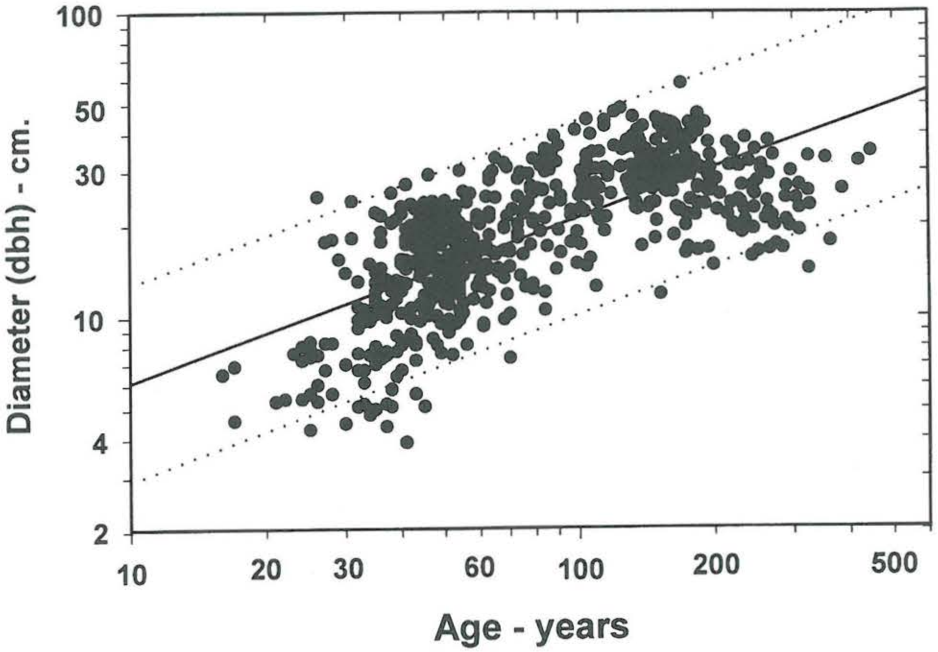

Figure 7.5 Relationship between age (years) and diameter at breast height (dbh, cm) for white spruce from the Kluane study area ($N = 624$). The log-log regression is log (dbh) = 0.5382 log (age) + 0.2480 ($r^2 = .49$). The 95% confidence limits for an individual predicted value of diameter at breast height are given by the dotted lines.

One factor that contributes to the variability of tree size as a function of age and to the generally slow establishment of spruce is the impact of snowshoe hares. Hares normally avoid eating small spruce trees, preferring willow and birch, probably because of the higher concentrations of the antifeedant chemical camphor in the juvenile trees compared to mature white spruce (Sinclair et al. 1988). At high hare densities, however, the apical shoot of the spruce is frequently eaten (Sinclair et al. 1993). In one sample area, of the 63 small spruce trees in a 20 m × 30 m plot, 55 trees had been clipped at least once and 10 twice or more. It is not clear what the overall effect of this clipping is on the trees' ultimate size and rate of growth, but it may be several hare cycles (decades) before a tree is tall enough to escape this periodic herbivory.

To determine the variability in white spruce growth rates, we compared age and diameter at breast height of 543 spruce trees measured throughout the study area. Because of differences among sites and genetic differences among trees, the linear relationship between the two is highly variable. Figure 7.5 shows a log-log plot of age and diameter at

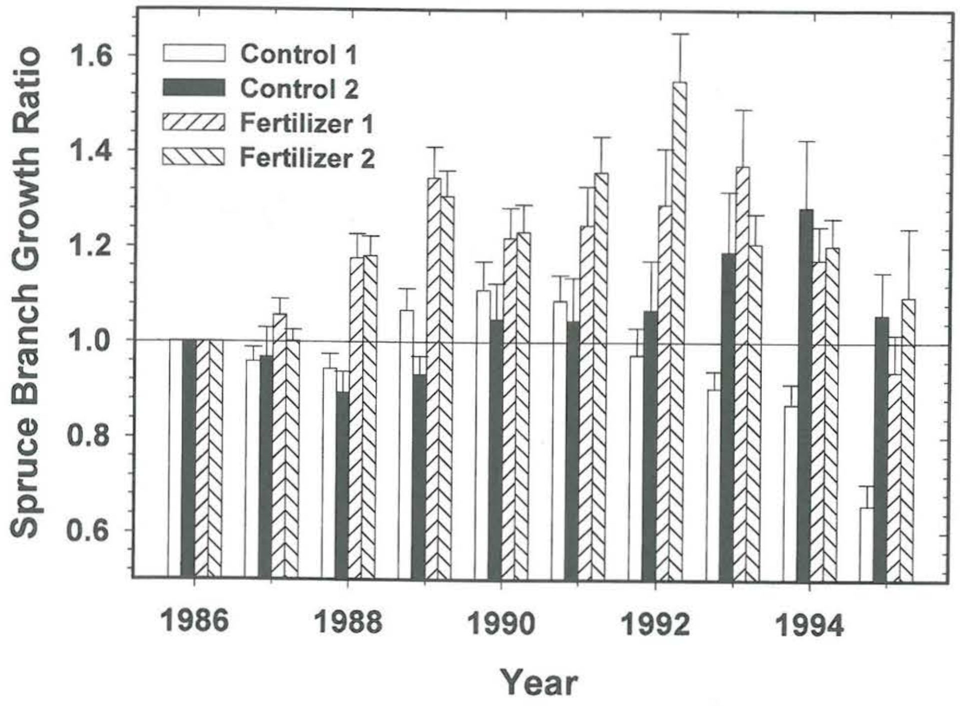

Figure 7.6 White spruce lateral branch extension growth on fertilized and control areas, 1986–1995. Extension growth is expressed as a ratio of the year's growth to the standard year of 1986 (+ 1 SE). Two control grids and the two fertilized grids were measured (*n* = 50 trees in each area).

breast height for white spruce in the Kluane area, which improves the linear regression fit over that of the untransformed data. This regression gives an average 19.5 cm dbh at 100 years, which is similar to the values found by Jozsa et al. (1984) for white spruce at Swan Hills (55° N) and Fort Vermilion (58° N) in Alberta. This indicates that, although the biological processes do occur slowly in our valley, they are comparable to those at other sites in the northern boreal forest.

7.4 Fertilizer Effects on Trees

Because one of the experimental treatments was the addition of fertilizer, we wanted to determine its effects on the growth and reproduction of white spruce. Seventy-five trees were studied in open spruce vegetation on control and fertilizer grids by measuring the annual growth of a single branch on each tree each year. The growth was compared, in each case, to the growth of the same branch in 1986 before the fertilizer was added. We also looked for fertilizer effects on reproductive effort by counting new cones each year.

The addition of fertilizer had a clear effect on the vegetative growth of the spruce trees. After the fertilizer treatment began in 1987, the branches grew 15–50% more than in the prefertilizer year. Figure 7.6 illustrates the strength of this response. On average, from 1987 to 1995 fertilized trees grew 22% per year more than control trees.

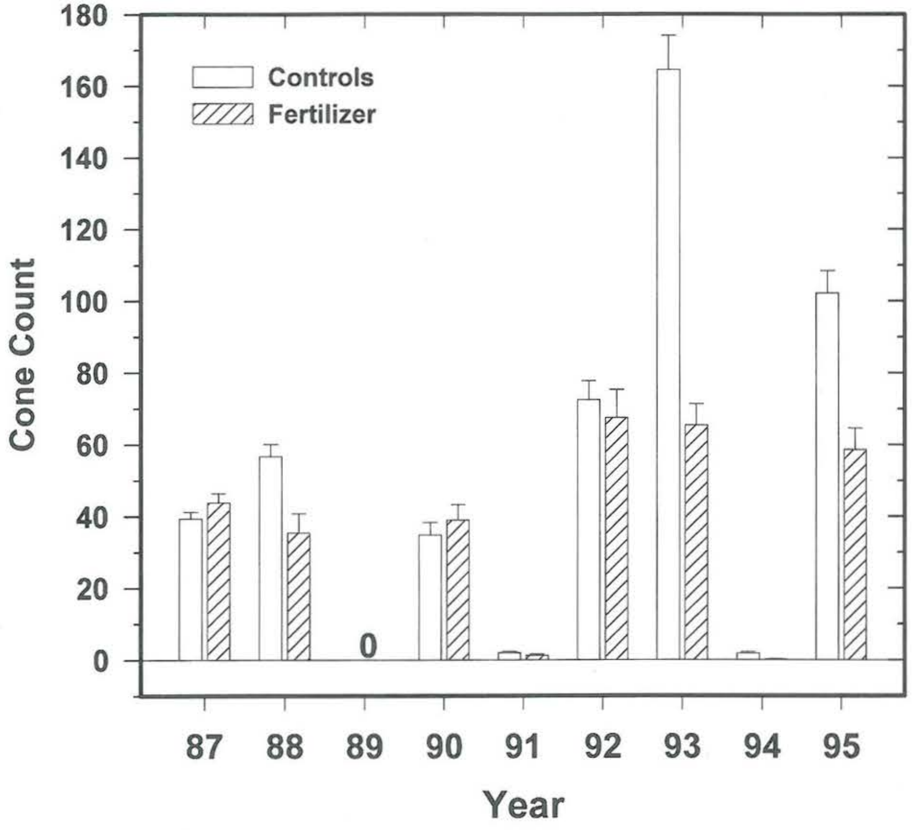

Figure 7.7 Average white spruce cone counts for 172 trees from control areas and 172 trees from fertilized areas (+ 1 SE). Counts were done in August of each year. Cone counts are an index of cone production and not an absolute estimate. There were no cones produced in 1989.

Although fertilizer increased vegetative growth, there was no significant effect on cone production (figure 7.7). Indeed, if there was any trend, it was for control trees to have more cones than fertilized trees, although these differences were not statistically significant. Spruce trees normally exhibit mast years, with little or no seed production between mast years. The addition of fertilizer did not seem to change the timing of masting, since fertilized trees produced many cones in the same years as control trees and no cones in the low years of 1989, 1991, and 1994. In spite of the similar cone production of spruce on control and fertilized areas, seed production was significantly higher on the fertilized area (figure 7.8). Over all 8 years, seed production was 44% higher on the fertilized areas. If the cone failure years of 1989, 1991, and 1994 are excluded from these data, the increase in seed production due to fertilization is 61%. The increased seed production on fertilized areas could have two explanations. First, red squirrels were less abundant on fertilized ar-

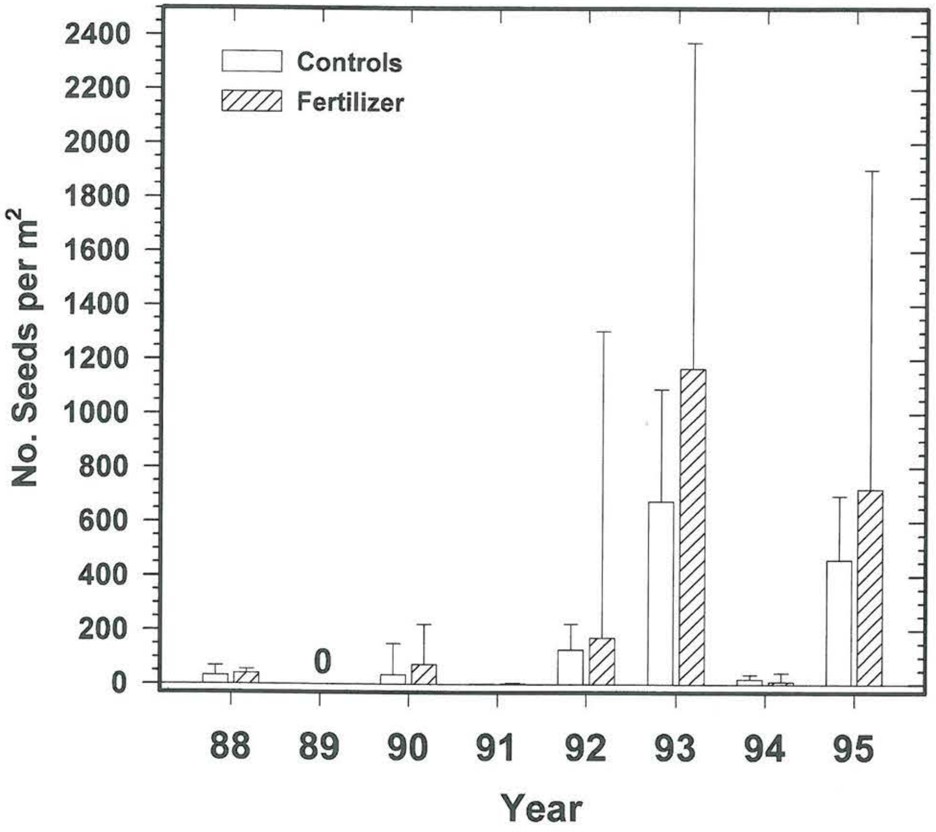

Figure 7.8 Seed production from white spruce, measured by 86 seed buckets on control 1 and fertilizer 1 grids, 1988–1995. Seeds falling to the ground were collected in the buckets over the winter and were counted the next spring. Year is the year of seed production. Error bars show 95% upper confidence limits.

eas, and thus fewer cones were harvested before they could shed seeds in the autumn. Second, cones on fertilized trees contained more seeds, either because of a higher fraction of fertile seeds in each cone or, alternatively, because they produced larger cones with more seeds. Unfortunately, we have no measurements of the viability of white spruce seeds or the number of viable seeds per cone for either controls or fertilized trees.

Fertilization could also affect the palatability of trees to herbivores. Small white spruce trees contain camphor, which acts as an antifeedant against snowshoe hares (Sinclair et al. 1988). The addition of fertilizer and the exclusion of herbivores both decreased the amount of camphor in the distal branches of small spruce (figure 7.9). The dynamics and importance of these effects are yet to be worked out. Aspen and balsam poplar are also protected to varying degrees by antifeedant chemicals that are produced in response to browsing by hares (Bryant 1981, Jogia et al. 1989). The chemistry of these plants may also be affected by the addition of fertilizer, but because of their rarity in the Kluane forests, we did not examine either *Populus* species for fertilizer effects.

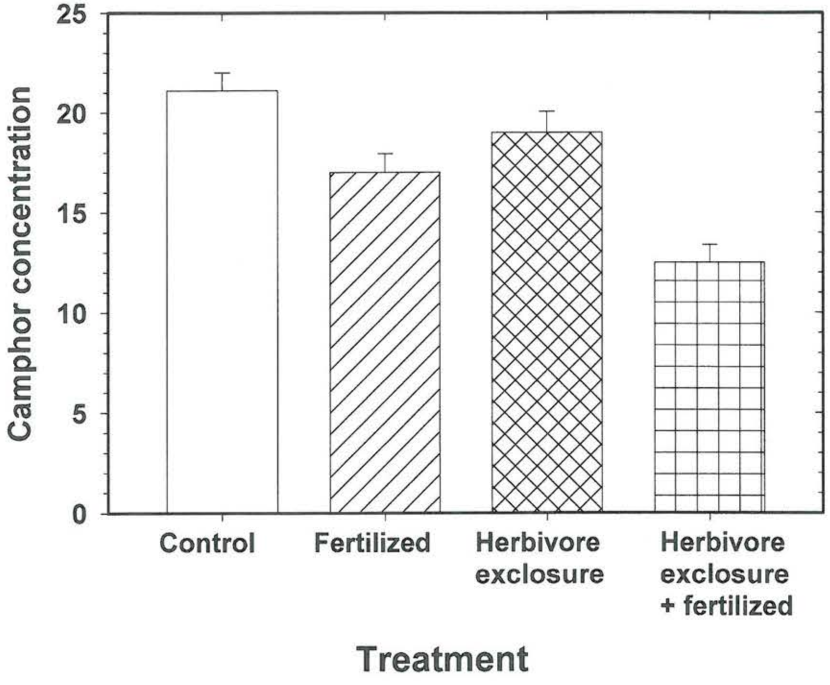

Figure 7.9 Camphor concentration in the distal branches of small white spruce trees in four treatment areas at Kluane (+1 SE). Camphor deters snowshoe hares from feeding on small spruce trees. Herbivore exclosures excluded snowshoe hares and moose after 1988. Camphor concentration is micrograms per gram dry mass. Measurements were made in spring 1995 (after G. Sharam, unpublished).

7.5 Summary

The boreal forest of the Shakwak Trench is dominated by white spruce, with considerably fewer trembling aspen and balsam poplar. The density of trees varies greatly in the nine main study areas. Much of the spatial variability of the tree vegetation is due to fire. Fire size is highly variable, with most burned area resulting from a few large fires in the 1840s, 1870s, and 1880s. Many of these large fires are synchronous with large fire events across western North America, indicating the importance of large-scale, characteristic weather systems coordinating extreme fire weather. The fire regime has changed over the past 200 years from large, infrequent fires to small, relatively frequent fires. There has not been a major fire in the Shakwak Trench since 1929. Human impact on this changing fire regime appears to be small.

Other disturbances have had little impact on the forests of the Kluane region. A spruce bark beetle outbreak began in the region in 1994 near the end of this study. Little evidence was found for a spruce beetle outbreak of the current magnitude having occurred in the last 100 years.

Vegetation recovery from fire and disturbance events is a lengthy and highly variable process. Some of the trees (*Populus*) can establish by surviving below-ground parts, but the dominant tree, white spruce, establishes only from seed. Reestablishment of white spruce may take 75 years or more in some habitats. Although several factors ensure that the spruce trees recruit and grow slowly, their average size at 100 years (19 cm dbh) is comparable with trees at other northern boreal sites.

White spruce trees showed a strong vegetative growth response to fertilizer, growing on average 22% more each year. In contrast, cone production was identical in fertilized and control spruce trees, and mast years occurred at the same time on all areas. Seed production, however, was higher on fertilized plots, with 44–61% more seeds falling to the ground on the fertilized site. This increase in seed production could be a result of fewer red squirrels on the fertilized grids or could be due to cones of fertilized trees containing more seeds. Fertilizer alters white spruce needle chemistry, reducing the concentration of the antifeedant chemical camphor.

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