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# Response of the Central Canadian Treeline to Recent Climatic Changes

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Dendrochronology and the analysis of historical records from eighteenth, nineteenth, and early twentieth-century expeditions are used to reconstruct the response of the central Canadian treeline to recent climatic variations. Cold summer temperatures during the early to mid-nineteenth century contributed to low rates of growth and poor recruitment of white and black spruce at treeline. Despite the harsh conditions, however, individuals of both species were able to persist at sites that define their northern range limits today. After 1880, increases in regional and hemispheric temperature are associated with increased growth rates and recruitment by both white and black spruce. A drop in temperatures during the 1960s and 1970s corresponds with declines in growth rates and recruitment. Growth rates have responded positively to higher temperatures in the 1980s, yet despite this positive response to recent temperature increases, dendrochronological and historical evidence suggest that there has been no significant northward extension of spruce range limits or continuous forest. It is likely that future climate warming, caused by the anthropogenic increases in greenhouse gases, will initially produce increased growth and higher rates of recruitment in treeline stands. The extension of the boreal forest northward, however, could experience a significant lag relative to climate warming. *Key Words: treeline, climate change, global warming, Canada, tree-rings, Arctic expedition maps.*

The arctic treeline of central Canada is an important biogeographic boundary, separating the boreal biome from the tundra to the north. Not only does the vegetation change from coniferous forest to tundra, but the fauna undergo a decrease in species richness and a transition in dominance from boreal taxa to tundra taxa (Pruitt 1978). Aquatic ecosystems also change markedly along this transition zone between forest and tundra (Pienitz and Smol 1993; Walker and MacDonald 1995). The proximal human dimension of this biogeographic boundary is apparent in the fact that the treeline formed a dividing line between northern lands, dominated by native peoples of the Eskimoan linguistic family, and southern areas, where the Athapaskan and Algonkian linguistic families were dominant (MacDonald and Gajewski 1992). In this regard, it is noteworthy that one plan for dividing Canada's Northwest Territories into two administrative districts uses the present treeline as a potential political boundary (MacDonald and Gajewski 1992). It is now becoming clear, however, that the northern treeline could exert a far more extensive impact on human activities. The potential exists for the treeline to move hundreds of kilometers northward in response to climate warming caused by increasing levels of atmospheric greenhouse gases (Rizzo and Wiken 1992; Smith et al. 1992). Such a movement could enhance the rate and magnitude of climate warming on a global scale (Bonan et al. 1992; Foley et al. 1994). The potential impact of the treeline change on global climate introduces a new urgency into the study of this biogeographic boundary, particularly in terms of its response to climate change.

Summer thermal conditions are likely the most important control on the geographic position of the treeline in central Canada (Halliday and Brown 1943; Larsen 1980; Elliott-Fisk 1988; Scott et al. 1988, 1993, 1997; Szeicz and MacDonald 1995a, 1995b). The location of the arctic treeline in central Canada (Figure 1) corresponds roughly with the mean position of the Arctic Front in July (Bryson 1966; Barry 1967). North of this position the summer climate is dominated by cold and dry arctic airmasses. The frontal zone is typified by a steep gradient of decreasing surface temperature from south to

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north. A general correspondence occurs between the 10–12.5° C-surface isotherms and the mean summer location of the front (Figure 1). North of the treeline, the length of the growing season and amount of available heat energy is insufficient for trees to support foliar and bud growth, and to produce viable pollen and seeds for reproduction. Severe winter temperatures and low snowfall, coupled with blowing snow and ice, also contribute to the poor growth and reproduction by promoting the destruction and desiccation of needles and buds (Wardle 1981; Hadley and Smith 1989; Payette et al. 1985; Elliott-Fisk 1988; Scott et al. 1993; Jacoby and D'Arrigo 1989).

The potential impact of greenhouse warming on the arctic treeline has been examined recently using linked vegetation-climate models (Rizzo and Wiken 1992; Smith et al. 1992). The results of model experiments suggest that warming in the high northern latitudes would be most significant in the winter, but would also affect summers, with annual temperatures increasing by 1–4° C. This would be sufficient to displace the treeline northward by hundreds of kilometers in central Canada. Although uncertainty remains in climate model results pertaining to global warming (Schlesinger and Mitchell 1987; Houghton et al. 1996), they consistently indicate northern warming and a potential for significant poleward displacement of the arctic treeline. A rapid displacement would, of course, be disruptive to ecosystems and human land use in the treeline zone. Even more alarming are the global climatic impacts of a large northward displacement of the treeline.

How would a northward shift in the treeline affect global climate? The albedo of the dark boreal forest is much lower than that of the tundra, particularly in winter (Hare and Ritchie 1972; Pielke and Vidale 1995). Even in summer, the albedo of the boreal forest is low (0.10) com-

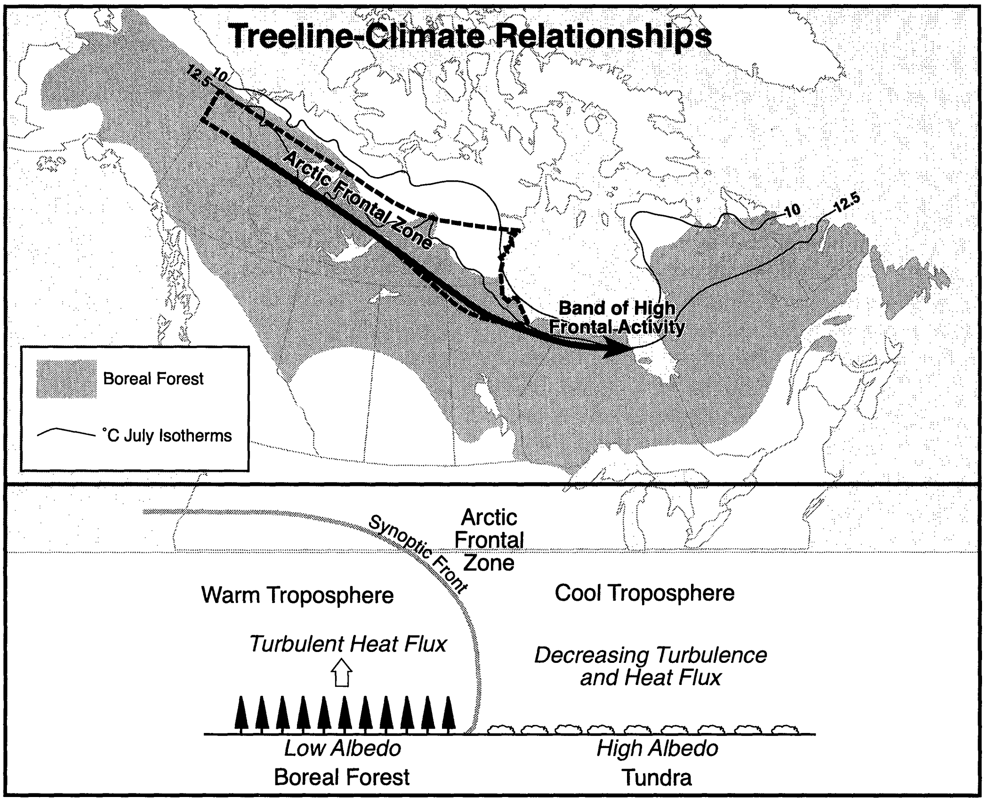

**Figure 1.** Relationship between the Arctic Frontal Zone, July isotherms, and the location of treeline. The inset presents the idealized relationship between forest, albedo, troposphere heating, establishment of a synoptic front due to differential heat fluxes from forest and tundra, and the location of the Arctic Front (partially after Pielke and Vidale 1995).

pared to the tundra (0.15–0.20) (Monteith 1975; Bonan et al. 1995). In and of itself, the lowering of the planetary albedo, by placing forests at high latitudes, could promote significant global warming (Bonan et al. 1992; Foley et al. 1994). In addition, changes in the position of the northern treeline could cause changes in the geographic position of the Arctic Front in summer. The low albedo of the boreal forest contributes to regional surface temperatures that are warmer than the adjacent tundra, causing large sensible heating of the overlying troposphere (Hare and Ritchie 1972; Pielke and Vidale 1995). Lafleur et al. (1992) showed that the boreal forest has a greater sensible heat flux than the adjacent tundra even in areas where local differences in the albedo of the forest and tundra were small. Pielke and Vidale (1995) calculated that the difference in heating rates between the boreal forest and adjacent tundra was on the order of 50 W $m^{-2}$. They concluded that the increased heating and turbulence was sufficient to create a relatively deep boundary layer over the forest, resulting in a steep thermal gradient in the atmosphere between the forest and tundra. This thermal gradient produces a synoptic barometric gradient, or front, that is strong enough to partially anchor the summer position of the Arctic Front (Pielke and Vidale 1995). It is possible that a northward movement of the treeline would move the mean summer position of the Arctic Front northward and change summer-storm patterns in the high and mid-latitudes. The northward movement of the treeline in central Canada could be particularly important for future climate change, as this region offers the greatest area of continental tundra for invasion by forest (Figure 1). The potential impact of treeline movement in central Canada raises two key questions that need to be addressed in order to anticipate the impacts of global warming: is the treeline sensitive to the magnitude of anticipated global warming, and at what rate might the treeline respond to climate warming? In this study, we use the analysis of tree-rings and historical maps and documents to address these questions.

## The Treeline and Global Warming: Research Considerations

The response of the treeline to warming could take three forms: first, the growth, stature and reproductive capability of individual trees may improve; second, the population density of trees near treeline may increase; third, the geographic distribution of tree species may expand northward. The relative rates at which these changes might occur are uncertain. Studies in Quebec indicate that several decades may elapse between climate warming and changes in tree physiognomy from the stunted krummholz (shrub-form) trees found at treeline to upright growth forms. Nevertheless, reproduction by seeds produced by krummholz trees may occur quickly (Payette et al. 1985). After reviewing available data, Scott et al. (1997) suggest that the density of tree populations in the forest-tundra would respond rapidly to increased warming. In contrast, due to limited seed dispersal and poor soil conditions, rates of northward range expansion by tree species could be extremely slow (Svoboda and Henry 1987).

One avenue for investigating the potential impact of greenhouse warming on the treeline is to examine the impact of past climatic changes. Climatic reconstructions based on instrumental records (Jones et al. 1986; Hansen and Lebedeff 1987; Houghton et al. 1996) and tree-rings (Jacoby and D'Arrigo 1989; D'Arrigo et al. 1992; D'Arrigo and Jacoby 1992) suggest that the northern treeline experienced a warming of 1–2° C in annual temperature following the close of the Little Ice Age (Grove 1988), ca. 1880. The cause of this warming is uncertain (Overpeck et al. 1997), but it could relate to solar variations (Friis-Christensen and Lassen 1991), decreased volcanic aerosols (Bryson and Goodman 1980), increased greenhouse gases (Houghton et al. 1996), natural climatic variability (Wigley and Raper 1990) or some combination of these factors (Kelly and Wigley 1992; Overpeck et al. 1997). Between 1950 and 1980, there was a significant drop in average temperatures and lower tropospheric circulation became similar to that of the Little Ice Age period (Bradley and Miller 1972). Starting in the 1980s, there has been a pronounced warming (Houghton et al. 1996). The magnitude of warming from the Little Ice Age to today may be only slightly less than that anticipated from future greenhouse warming. The impact of these recent climatic variations on the central Canadian treeline can be reconstructed using two approaches.

First, analysis of tree rings (dendrochronology) can provide evidence of the growth response of trees to past climatic changes. Many studies have found a positive response between summer temperatures and/or annual temperatures and the radial growth of *Picea glauca* (white spruce) in northern Canada and Alaska (e.g. Scott et al. 1988; Jacoby and D'Arrigo 1989; D'Arrigo et al. 1987, 1992; D'Arrigo and Jacoby 1992; Schweingruber et al. 1993; Szeicz and MacDonald 1995a). Tree rings can also be used to date the establishment of trees and measure the impact of climate on tree recruitment and range extension. Such studies conducted in other parts of Canada suggest that there was increased recruitment of treeline spruce after 1880 (e.g. Payette and Filion 1985; Payette et al. 1985; Scott et al. 1987; Szeicz and MacDonald 1995b). This response, however, was restricted to stands at the extreme limits of trees. In addition, there is little evidence of significant range extensions to higher latitudes or elevations.

Second, remarkable written records and maps of past treelines are available for central Canada. European exploration began with the establishment of trading posts at York Factory (1664) and Fort Prince of Wales (1717) by the Hudson's Bay Company. These historical documents provide eyewitness accounts of treeline conditions during the Little Ice Age, which can be compared with modern conditions. Ball (1986) analyzed the journals and maps of Samuel Hearne (1770–1772) and concluded from Hearne's mapping of the "woods edge" that the "tree limit" in central Canada has advanced up to 200 km north since the end of the Little Ice Age. If this is correct, we might expect a rapid northward movement of the boreal forest as temperatures warm in the future due to the greenhouse effect. Neither Hearne nor Ball, however, specify whether the terms "wood edge" and "tree limit" refer to the edge of continuous forest, the edge of upright tree-form growth, or the range limits of coniferous tree species. Nevertheless, there are many other historical sources of information on treeline conditions that might be compared with Hearne's accounts and the analysis of Ball (1986).

In this study, dendrochronology is combined with the analysis of historical records from the period 1770–1907 to examine the impact of recent climatic changes on the treeline in central Canada and to provide some insights into the sensitivity and likely response of the treeline to future warming. The investigation is framed around three hypotheses. First, in order to assess whether the study area is sensitive to recent temperature variations, tree-ring records are used to test the hypothesis that increases in temperature following the Little Ice Age are reflected in increased radial growth of white and black spruce (*Picea mariana*) at seven sites along the Kazan River (Figure 2). If the growth of trees was sensitive to this warming, a similar degree of sensitivity to future warming might be expected. Second, dendrochronological evidence is used to test the hypothesis that climatic warming following the Little Ice Age is associated with increased rates of establishment and survival of white and black spruce in central Canada. Examining the timing and magnitude of establishment and survival since that period provides insights into the potential response of northern tree populations to future warming. Finally, the most pronounced impact of treeline change on future climate would be due to a northward extension of the boreal forest. Historical records and tree-ring data from sites across the treeline zone are used to test the hypothesis proposed by Ball (1986) that there has been a significant northward shift in the range limits of the forest following the Little Ice Age. If post-Little Ice Age warming is associated with a large shift in the northern range limits of spruce, a rapid rate of northward movement by tree species and forest following future warming might be expected.

## Study Area

The study area (Figure 2) is underlain by the crystalline rock of the Canadian Shield. Glacial, glaciofluvial, and glaciolacustrine deposits form discontinuous cover over glacially smoothed bedrock (Dyke and Prest 1987). Topographic relief is generally less than 100 meters. Permafrost is discontinuous in the boreal forest and becomes continuous in the tundra (Brown and Pewe 1973).

The climate at the treeline is typified by long cold winters and short cool summers. A climate station operated in the treeline zone at Ennadai Lake from 1950 to 1979 was the nearest meteorological station to the Kazan River sites (Figure 2). During the time that the station at Ennadai Lake operated, the mean daily January and July temperatures were –30.9° C and 13.0° C, respectively. For comparison, the mean daily January and July temperatures for the same period south of the treeline zone at Yellowknife (Figure 2) were –28.8° C and 16.3° C. North of the treeline zone at Baker Lake (Figure 1), the mean January and July temperatures were –33.0° C and 11.0° C (Environment Canada 1982b). Mean annual precipitation at Yellowknife, Ennadai Lake, and Baker Lake was 267 mm, 295 mm, and 235 mm respectively (Environment Canada 1982a).

The central Canadian treeline is not a distinct boundary, but rather an ecotonal gradation from continuous boreal forest to forest-tundra to tundra. We define the treeline as a zone of transition between closed continuous forest and tundra. The width of this transition can extend almost 300 km (Elliott-Fisk 1983). Timoney et al. (1992) used extensive analysis of airphotos and groundtruth to divide the treeline zone into a southern forest-tundra where the ratio of tree cover to tundra is ≥ 1:1, and a northern forest tundra where the ratio decreases to 1:1000 (Figure 2).

The western boreal forest is dominated by white spruce, paper birch (*Betula papyrifera*), and aspen poplar (*Populus tremuloides*) on mesic sites. Black spruce and larch (*Larix laricina*) dominate on moist sites and peatlands. Jack pine (*Pinus banksiana*) can be found on very well-drained sites and as a post-fire dominant. Balsam poplar (*Populus balsamifera*) is found along rivers. In the forest-tundra zone, the canopy becomes open and stands of trees become interspersed with tundra. Pine, larch, poplar, and paper birch become increasingly rare, and the final trees encountered are spruce. In most cases, the stature of the spruce decreases northward until they occur as scattered low krummholz. Studies conducted in the 1960s and 1970s at Ennadai and Dubawnt Lakes (Figure 2) found that sexual reproduction of spruce at treeline was rare, and regeneration for both white and black spruce occurred primarily

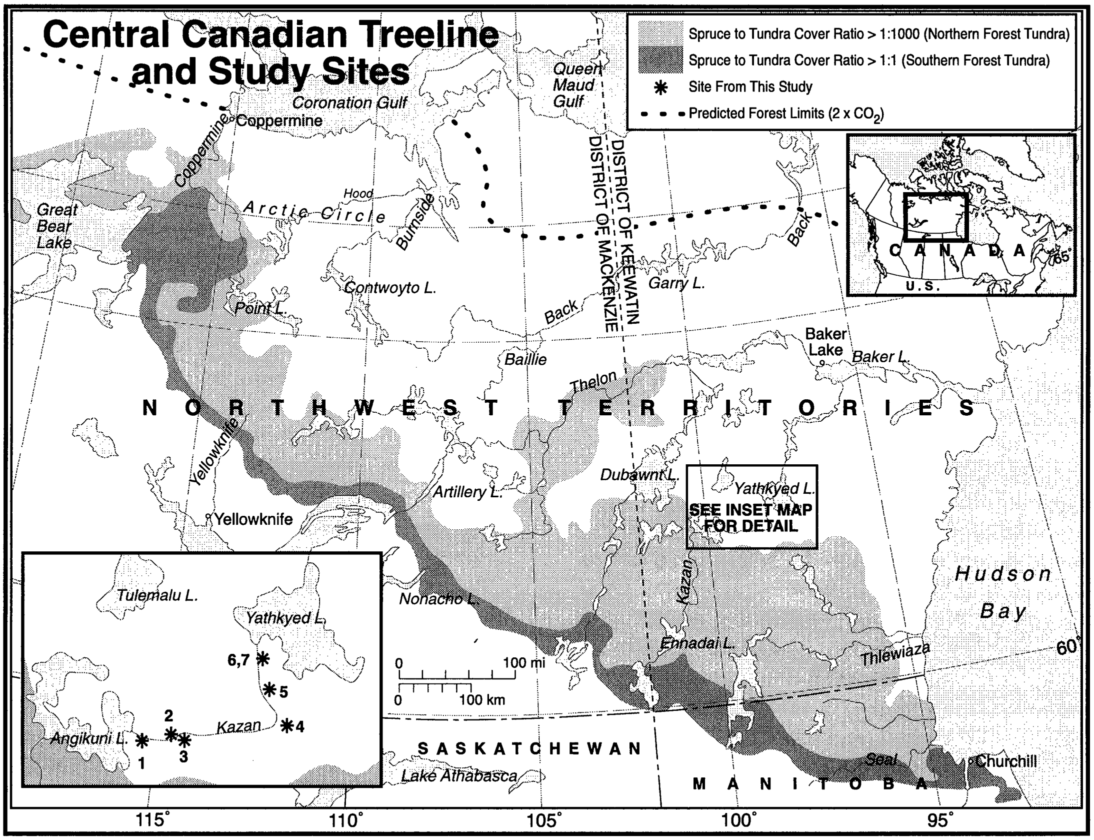

**Figure 2.** The treeline zone of central Canada, Kazan River sampling sites and locations mentioned in text. Mapping of southern and northern forest-tundra follows Timoney et al. (1992). The predicted northern limits of boreal forest following a doubling of CO$_2$ follow Rizzo and Wiken (1992).

by layering (Larsen 1965; Elliott 1979; Elliott-Fisk 1983).

## Methods

### Dendrochronological Analysis and Observations on the Present Treeline

Increment cores and disks from seven stands of spruce located along the Kazan River were collected in 1988 (Figure 2). The sites are in the middle of the central Canadian treeline zone and lie approximately 200 km north of the Ennadai Lake stands and 200 km east of the Dubawnt Lake stands studied previously (Larsen 1965; Elliott-Fisk 1983). A canoe transect to the mouth of the Kazan near Baker Lake assured that the samples were taken from the absolute northern range limits of white and black spruce along the river.

A line transect of length 118–250 m was established through the center of each stand and divided into approximately 30 equally spaced nodes. Spacing between nodes varied from 3.8 m to 8.2 m, depending on the stand. The nearest tree to each node was disked or cored near the base. In the case of layered (vegetatively regenerated) clones, the largest central stem was sampled. A number of attributes were recorded for each stand. These included the height of trees, percentage of trees with male and female cones, and growth form (erect or prostrate/krummholz). Quadrats were established adjacent to each transect to determine the density of individual trees, stems attached to layered trees, seedlings (diam. < 0.5 cm), and dead trees.

Dendrochronological analysis followed standard practices (Fritts 1976; Holmes 1992). Samples were cross-dated using light rings (Szeicz 1996) and/or narrow marker rings when possible. Rings were measured using a Nikon stereomicroscope and a Velmex measuring table (0.001 mm precision). The age of the pith was taken as the age of tree establishment. Based on aging of root-collar sections taken from a subsample of trees, 10 years were added to core samples to compensate for the time it took the trees to reach the coring height of 20–25 cm. This is still a somewhat crude method of age determination, so samples were placed into 10-yr age classes.

Ring-width chronologies for white and black spruce were developed from a subset of the transect samples. Radii that could not be reliably cross-dated, or that had reaction wood, were eliminated from the analysis, leaving 38 white spruce and 35 black spruce samples to develop the chronologies. Sample sizes decrease back in time, to a minimum of 5 for both species in the late nineteenth century. In order to preserve long-term growth trends that may be climate-related, radii were standardized and detrended conservatively, using negative exponential curves or straight lines of negative or horizontal slope (cf. D'Arrigo et al. 1992; Szeicz and MacDonald 1995a). The final chronologies were constructed by biweight robust averaging of individual indices. Autoregressive modeling, a common procedure in many dendrochronological analyses, was not carried out, as it may remove some potentially climate-driven variance in the tree rings (Jacoby and D'Arrigo 1989).

The chronologies were compared with the relatively long climate record from Churchill, Manitoba (1933–1987) using response function analysis (Fritts 1976), which involves multiple regression, using the principal components of monthly climate data as the predictors and the tree-ring chronologies as predictands. This procedure identifies the climatic variables having the greatest influence on radial growth, and includes data extending from the previous May to September in the year of growth. The principal components analysis of climate data reduces the effects of multicollinearities between predictor variables in a multiple regression. Although Churchill is located nearly 500 km from the sampling sites, it has the longest climatic record available for the boreal forest-tundra transition zone of central Canada. August temperatures at Churchill correlate closely with those at Ennedai Lake ($r=0.87$, 1950–1979; $p \leq 0.001$) and Fort Reliance ($r=0.71$, 1949–1989; $p \leq 0.001$), suggesting that the central Canadian treeline zone has a relatively homogeneous pattern of variations in summer temperature.

As air temperatures and the growth of high latitude trees has been shown to have a strong correlation with hemispheric temperature trends (Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1993), correlation coefficients were also calculated between the ring-width chronologies and arctic/subarctic annual temperature departures (Hansen and Lebedeff 1987), and between ring-width chronologies and northern hemisphere annual, August, and January temperature departures (Jones et al. 1986) for the period 1884–1987 (for white spruce) and 1890–1987 (for black spruce). Finally, the radial growth of evergreen conifers may be influenced by climate for several years preceding ring formation, and so correlation coefficients were also calculated between the white and black spruce chronologies and the same four temperature records averaged over the five years up to and including the year of growth (cf. Jacoby and D'Arrigo 1995).

To document the current northern limits of spruce at other sites in central Canada, we relied upon observations made during helicopter reconnaissance trips and information collected from published reports (Hansell et al. 1971; Kay 1978; Guerts 1985; Larsen 1989). The helicopter trips were taken between 1986 and 1996 for the purpose of identifying the northern range limits of trees in order to select sites for tree-ring and lake-sediment coring. The altitude on most flights ranged from 200–1500 m above the land surface. The helicopter was brought in close to the ground to confirm identification of krummholz trees. Trees spotted from the air were marked on 1:250,000 topographic maps. When possible, tree-ring cores and disks were collected and analyzed in order to ascertain the age of the oldest trees at the northern limits.

## Analysis of Historical Records

Historical records from British, Canadian, and American expeditions provide an important source of information on past treeline conditions (Ball 1986), and these can augment and geographically extend the dendrochronological record. The location of trees was extremely important to explorers. Even small stands of krummholz provided shelter in the winter, and were sources of firewood, material for snowshoes and sleds, and game. In addition, the treeline was a significant spatial boundary. Naturalist Ernest Thompson Seton describes his emotions when encountering trees again after exploring the tundra in 1907: "How shall I set forth the feeling it stirred? None but the shipwrecked sailor, long drifting on the open sea, but come at last to land, can fully know the thrill it gave us" (Seton 1912:251).

Observations were therefore often made on both the location and nature of the treeline. For example, Samuel Hearne, an employee of the Hudson's Bay Company, wrote about the Coppermine River: "The woods grow gradually smaller as you approach the sea; and the last tuft of pines that I saw is about thirty miles from the mouth of the river, so that we meet nothing between that spot and the sea-side but barren hills and marshes" (Hearne 1911:188). The "pines" mentioned by Hearne and the early nineteenth-century explorers were undoubtedly spruce (Ball 1986). In July, 1821, a British naval expedition led by Lieutenant John Franklin descended the Coppermine by canoe. Close to the spot where Hearne had stood, John Richardson recorded in precise terms: "Situation of encampment, 67°34'20" North(R), 115°55'45" West(R). No trees beyond this place" (Richardson 1984:76). George Back also provided information on the location and stature of the trees he observed during his 1833–1835 British naval expedition. In addition, he speculated on the age of the trees and offered impressions of them: "Still further south, in latitude 63°14'00" N we saw the first dwarf pines, from fourteen inches to two feet high, which my bowman humourously called *des petits vieux* . . . nevertheless, such as they were, they were welcome to us, who had not seen any since the 20th of August, and as all enjoyment is comparative, we looked forward to delight to the comfort of a good fire" (Back 1970:166).

We used the published records and maps of Hearne (1911, 1971), Richardson (1981), Back (1970, 1994), J. W. Tyrrell (1897, 1902), and Hanbury (1904), and the unpublished fieldnotes of J. B. Tyrrell (1894) to reconstruct expedition routes (Figure 3) from the years 1770–1771, 1819–1822, 1833–1835, 1893–1894, 1899, 1901, and 1902, and to plot the approximate position of first and last sightings of trees on modern 1:250,000 topographic maps. We also used published accounts to determine the locations of trees encountered by Russell (1898), during his expedition of 1893, and Seton (1912) in 1907. Longitudinal positions have poor fidelity in the early records, so matching expedition records with known lakes and rivers was particularly important. Previous reconstructions of the routes proved extremely useful (e.g., Tyrrell in Hearne 1911; Speck 1963; Houston in Richardson 1984; Ball 1986; Houston in Back 1994). Earlier maps of the treeline are available, beginning with the sketch map of Governor James Knight (Figure 4). Based on information provided in 1716 by Hudson's Bay Company employee William Stewart and his native guides, this map was later revised with information from the 1741–1742 voyage of Captain Middleton. Cardinal directions are not represented realistically, however, making the map unreliable for our purposes. The maps of Samuel

Hearne have much greater fidelity to cardinal directions and the shapes of rivers and lakes. He provided both a general map of the "wood's edge" (Figure 5) and details of the last stands of trees along the Coppermine (Figure 6). The routes taken by Hearne (Figure 3) indicate that he could not actually have seen all of the features depicted on his general map (Figure 5) and must have relied upon accounts from his native guides. The maps provided by the Franklin and Back expeditions (Figure 7) were the products of disciplined naval navigators and can be relatively easily compared and correlated with modern topographic maps. The government survey maps of J. B. and J. W. Tyrrell (Figure 8) are also of good geographic fidelity. A common feature on all these maps is the attention paid to depicting the position of the treeline or the last trees encountered.

Hearne's map of the woods edge (Figure 5) is particularly important as it was used by Ball (1986) to infer movement of the treeline in historical times. Using the reconstruction of Ball, and our own comparison of Hearne's notes and maps with modern maps, we have plotted the position of the "wood's edge" as portrayed by Hearne as an overlay on the modern treeline zones of Timoney et al. (1992) (Figure 3).

A final line of evidence regarding the past treeline is provided by the drawings, watercolors, and photographs made by explorers. For example, Hearne drew the spruce, poplar, and birch forest he encountered near the southern shore of Great Slave Lake in 1772 (Figure 9), and commented: "The woods about the river, particularly the pines and poplars, are the tallest and stoutest I have seen in any part of North America. The birch also grow to a considerable size . . ." (Hearne 1911:268). The vegetation described and depicted by Hearne is very similar to the boreal forest found at the site today. Back provided

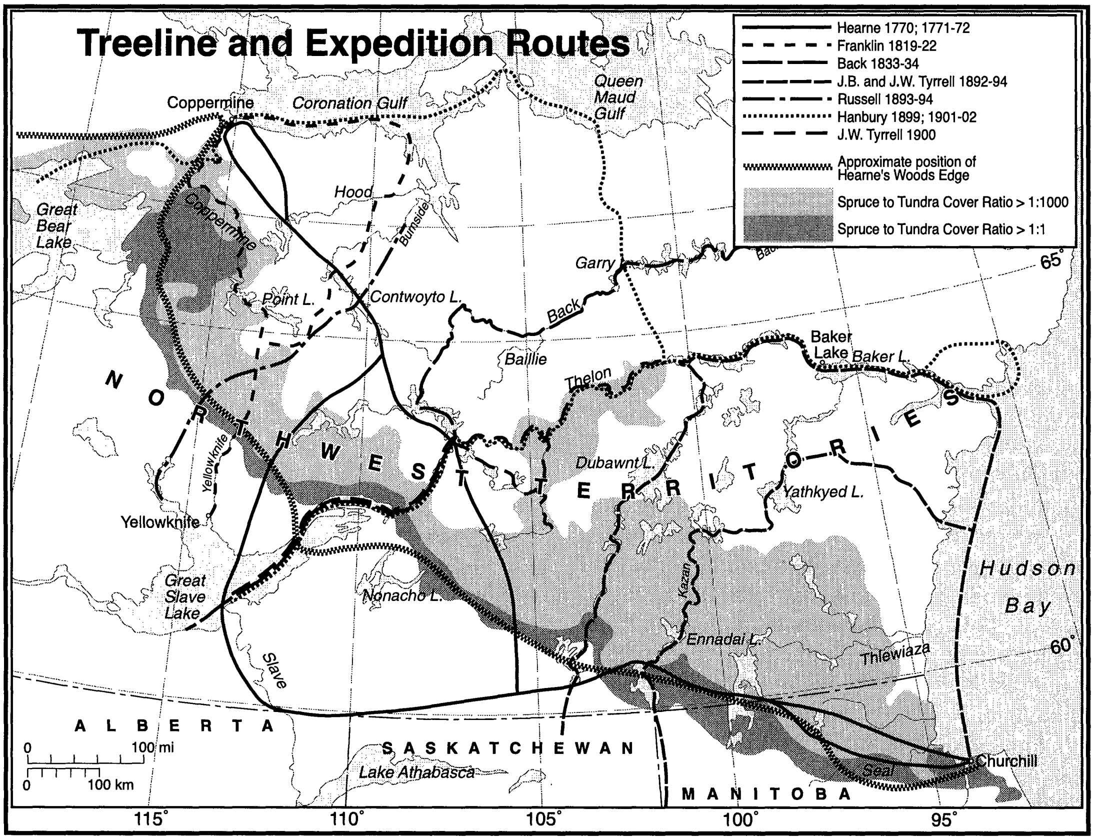

Figure 3. Central Canadian treeline and exploration routes plotted from journals and maps of eighteenth, nineteenth and early twentieth-century explorers, and interpreted position of the "woods edge" from the 1772 map by Hearne.

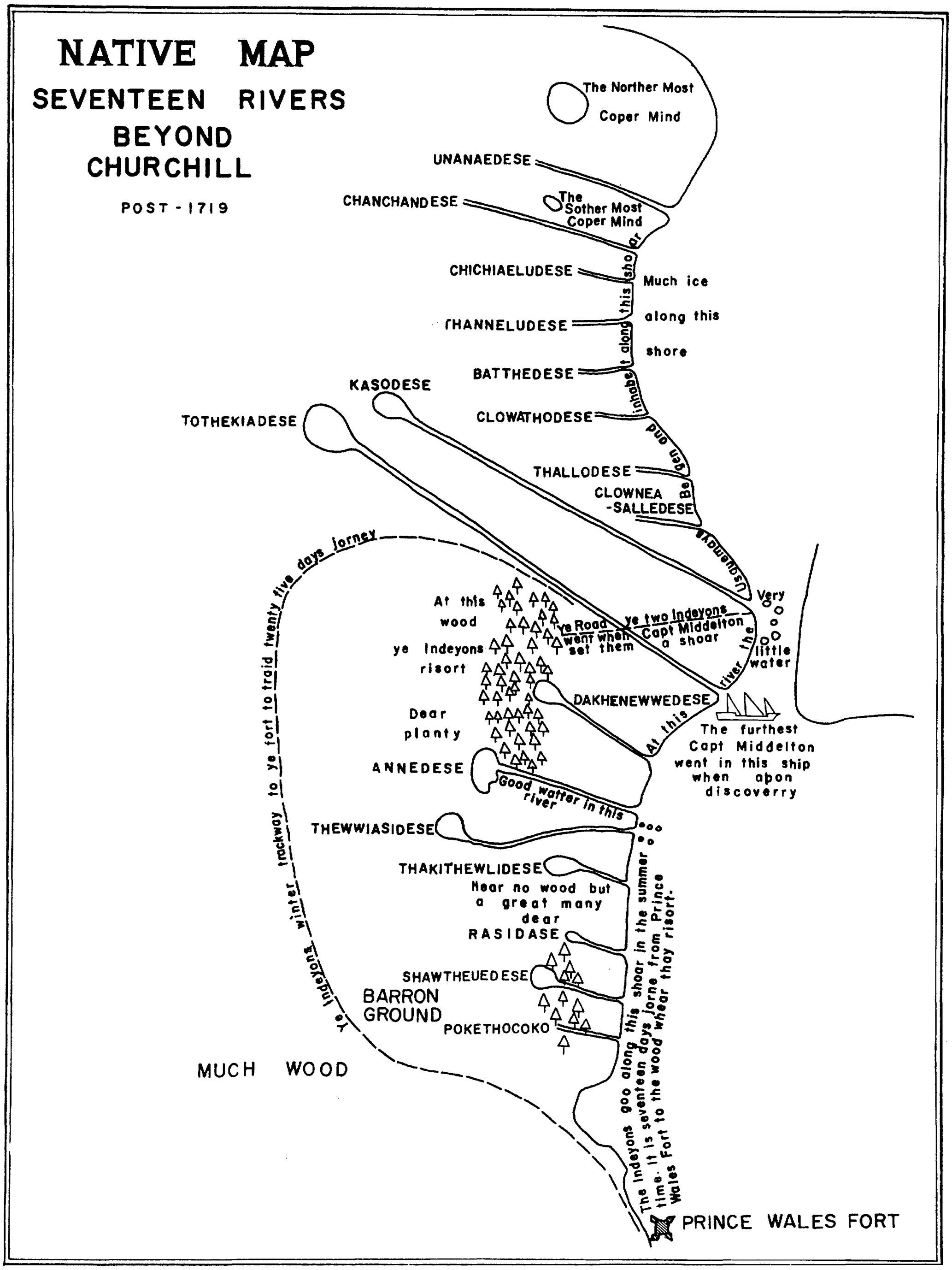

**Figure 4.** The post-1742 "Native Map" of the region between Hudson Bay and the Coppermine River prepared by Governor James Knight, partly based on information from native guides. Note the lack of fidelity to cardinal directions (reproduced from Warkentin and Ruggles 1970).

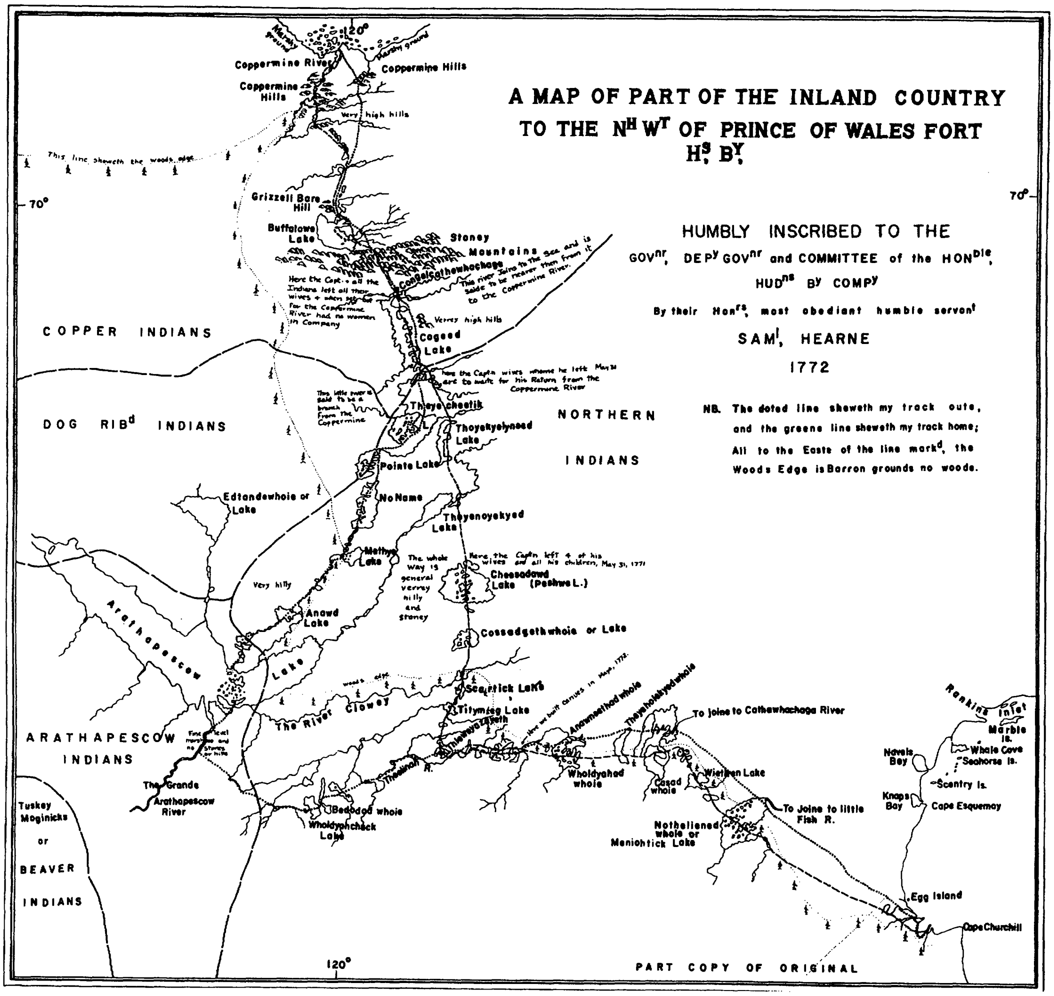

Figure 5. The 1772 general map of the region between Hudson Bay and the Coppermine River prepared by Samuel Hearne (reproduced from Warkentin and Ruggles 1970). This includes the mapping of the "woods edge."

watercolors of the last stands of spruce along the Coppermine River in 1821 that clearly show open groves restricted to the lowlands (Back 1994). As a final example, Seton photographed the "Last Woods" along the west shore of Artillery Lake. The location is approximately 63°12'N and 107°56'W, and spruce can be found in the region today. The final stands of spruce in this vicinity were noted by Back (1970), Tyrrell (1902), Hanbury (1904), and Seton (1912). His 1907 photograph (Figure 10) is of particular historical importance as it shows the first dendrochronological sampling at the arctic treeline in North America. Of the sampling, Seton writes:

> A tall, dead, white spruce at the camp was 30 feet high and 11 inches in diameter at 4 feet from the ground. Its 190 rings were hard to count, they were so thin. The central ones were thickest, there being 16 to the inmost inch of radius; on the outside to the north 50 rings made only 1/2 an inch and 86 made one inch. Numbers 42 and 43 counting from the outside were two or three times as thick as those outside of them and much thicker than the next within; they must have represented unusual summers. No. 99 was also of great size. What years these corresponded with one could only guess, as the tree was a long time dead. Another, a dwarf but 8 feet high, was 12 inches through. It had 205 rings plus a 5-inch hollow we reckoned at about 100 rings of growth . . . (Seton 1912:217–18).

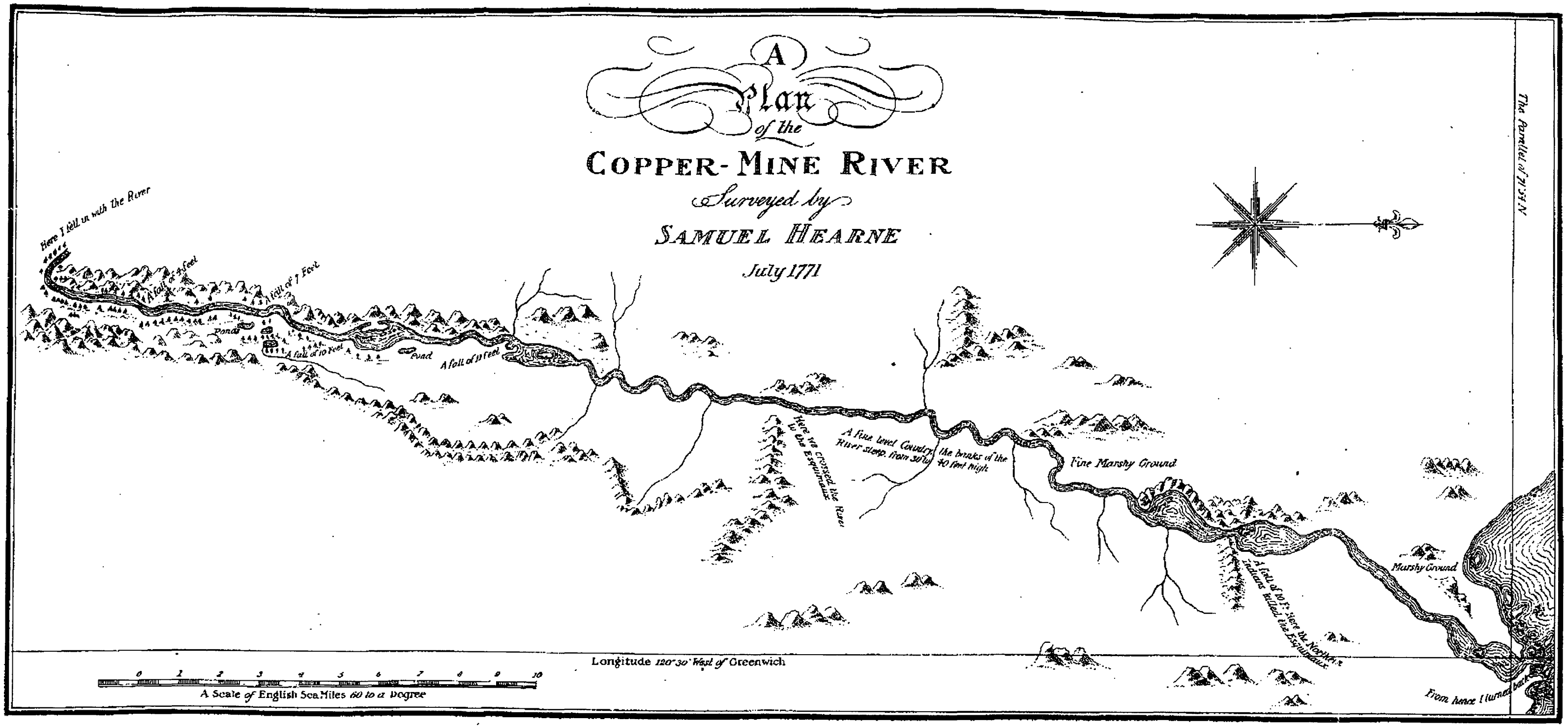

**Figure 6.** The 1771 detailed map of the treeline along the Coppermine River by Hearne (reproduced from Hearne 1911). Trees are indicated by small sketched shapes of trees along the river.

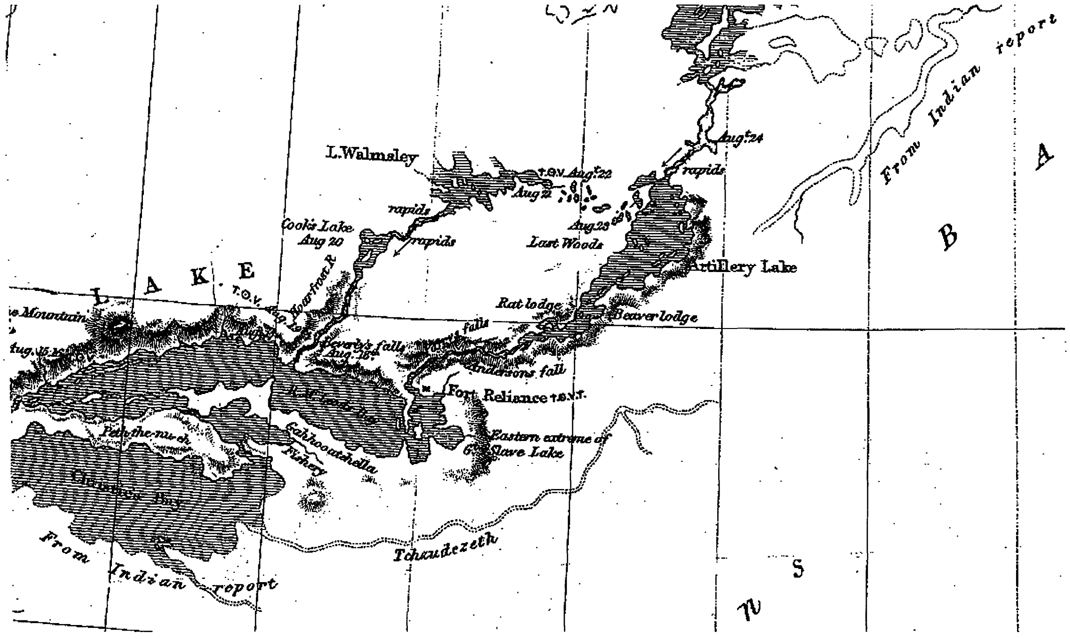

Figure 7. The 1833 map, indicating the "last woods" along the western shore of Artillery Lake, by George Back (reproduced from Back 1970). A picture of this stand in 1907 taken by Seton is reproduced in Figure 10.

Thus, ninety years ago, Seton began the tree-ring work in central Canada that continues today, anticipating the positive correlation that has been found between ring widths and summer conditions at the Canadian treeline.

## Results and Discussion

### The Current Kazan River Stands

Both white and black spruce were encountered at most stands along the Kazan River (Table 1). Both krummholz and upright growth forms occur, with maximum heights reaching over 750 cm. Mean heights, however, tended to be under 200 cm. Male and female cones were common for both species. Fresh male cones and immature female cones indicate cone development in 1987–1988. Seedlings were extremely rare, being present only at the northernmost sites. Densities of stems were generally low, particularly for individual, nonclonal stems. Maximum densities of stems were found at sites dominated by black spruce krummholz with extensive layering (Transect numbers 3 & 5).

### Temperature and Radial Growth of White and Black Spruce

Ring-width chronologies were constructed from 1874–1987 for white spruce and 1898–1987 for black spruce (Table 2; Figure 11). Although several trees dated to the eighteenth century or earlier, sample sizes were small (<5) and cross-dating unreliable before the nineteenth century. The mean sensitivities and first-order autocorrelations for the chronologies are similar to those of other studies in subarctic Canada (Cropper 1984; Szeicz and MacDonald 1995a), and indicate that low-frequency signals are stronger than high-frequency, interannual variations. Two indications of the common signal strength in these data are the mean correlation between individual indices and the variance explained in the first eigenvector of a principal components analysis (PCA) of the individual indices. Both of these statistics are substantially greater for white spruce than for black spruce. As many of the black-spruce radii come from dense clonal clumps, the effects of competition between closely spaced stems may contribute to the lower common signal. White spruce also has a much greater ten-

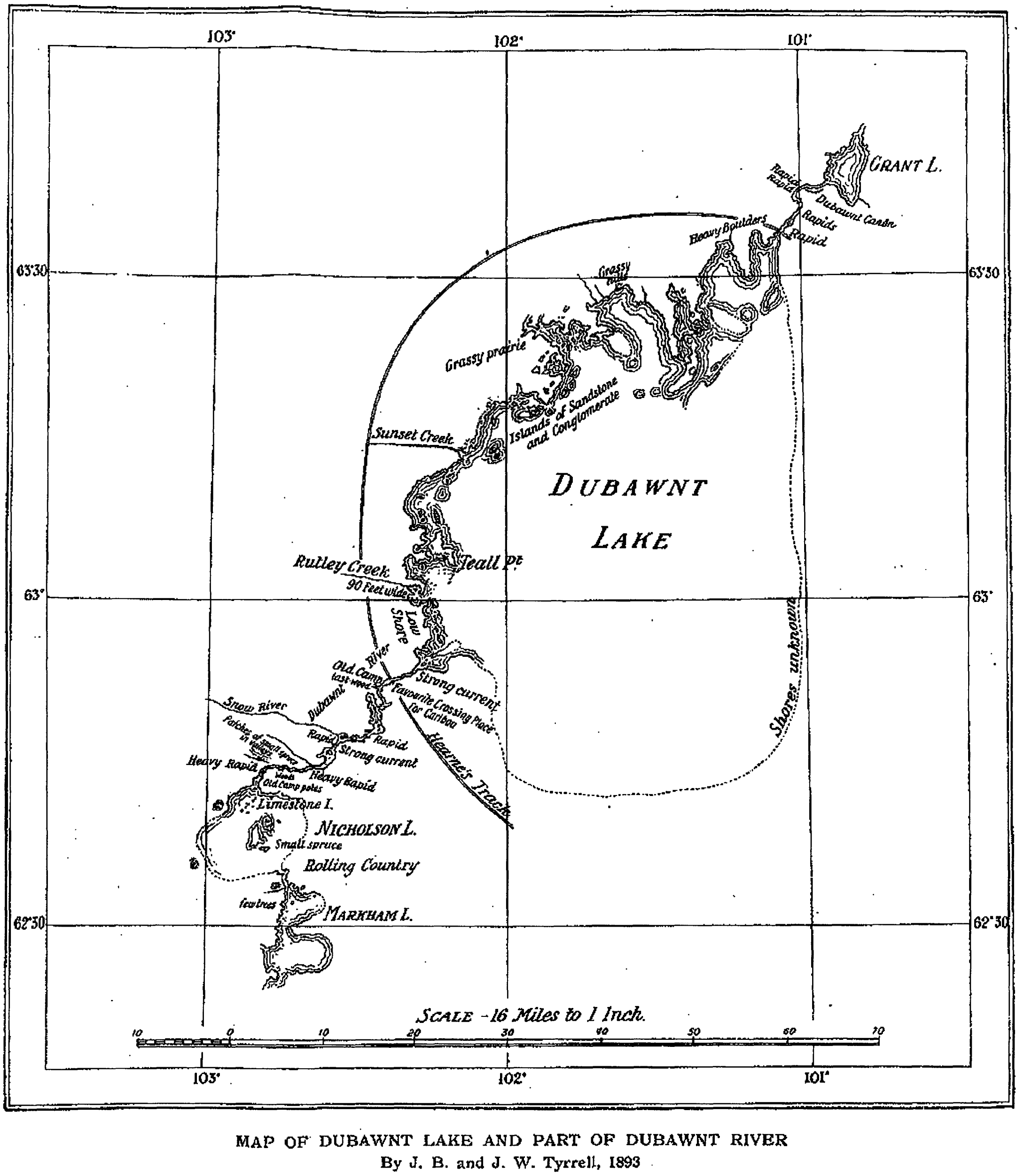

**Figure 8.** The 1893 detailed map of treeline along the Dubawnt River by the Tyrrells (reproduced from Seton 1912). Note that Hearne also traversed this region.

dency toward erect as opposed to prostrate or krummholz growth forms (Table 1), and its growth is therefore more likely to reflect macroclimates than local microclimates.

Despite the relatively weak common-growth signal among the black spruce, the two chronologies still compare very closely to one another ($r=0.85$ and $p \leq 0.001$ for 1898–1987). The radial growth of both white and black spruce generally increased from the late nineteenth century to the 1940s, with the most dramatic increase occurring between 1920 and 1945 (Figure 11). This was followed by a marked decline and second nadir in growth during the 1960s and 70s. A rapid

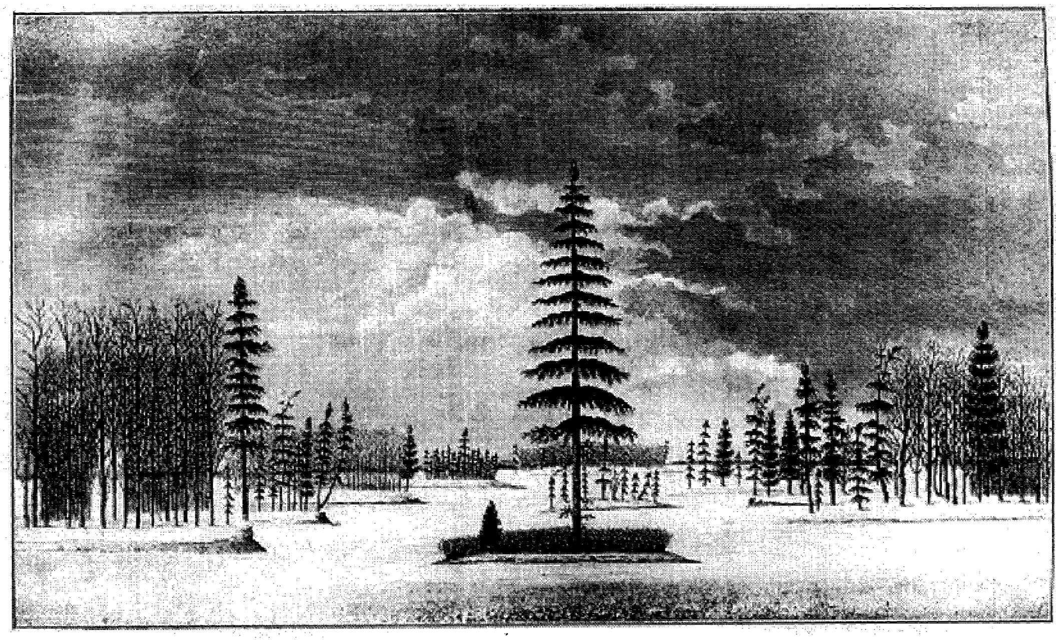

**Figure 9.** Hearne's 1771 sketch of mixed-woods forest near the southern shore of Great Slave Lake (reproduced from Hearne 1911).

**Figure 10.** Seton's photograph of dendrochronological sampling at the last woods along the western shore of Artillery Lake (reproduced from Seton 1912). This stand is shown on the 1833 map by Back (Figure 7).

**Table 1.** Stand Characteristics of Kazan River Sites

| Transect Data | | | | | | | | | Quadrat Data | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Transect No.<br>lat., long.<br>altitude | Species | n | Mean Height (cm) | Max Height (cm) | Trees with Cones (%) | | Form of Trees > 2 cm Diam. (%) | | Quadrat Area (m$^2$) | Density (stems/100m$^2$) | | | |
| | | | | | male | female | Prostrate/ Krummholz | Erect | | Indivi- duals | Attached Layers | Seedlings | Dead |
| 1<br>62°15'N, 99°35'W<br>(260–270 m) | WS | 25 | 144 | 400 | 52 | 36 | 44 | 56 | 540 | 3.0 | 1.7 | 0 | 2.4 |
| | BS | 7 | 129 | 275 | 14 | 57 | 71 | 29 | | 2.4 | 21.9 | 0 | |
| 2<br>62°15'N,99°12'W<br>(250 m) | WS | 21 | 252 | 460 | 81 | 57 | 29 | 71 | 300 | 2.0 | 0 | 0 | 1.6 |
| | BS | 12 | 191 | 270 | 50 | 67 | 92 | 8 | | 5.0 | 10.7 | 0 | |
| 3<br>62°15'N,98°55'W<br>(240 m) | WS | 3 | 191 | 260 | 67 | 67 | 33 | 67 | 260 | 0.4 | 0 | 0 | 13.8 |
| | BS | 27 | 148 | 310 | 11 | 52 | 96 | 4 | | 38.5 | 65.0 | 0 | |
| 4<br>62°12'N,98°15'W<br>(170–180 m) | WS | 2 | 197 | 225 | 0 | 50 | 50 | 50 | 396 | 0 | 0 | 0 | 1.0 |
| | BS | 28 | 78 | 120 | 4 | 18 | 100 | 0 | | 19.9 | 0.2 | 0 | |
| 5<br>62°26'N,98°15'W<br>(160 m) | WS | 0 | – | – | – | – | – | – | 300 | 2.3 | 2 | 0 | 5.7 |
| | BS | 30 | 124 | 245 | 30 | 40 | 90 | 10 | | 65.7 | 58.7 | 0 | |
| 6<br>62°35'N,98°22'W<br>(140–150 m) | WS | 30 | 262 | 750 | 57 | 57 | 0 | 100 | 456 | 2.2 | 0.4 | 0.4 | 2.6 |
| | BS | 0 | – | – | – | – | – | – | | 0 | 0 | 0 | |
| 7<br>62°35'N,98°22'W<br>(140–150 m) | WS | 30 | 309 | 520 | 77 | 87 | 3 | 97 | 420 | 2.4 | 2.4 | 2.0 | 0.7 |
| | BS | 0 | – | – | – | – | – | – | | 0 | 0 | 0 | |

WS = White spruce (*Picea glauca*)
BS = Black spruce (*Picea mariana*)

**Table 2.** Characteristics of Ring-Width Data and Results of Response Function and Linear Regression Analyses (All Sites Combined)

| | | | | | | Response Function Results | | Correlations (r) between Tree-Ring Indices and Large-Scale Temperatures[b] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | n | Mean Sensitivity[a] | 1st Order Autocorrelation | % Variance in 1st Eigenvector | Mean Correlation between Indices | % Variance Explained | Climate Variables Significant at $p<0.05$ | Arctic Annual temp. | N. Hem. Annual temp. | N. Hem. August temp. | N. Hem. January temp. |
| White spruce | 38 | 0.13 | 0.77 | 39 | 0.32 | 45 | August temp., growth year | 0.65/0.78 | 0.65/0.80 | 0.59/0.73 | 0.42/0.54 |
| Black spruce | 35 | 0.14 | 0.70 | 26 | 0.18 | 53 | August temp., growth year;<br>October temp., previous year | 0.48/0.57 | 0.50/0.60 | 0.37/0.56 | 0.31/0.45 |

[a] A measure of the year-to-year variation in ring widths (Fritts 1976).

[b] First value is for the unaveraged temperature data; second value is for the temperature data averaged over 5 yrs up to and including the year of growth. All values significant at $p<0.001$ except unaveraged Northern Hemisphere January temperature, which is significant at $p>0.002$.

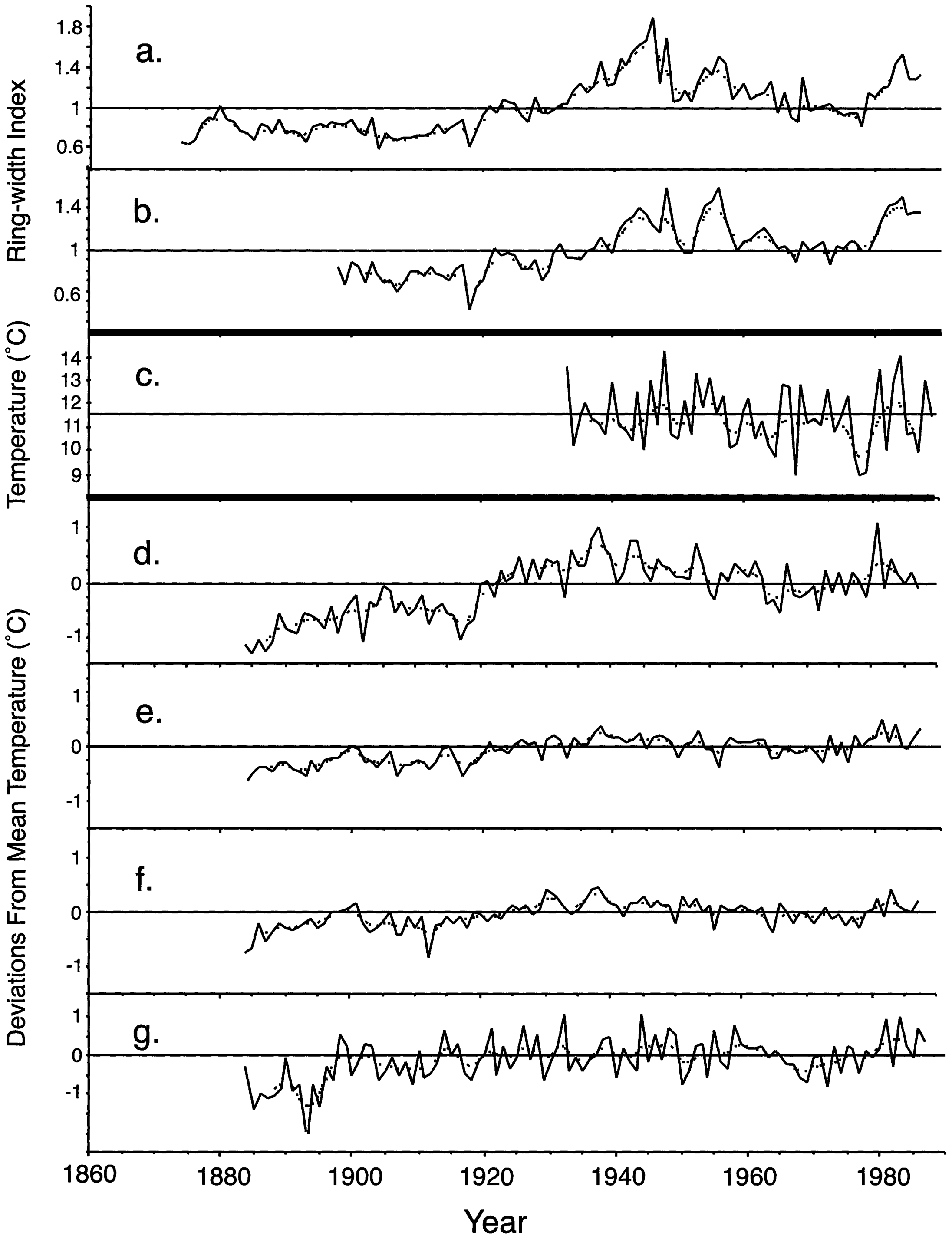

**Figure 11.** Comparison of Kazan tree-ring data with temperature data. (a,b) Tree-ring chronologies from (a) white spruce and (b) black spruce; (c) mean August temperature from Churchill; (d-g) temperature departures for (d) arctic/subarctic mean annual temperature, (e) mean annual, (f) mean August, and (g) mean January temperatures for the Northern Hemisphere. Dotted lines indicate smoothing with 7-yr binomial filters. (Temperature data from Environment Canada 1982b; Jones et al. 1986; Hansen and Lebedeff 1987).

increase in radial growth is apparent during the 1980s (Figure 11).

Response function results indicate that 45 percent of the variance in white-spruce growth and 53 percent of the variance in black-spruce growth can be accounted for by the Churchill climate data (Table 2). These values compare well with results from other tree-ring sites in northern Canada (e.g., Kay 1978; Jacoby and Cook 1981; Szeicz and MacDonald 1995a) and indicate a strong local-regional climate signal in the ring-width data from these sites. August temperature in the year of growth is a significant variable for the radial growth of both species, and October temperature in the year preceding growth is also significant for black-spruce ring widths. Ring widths are not significantly correlated with temperature or precipitation for any other month recorded in the Churchill data. The spruce ring widths, particularly white spruce, are highly positively correlated with arctic annual temperature, northern hemisphere annual temperature, and northern hemisphere August temperature, with a weaker but significant correlation with northern hemisphere January temperatures (Table 2; Figure 11). These correlations increase further when the temperature records are averaged over the five years up to and including the year of growth (Table 2).

The significant correlations between the ring widths and temperature over the period 1884 to 1987 support the hypothesis that the sites in central Canada are sensitive to post-Little Ice Age warming. Although significant correlations were found with annual, summer, and winter temperatures, the comparison of tree rings with temperature at Churchill suggests that summer temperature is the most important factor. This is to be expected, as warmer temperatures during the growing season result in higher rates of photosynthesis and the production of carbohydrates used in ring production (Fritts 1976). As a secondary factor, longer and better growth during the summer can produce thicker cuticles, making needles more resistant to damage and desiccation during winter and spring (Wardle 1981; Hadley and Smith 1989). The significant correlations between tree-ring growth and Northern Hemisphere winter temperatures may be an artifact of the general covariance between low frequency variations in summer and winter temperatures in the 1880–1987 records. Winter conditions, however, can also affect trees through desiccation, frost damage to buds and roots, and abrasion by blowing snow and ice (Wardle 1981; Hadley and Smith 1989; Payette et al. 1985; Scott et al. 1993).

The high degree of correlation between arctic and hemispheric temperature trends and the growth of the Kazan trees is consistent with climatological studies that suggest that north-central Canada is particularly sensitive to northern hemisphere temperature variations (Diaz and Andrews 1982). In addition, the degree of correlation between hemispheric temperature variations and tree growth may be increased by northward shifts in the mean summer position of the Arctic Front in central Canada during warm decades (Scott et al. 1988). The spruce growing in these marginal stands are clearly responding to climate changes over the preceding several years. Long-term storage of photosynthates and needle retention for up to a decade (Jacoby and D'Arrigo 1995) are likely to contribute to the highly significant correlations between the chronologies and large-scale temperatures averaged over five years (Table 2).

Our sites link studies from northern Quebec and Churchill (Payette et al. 1985; Scott et al. 1988) with those from northwestern Canada and Alaska (Jacoby and D'Arrigo 1989; D'Arrigo et al. 1992; D'Arrigo and Jacoby 1992) to show a general North American pattern of: (1) significant warming and increased radial growth of trees between ca. 1880 and 1950; (2) decreased temperatures and growth during the 1960s and 70s; and (3) sharply increasing temperatures and growth rates in the 1980s.

## Spruce Establishment and Recent Climatic Change

The age structure of the stands (Figure 12) indicates that trees have been present in the region since at least the mid-seventeenth century. At most sites there are a few trees that persisted through the extremely cold portion of the Little Ice Age from 1800 to 1850 (Jacoby and D'Arrigo 1989; D'Arrigo et al. 1992; D'Arrigo and Jacoby 1992; Szeicz and MacDonald 1995a, 1995b). Most of the present stems were established during the period 1880–1950. This tendency is most evident in the northernmost sites. There has been little establishment following the 1940s, and although seedlings were present in Transects 6 and 7 (Table 1), none of the sampled individuals was established after 1960.

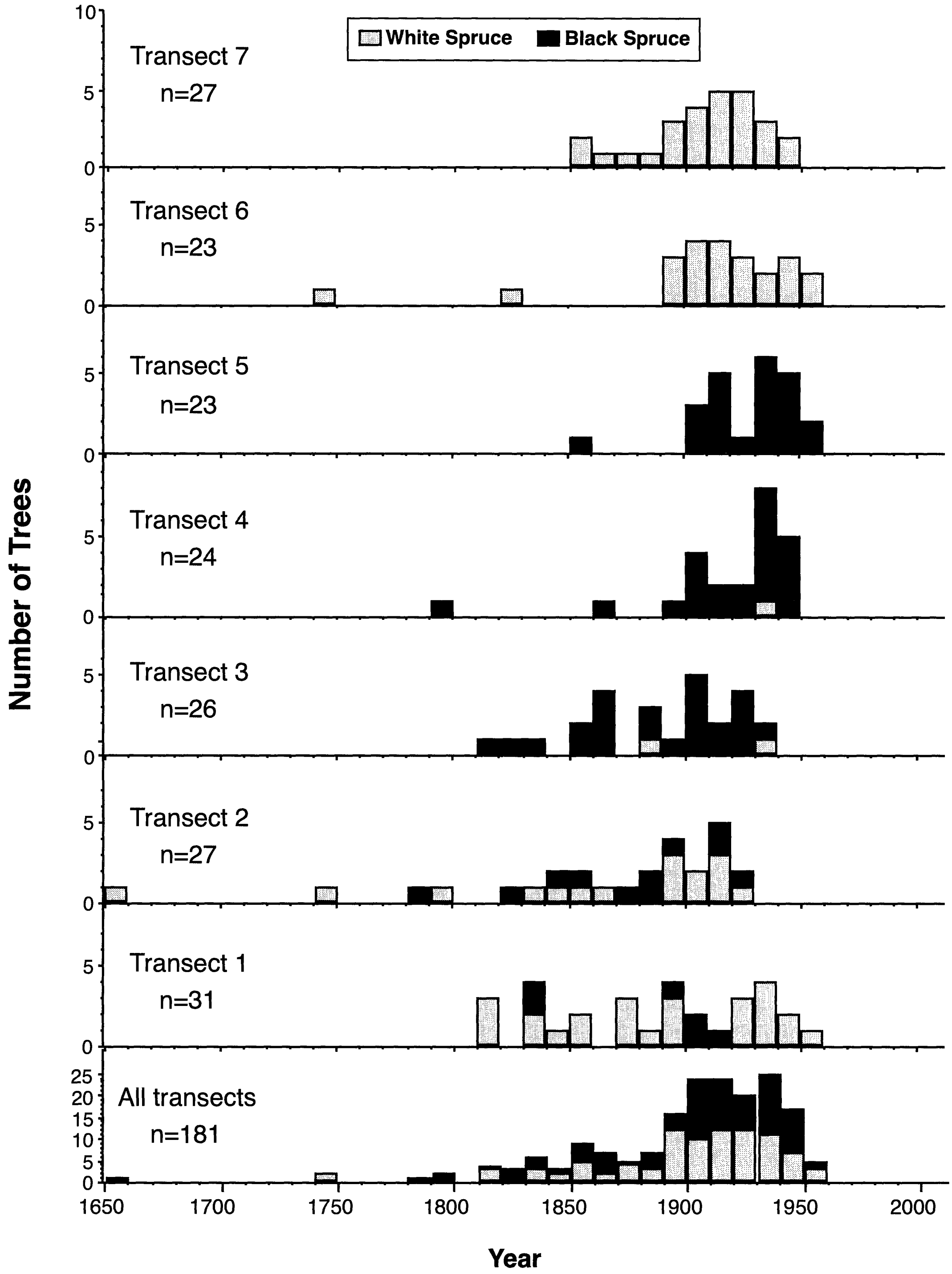

Figure 12. Establishment histories of the Kazan River stands. White spruce are represented by gray bars, and black spruce are represented by black bars. Sample sizes (n) are lower than in Table 1, as a proportion of trees at each site could not be reliably dated.

The age structures of the seven Kazan stands indicate that the majority of trees, particularly at the northern stands, were established between 1890 and 1950. This supports the hypothesis that there was an increase in stand density following the close of the Little Ice Age. This effect is most evident at extreme northern sites. Our sites, together with similar evidence from northern Quebec (Payette and Filion 1985), Churchill (Scott et al. 1987), and the arctic-alpine treeline of the Mackenzie Mountains (Szeicz and MacDonald 1995b), suggest that this was a continent-wide phenomenon at the treeline.

The large number of trees dating from the period 1890–1950 is likely due to a combination of higher natality and lower mortality. Warmer summer temperatures promote higher rates of photosynthesis that supply more carbohydrates for radial and longitudinal growth, and for seed and pollen development (Fritts 1976; Kramer and Kozlowski 1979). In addition, warm summers promote apical bud differentiation and the development of fertile male and female gametophytes (Kramer and Kozlowski 1979). Seedling establishment and survival is also promoted by warmer summer conditions (Black and Bliss 1980). Winter temperatures and precipitation also increased following the Little Ice Age, making needles and apical buds less subject to desiccation or mechanical damage (Payette and Filion 1985; Scott et al. 1993). Moderate amounts of snow would also aid seedlings by protecting them during winter and increasing soil moisture content (Black and Bliss 1980; Scott et al. 1997). The growth of previously established trees and the establishment of new trees can serve as a positive feedback mechanism that enhances regeneration in spruce stands. Increases in the size and number of trees leads to decreased wind velocity and increased trapping of snow in the stand. This condition has the effect of protecting seedlings and the buds and needles of mature trees, which enhances rates of seed production and seedling survival (Payette and Filion 1985; Scott et al. 1993, 1997).

The lack of regeneration during the 1960s and 1970s is consistent with the reproductive biology studies carried out at Dubawnt Lake and Ennadai Lake during that period by Larsen (1965) and Elliott-Fisk (1983). It was found that pollen and seeds were infertile and there was little indication of recent establishment (Elliott-Fisk 1983). The decline in regeneration in the 1960s and 1970s likely reflects the return of the climate to cold conditions, similar to the Little Ice Age (Bradley and Miller 1972). It appears, however, that climate during the 1960s and 1970s was not quite as severe as pre-1880 conditions (Figure 11). In addition, growth rates for white and black spruce were slightly better than during the Little Ice Age (Figure 11). It is possible that limited recruitment occurred following the 1950s but was missed in our sampling.

## Post-Little Ice Age Changes in the Range Limits of White and Black Spruce

Scattered stands of spruce can be found more than 50 km beyond the mapped limits of the northern forest-tundra. The northernmost trees recorded in expedition records are in the general vicinity of the present-day species limits of black and white spruce (Figure 13; Table 3). In a few cases, living trees can be found more than 50 km beyond the historical observations of the expedition records. Dendrochronological analysis of these stands (Figure 13; Table 3) indicates there are some trees greater than 125 years in age. Trees were able to persist at the present northern limits of spruce during the coldest period of the Little Ice Age.

Hearne records a number of sightings of trees (Figure 13) well beyond the limits of his mapped "woods edge" (Figure 3). It is clear that the "woods edge" was not meant to represent the species limits of spruce. It should also be remembered that Hearne's route (Figure 3) did not always take him to the "woods edge." It is likely that the "woods edge" represents the edge of continuous forest as inferred by Hearne, while his mapping at times draws upon secondary accounts from guides. The interpreted position of the limit of the woods from Hearne (Figure 3) coincides generally with the present boundary between the boreal forest and the southern forest-tundra, and does not provide evidence of a significant northward shift in either the ranges of tree species or the continuous boreal forest.

Our dendrochronological and historical analyses refute the hypothesis that there has been significant northward range extension of tree species following the close of the Little Ice Age. In addition, comparison of Hearne's map with the present treeline does not provide evidence of a major shift in the northern forest limit (Figure 3). This is contrary to the assertions of Ball (1986), who compared Hearne's map of the "woods edge"

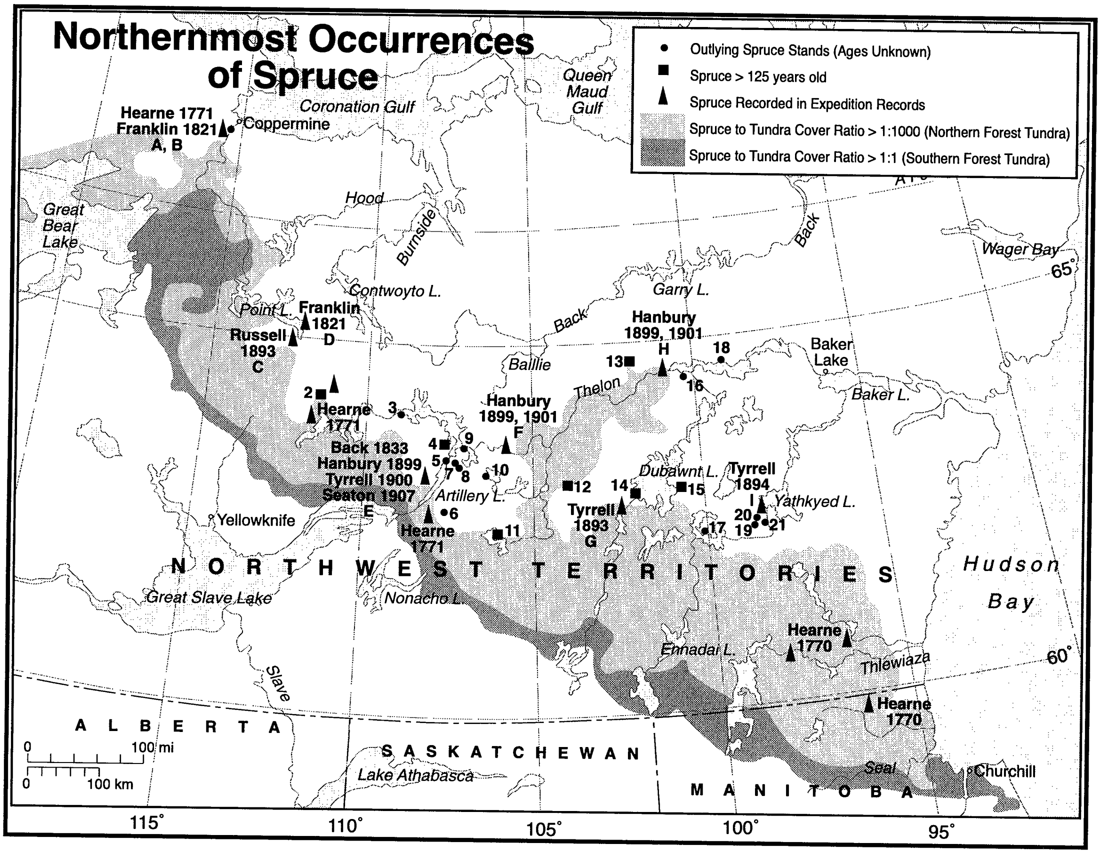

**Figure 13.** Location of first or last trees encountered by eighteenth, nineteenth and early twentieth-century explorers. Location of northernmost trees observed during late twentieth century (from Table 3) and locations where trees >125 years in age occur.

with the map of the extreme northern "tree limit" provided by Elliott-Fisk (1983), when it would have been more appropriate to compare it with her more southerly treeline, which she defined as the northern limits of boreal woodland.

The lack of evidence for significant northward range extension following the Little Ice Age is strikingly similar to the situation in northern Quebec. Evidence from tree rings and radiocarbon-dated wood and charcoal indicates that the species limits of spruce have not changed significantly over the past 3,000 years (Payette and Filion 1985; Payette and Gagnon 1985; Payette et al. 1989; Payette and Lavoie 1993; Lavoie and Payette 1996). The apparent geographic stability of the northern limits of spruce indicates an ability to persist through periods of harsh climate coupled with an inability to quickly expand in range during favorable periods.

The ability of spruce to persist once established, even in the face of severe climatic stress, is a product of longevity, phenotypic plasticity, and vegetative reproduction. Longevity allows individuals to persist for centuries, and thus to maintain populations during periods of climatic stress, when sexual reproduction is not possible (Brubaker 1986). Plasticity allows the species to survive in a krummholz form during harsh winters. In addition, the low stature allows the trees to optimize warming by long-wave radiation at the ground surface during the summer. This aids in photosynthesis and in the production of viable seeds and pollen. When conditions improve, the trees can again grow upright. Finally, both white and black spruce can regenerate vegetatively by layering (Elliott 1979; Elliott-Fisk 1983; Payette and Filion 1985; Szeicz and MacDonald 1995b). This allows both for a rapid increase in the number of stems and for microclimatic changes that can benefit the trees during climatic amelioration, even when conditions remain too harsh for sexual reproduction. Given this ability, it is

**Table 3.** Location of Spruce Outliers

Nineteenth and Early Twentieth-Century Records of *Picea* sp.

| Site (Fig. 8) | Lat. | Long. | Expedition | Year Recorded |
|---|---|---|---|---|
| A | 67° 34' N | 115° 55' W | Franklin | 1821 |
| B | 67° 35' N | 115° 30' W | Franklin | 1821 |
| C | 64° 55' N | 112° 20' W | Russell | 1898 |
| D | 65° 00' N | 111° 59' W | Franklin | 1821 |
| E | 63° 11' N | 107° 55' W | Back, Tyrrell, Hanbury, Seaton | 1833, 1899, 1900, 1907 |
| F | 63° 35' N | 106° 00' W | Hanbury | 1899, 1901 |
| G | 62° 53' N | 102° 13' W | Tyrrell | 1893 |
| H | 64° 30' N | 101° 15' W | Hanbury | 1899, 1901 |
| I | 62° 32' N | 98° 20' W | Tyrrell | 1894 |

Sitings recorded by Hearne are omitted due to uncertainty over exact coordinates. The general location of his sitings can be estimated from geographic features and are indicated on Fig. 8.

Modern Observations

| Site (Fig. 8) | Lat. | Long. | Species | Age | Source |
|---|---|---|---|---|---|
| 1 | 67° 37' N | 115° 30' W | *Picea* sp. | ? | Guerts 1985 |
| 2 | 64° 05' N | 111° 15' W | *Picea mariana* | >125 yr | This study |
| 3 | 64° 02' N | 109° 10' W | *Picea* sp. | ? | Larsen 1989 |
| 4 | 63° 39' N | 108° 02' W | *Picea mariana* | >125 yr | This study |
| 5 | 63° 27' N | 107° 40' W | *Picea* sp. | ? | Larsen 1989 |
| 6 | 62° 50' N | 107° 28' W | *Picea* sp. | ? | Larsen 1989 |
| 7 | 63° 35' N | 107° 23' W | *Picea* sp. | ? | Larsen 1989 |
| 8 | 63° 40' N | 107° 05' W | *Picea* sp. | ? | Larsen 1989 |
| 9 | 63° 57' N | 106° 58' W | *Picea* sp. | ? | Larsen 1989 |
| 10 | 63° 45' N | 106° 30' W | *Picea* sp. | ? | Larsen 1989 |
| 11 | 62° 35' N | 106° 20' W | *Picea glauca* | >125 yr | This study |
| 12 | 63° 13' N | 104° 30' W | *Picea glauca* | >125 yr | This study |
| 13 | 64° 40' N | 102° 26' W | *Picea glauca* | >125 yr | This study |
| 14 | 62° 54' N | 102° 09' W | *Picea glauca* | | |
| | | | *Picea mariana* | ~125 yr | Hansell et al. 1971 |
| 15 | 63° 02' N | 100° 47' W | *Picea mariana* | >125 yr | Kay 1978 |
| 16 | 64° 30' N | 100° 20' W | *Picea* sp. | ? | Hansell et al. 1971 |
| 17 | 62° 15' N | 100° 15' W | *Picea* sp. | ? | Larsen 1989 |
| 18 | 64° 40' N | 99° 00' W | *Picea* sp. | ? | Hansell et al. 1971 |
| 19 | 62° 26' N | 98° 43' W | *Picea* sp. | ? | Larsen 1989 |
| 20 | 62° 35' N | 98° 25' W | *Picea* sp. | ? | Larsen 1989 |
| 21 | 62° 24' N | 98° 18' W | *Picea* sp. | ? | Larsen 1989 |

possible that the northernmost individuals of white and black spruce found today (Table 3; Figure 13) represent the maximum range of spruce in the Holocene in central Canada. Extensive studies using fossil pollen, charcoal, tree rings, and soils have determined this to be the case in northern Quebec (Lavoie and Payette 1996). The inability of white and black spruce to extend their ranges significantly following the end of the Little Ice Age may reflect several factors. First, reproduction at treeline may be greatly aided by the positive feedback between increased growth of existing trees and newly established individuals (Payette and Filion 1985; Scott et al. 1993, 1997). The increased protection from wind and enhanced snow-holding capacity is not available to aid establishment beyond the species limits. Second, although the small trees and krummholz at treeline can produce seeds, the numbers of viable seeds are limited (Elliott 1979;

Elliott-Fisk 1983). Third, despite possessing winged seeds, most seeds dispersed by large white and black spruce trees fall close to the parents (Nienstaedt and Zasada 1990; Viereck and Johnston 1990). The height of seed release from the small spruce at treeline is too low to provide for large dispersal distances, and as a result, seed densities beyond the immediate vicinity of the parent trees will be extremely low. Fourth, the presence of water-logged and disturbed areas associated with continuous permafrost, coupled with areas of thick organic layer or bare rock, makes many sites unsuitable for establishment. Therefore, the probability of a seed being carried to a hospitable spot during a suitable year for establishment at the extreme limits of the species must be very small.

## Conclusion

The potential for a large northward displacement of treeline in central Canada (Figure 2) and the impact of such a displacement on climate (Figure 1) makes it important to understand the potential response of this region to climate warming. Based upon the analysis of dendrochronological and historical records, it can be concluded that the treeline zone of central Canada is sensitive to recent temperature variations associated with the close of the Little Ice Age. There has been an increase in recruitment of trees at the northern edge of the treeline in concert with warming between 1880 and 1950. It does not appear, however, that there has been a significant northward advance of the forest or of the range limits of tree species during this period. These results are comparable to the findings of similar tree-ring-based studies in eastern and western Canada and indicate that the response of the treeline in central Canada to recent climatic changes is part of a transcontinental phenomenon. What are the implications of these results for anticipating the impact of future warming due to the greenhouse affect?

Global warming scenarios anticipate a seasonal or annual warming of 1–4°C in the treeline zone of Canada in the next century (Houghton et al. 1996). This scale of warming is not much greater than that experienced at the close of the Little Ice Age. Based on the results presented here, it is likely that such warming would initially be registered as an increase in sexual reproduction at the northernmost stands of white and black spruce. Research from Quebec suggests that increased sexual reproduction might even occur more rapidly than changes in the form of trees from krummholz to upright growth (Payette et al. 1985). The feedbacks between stand density and reproduction should enhance the rate of infilling during warming (Pastor 1993; Scott et al. 1997). The small disjunct populations that occur at the northern limits of spruce will serve as inoculation foci for increases in tree density beyond the mapped forest-tundra zone (MacDonald et al. 1993). This could allow for a relatively rapid infilling by forest of the forest-tundra zone of central Canada, where trees are now present (Figure 13), with significant changes seen within perhaps 100–150 years (MacDonald et al. 1993).

The movement of tree species north will probably be slower than changes in stand density. The potential for transport of seeds to suitable spots beyond the limits of spruce will rise as tree height and reproductive capacity increase. The average height of the treeline spruce is relatively short (Table 1), however, so it may take decades for significant changes in the form and height of the trees to occur (Payette et al. 1985). Yet once trees are established beyond the current range limits, they will be extremely persistent and will serve as inoculation foci promoting infilling of the new range limits (MacDonald et al. 1993; Scott et al. 1997). Given the limited response of tree range limits and the forest boundary to warming between 1880 and the present, it is quite likely that significant changes in spruce range limits and infilling of forest behind the new range limits could well take centuries in central Canada. Thus, even if increases in greenhouse gases stabilize in the next century, the continued spread of boreal forest to its new, climatologically controlled range limits could cause a continued rise in temperatures until the treeline reaches some equilibrium with climate.

## Acknowledgments

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