

1991

Reversion of forest to tundra in the central Yukon

Les C. Cwynar

Ray W. Spear
SUNY Geneseo

Follow this and additional works at: <https://knight scholar.geneseo.edu/biology>

Recommended Citation

Cwynar L.C., Spear R.W. (1991) Reversion of forest to tundra in the central Yukon. *Ecology* 72: 202-212.
doi: 10.2307/1938915

This Article is brought to you for free and open access by the By Department at KnightScholar. It has been accepted for inclusion in Biology Faculty/Staff Works by an authorized administrator of KnightScholar. For more information, please contact KnightScholar@geneseo.edu.

REVERSION OF FOREST TO TUNDRA IN THE CENTRAL YUKON¹

LES C. CWYNAR

Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 6E1

RAY W. SPEAR²

Fulton Montgomery Community College, Johnstown, New York 12905 USA

Abstract. Pollen and plant macrofossil analyses of sediments from three sites in the central Yukon that are presently in shrub tundra provide a record of former forest establishment. Shrub tundra with groves and gallery forests of balsam poplar occupied the region between 10 000 and 8000 BP. At 9400 BP white spruce (*Picea glauca*) populations expanded, and open white spruce woodlands persisted until 6500 BP when black spruce (*Picea mariana*) and green alder (*Alnus viridis*) populations increased, resulting in open spruce woodlands with a distribution of species probably similar to that commonly found today in the northern boreal forest: white spruce on drier south-facing slopes and on alluvial sites with balsam poplar, and black spruce on colder, wetter sites on north-facing slopes and valley bottoms. At 5000 BP forest began to revert to shrub tundra, abruptly at first but then more gradually. The modern groves of spruce in the region, which are mostly white spruce, therefore are probably relict populations surviving in favorable microsites. These results support the conclusion from other recent studies that Alaska and northwest Canada experienced warmer summers than today from as early as 10 000 BP to ≈6000 BP in response to increased summer insolation arising from changes in the earth's orbital parameters as predicted by the Astronomic Theory of climate change. The decline of forest after 5000 BP is not associated with any significant changes in the abundance of shrub or herb pollen types, suggesting that the ground vegetation has behaved independently of the tree populations.

Key words: Astronomic Theory; black spruce; central Yukon; forest history; paleoecology; palynology; plant macrofossils; tundra; white spruce.

INTRODUCTION

Ecologists and paleoecologists both attempt to study “the interactions that determine the distribution and abundance of organisms” (Krebs 1978). In general, the ultimate factor affecting the distribution and abundance of vegetation is climate (Woodward 1981). The relationship of vegetation to climate is clearest at vegetation boundaries, a fact that has proved of great value in reconstructing the past dynamics of climate and vegetation, as in the study of changes in the prairie–forest boundary (McAndrews 1966) and arctic tree line (Ritchie and Hare 1971, Spear 1983, Payette et al. 1985, Payette and Filion 1985). Vegetation boundaries and ecotones are especially sensitive to climate change, making them ideal for reconstructing past climates and for studying the dynamics of community change.

Yukon Territory is transected by westward extensions of the Mackenzie Mountain system, resulting in a broad belt of tundra (Fig. 1) between closed boreal forest to the south and forest-tundra to the north (Rowe

1972). Groves of white spruce (*Picea glauca*), and occasionally black spruce (*P. mariana*), are scattered throughout this mountainous region on climatically favorable sites on south- to southwest-facing slopes (Fig. 2). Previous studies (Brubaker et al. 1983, Ritchie et al. 1983, Ritchie 1984a, Edwards et al. 1985) have shown that areas north of the central Yukon and adjacent Alaska experienced a period of warmth greater than modern climate from ≈10 500 to 5500 BP, coincident with higher insolation values predicted by the Astronomic Theory for high northern latitudes (Berger 1981, Kutzbach and Guetter 1986, COHMAP 1988).

We undertook this study to answer a number of related questions: (1) Was this belt of tundra previously forested? Valley floors in the region are scarcely higher than the altitudinal limit of trees in the boreal forest to the south, and as groves of trees occur in favorable localities today, the study area is sensitively located to respond to past changes of climate. The area would likely have been forested during the warm interval centered around 10 000 BP. A somewhat abbreviated pollen diagram from a bog near Chapman Lake (Fig. 1) analyzed by Terasmae and Hughes (1966) suggests that spruce forests may have grown in the region previously. However, Terasmae and Hughes (1966) drew no conclusions regarding the past vegetation since they were

¹ Manuscript received 23 October 1989; revised 6 April 1990; accepted 20 April 1990.

² Present address: Empire State College, State University of New York, 317 Washington Street, Watertown, New York 13601-3744 USA.

chiefly interested in the chronology of glaciation. (2) What is the origin of these isolated spruce groves? These groves may simply represent populations established by long-distance dispersal to favorable local habitats in what has always been essentially tundra, or they may be relict populations from a time when forest was more extensive. (3) If the area was previously forested, is the present tundra, then, simply the past vegetation minus the trees or is it fundamentally different from the understory vegetation of past forests? Ritchie (1986) has drawn the important distinction between "tree line" and "tree-line vegetation," noting that changes in tree-line species are "better thought of as responses of particular species populations to climate variations" rather than changes in vegetation. He also noted that few species limits coincide with tree line and that in northern Québec Morisset et al. (1983) demonstrated that most arctic and boreal taxa occur on both sides of tree line. If our study area was forested, it would provide a test of the hypothesis that shrubs and plants composing the ground vegetation in forested areas may act independently of tree populations, and therefore tree line, in the face of climate change.

SITE DESCRIPTIONS

The study area lies within the Southern Ogilvie Ranges, which have been glaciated repeatedly by montane glaciers that were independent of the Cordilleran ice sheet (O. L. Hughes, *personal communication*). Grayday Pond (64°57' N, 138°15' W, 915 m above sea level (asl); Fig. 2b) lies within the old floodplain of the Blackstone River in a region that was last glaciated more than a million years ago. Both Honeymoon Pond (64°38' N, 138°24' W, 1160 m asl; Fig. 2c) and Monkshood Pond (64°34' N, 138°15' W, 1280 m asl; Fig. 2d) lie just within terminal moraines of valley glaciers that spilled into the North Fork Pass during late Wisconsin time (Fig. 1). All of the ponds have a surface area < 1 ha, and none has an inflowing stream. The names that we have assigned to our sites are informal.

The three sites are located in shrub tundra. Isolated stands of predominantly white spruce are scattered throughout the area (Fig. 2a, b) and the largest of these, which are noted on 1:250 000 scale topographic maps, are shown in Fig. 1. Black spruce groves are generally much less common. Balsam poplar groves are restricted to alluvial sites and bluffs along the lower third of the Blackstone River in our study area and appear to be absent in interfluvies. We did not, for example, find balsam poplar in any of the white spruce groves that we visited, although such an admixture is commonplace in the boreal forest. Fingers of continuous forest of black spruce on valley bottoms and north-facing slopes and white spruce on drier and warmer sites extend to within 6 km of Monkshood, the southernmost site, and 3 km of Grayday, the northernmost site. The main body of the boreal forest lies ≈22 km south of

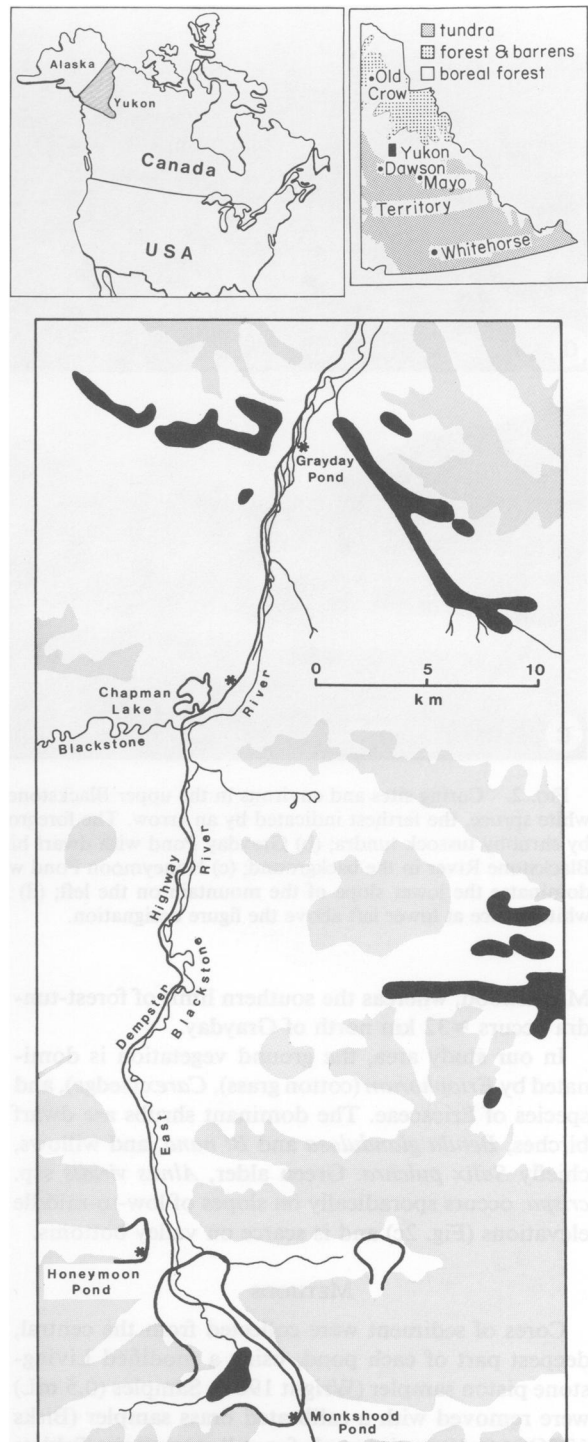


FIG. 1. Map showing the location of the study area. Shaded areas indicate land >1370 m above sea level, blackened areas represent stands of trees that appear on 1:250 000 map sheets, and heavy lines in lower part of map show the limits of Late Wisconsin valley glaciers. The insert shows the vegetation regions according to Rowe (1972).

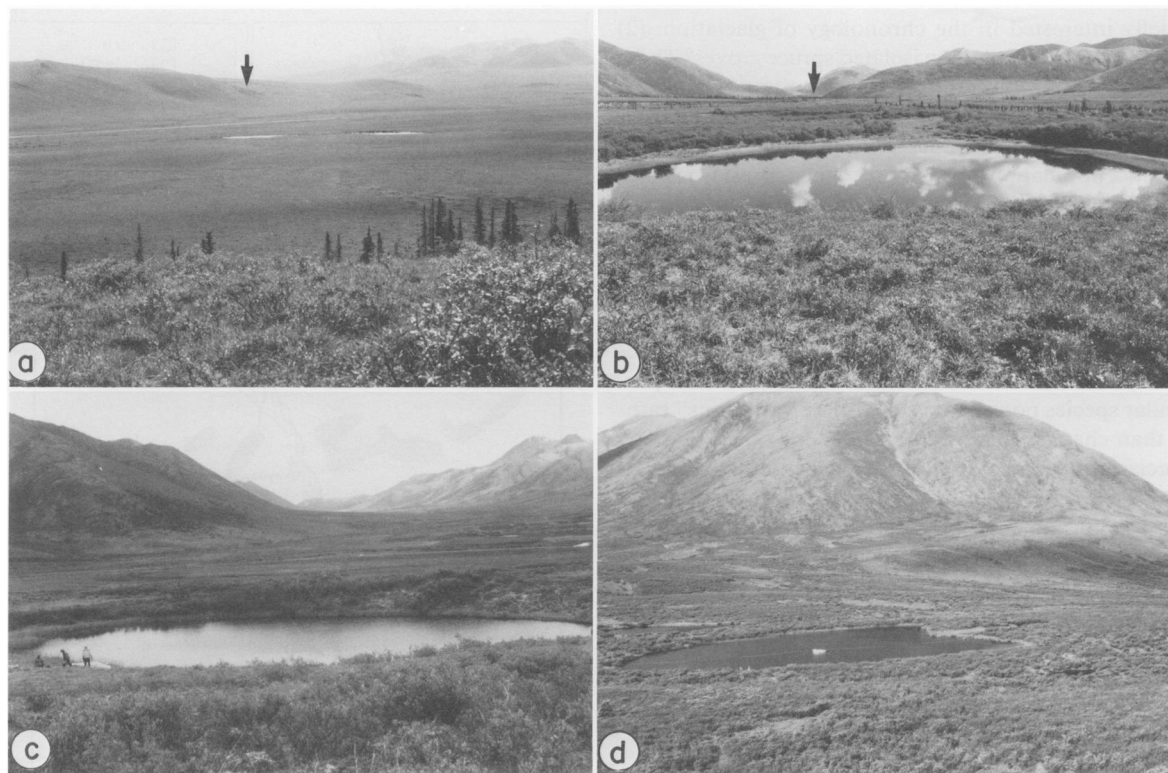


FIG. 2. Coring sites and environs in the upper Blackstone River. (a) Central portion of the study area with two stands of white spruce, the farthest indicated by an arrow. The foreground is dominated by willows and the valley bottom is covered by shrubby tussock tundra; (b) Grayday Pond with dwarf birch shrub tundra in the foreground and white spruce along the Blackstone River in the background; (c) Honeymoon Pond with willows dominating the shrub tundra locally, although alder dominates the lower slope of the mountain on the left; (d) Monkshood Pond surrounded by shrub tundra with a solitary white spruce at lower left above the figure designation.

Monkshood, whereas the southern limit of forest-tundra occurs ≈ 32 km north of Grayday.

In our study area, the ground vegetation is dominated by *Eriophorum* (cotton grass), *Carex* (sedge), and species of Ericaceae. The dominant shrubs are dwarf birches, *Betula glandulosa* and *B. nana*, and willows, chiefly *Salix pulchra*. Green alder, *Alnus viridis* ssp. *crispa*, occurs sporadically on slopes of low-to-middle elevations (Fig. 2c) and is scarce on valley bottoms.

METHODS

Cores of sediment were collected from the central, deepest part of each pond, using a modified Livingstone piston sampler (Wright 1967). Samples (0.5 mL) were removed with a calibrated brass sampler (Birks 1976) at 2–10 cm intervals for pollen analysis. Tablets of *Lycopodium* spores (Stockmarr 1971) were added to each sample before preparation by standard methods (Faegri and Iversen 1975), which included sieving through 7- μ m mesh screens to remove fine inorganic sediment (Cwynar et al. 1979). A minimum sum of 300 pollen and spores of terrestrial taxa was tallied for each sample and used to calculate pollen percentages. Black and white spruce pollen grains were identified using the qualitative technique of Hansen and Eng-

strom (1985). After sampling for pollen, cores were cut into 5-cm sections, which were washed through a sieve with meshes of 0.5 mm in order to extract plant macrofossils. All macrofossils were identified by comparison with modern reference collections. Bulk samples of sediment for radiocarbon dating were submitted to either the Radiocarbon Laboratory of the Geological Survey of Canada or Beta Analytic. Two samples of terrestrial macrofossils were submitted to the IsoTrace Laboratory of the University of Toronto for accelerator-mass spectrometer (AMS) ^{14}C dating.

RESULTS

Chronology

The radiocarbon dates fall into proper chronological order, except for one reversal at the base of Grayday (GSC-3868) and three anomalous dates (Beta-20913, -26560, and -20915) at Honeymoon (Table 1). The uppermost 10 cm of Honeymoon, which contained mollusc shells, were calcareous, but none of the other sediments reacted with 10% HCl. In order to test the validity of the oldest conventional radiocarbon date at Honeymoon, which was based on a bulk-sediment sample, we submitted two samples from the base of the section for AMS ^{14}C dating, 23 mg of twigs (TO-

1539) and 16 mg of wood fragments (TO-1538). As a result of the AMS dates, we reject as too old Beta-20919 and have excluded it from age–depth regressions. To calculate a time scale for the paleoecological record, we fit second-degree polynomial curves to plots of age vs. depth for Grayday and Honeymoon, and a linear regression to the data from Monkshood (Fig. 3). All three of our sites begin organic sedimentation at $\approx 10\,000$ BP, although older dates have been reported from the region (Terasmae and Hughes 1966, Lowden and Blake 1968).

Paleoecological record

Pollen percentages and plant macrofossils

1. *Tree species*.—At all three sites, populations of trees became quickly established (Fig. 4). Balsam poplar (*Populus balsamifera*) pollen percentages are maximal (15%) at the start of the record at Grayday and remain relatively high until ≈ 6500 BP. The local presence of balsam poplar at Grayday is confirmed by the occurrence of its bud scales in several samples. At Honeymoon a small peak of balsam poplar pollen occurs at ≈ 9400 BP, whereas at Monkshood balsam poplar pollen occurs at $10\,000$ BP, rises to a maximum of 12% at 9000 BP, and gradually declines to low values after 8000 BP.

Shortly after the increase of poplar pollen, spruce (*Picea*) pollen percentages increase. At all sites the initial increase of spruce pollen is attributable to white spruce (*P. glauca*), which reaches values of 10%, the value generally used to presume local presence, by 9900 BP at Grayday, 9000 BP at Honeymoon, and 8700 BP at Monkshood. Spruce needles also occur early in the records of each site, first appearing at 9400 BP at Grayday, 8900 BP at Honeymoon, and 8500 BP at Monkshood. The occurrence of spruce needles establishes the presence of spruce populations nearby since spruce needles are not dispersed far from their source (Glaser 1981). Unfortunately no reliable method for identifying spruce needles to species has been developed so their identities are unknown. At Grayday the local presence of white spruce between 7000 and 8000 BP is confirmed by the occurrence of intact ovulate cones of white spruce.

At all sites there is a shift in the spruce pollen curves from predominantly white spruce to black spruce, beginning at 6000 BP at Grayday, 6700 BP at Honeymoon, and 6500 BP at Monkshood. This rise in prominence of black spruce coincides with increasing percentages of green alder (*Alnus viridis*) pollen. From 6000 BP to the present, total spruce percentages remain relatively constant. Percentages of white spruce decline, especially after 2000 BP, while those of black spruce increase to 15% or more at the three sites. At Grayday there are two anomalously high values for black spruce.

Pollen of lodgepole pine (*Pinus contorta*) becomes increasingly abundant at each of the sites beginning at

TABLE 1. Radiocarbon dates from sediment cores.

Laboratory no.	Depth of sediment (cm)	Radiocarbon age (yr BP ± 1 sd)
Grayday Pond		
GSC-3805	25–30	1240 \pm 70
GSC-3790	55–60	2600 \pm 70
GSC-3876	71–75	4230 \pm 70
GSC-3779	86–89	6160 \pm 80
GSC-3870	99–102	8130 \pm 100
GSC-3770	110–113	9520 \pm 110
GSC-3868	121–126	8380 \pm 90
Honeymoon Pond*		
Beta-20909	55–60	1590 \pm 50
Beta-26554	110–115	2410 \pm 70
Beta-20910	155–160	3240 \pm 60
Beta-26555	195–200	3840 \pm 80
Beta-26556	220–225	4290 \pm 70
Beta-20911	239–244	5390 \pm 60
Beta-26557	265–270	6050 \pm 80
Beta-26558	280–285	6480 \pm 80
Beta-20912	288–293	6620 \pm 100
Beta-26559	300–305	6770 \pm 70
Beta-20913	310–315	6680 \pm 80
Beta-26560	320–325	8970 \pm 200
Beta-20914	330–335	7770 \pm 100
Beta-20915	353–357	7300 \pm 100
Beta-20916	360–365	8900 \pm 100
Beta-20917	368–372	9260 \pm 100
TO-1538†	372–375	9220 \pm 80
Beta-20918	375–379	9540 \pm 100
Beta-20919	382–388	11 100 \pm 100
TO-1539†	388–391	9390 \pm 100
Monkshood Pond*		
GSC-3899	60–65	2440 \pm 90
GSC-3893	95–100	3930 \pm 100
GSC-3890	125–130	4690 \pm 80
GSC-3879	155–160	6590 \pm 90
GSC-3881	175–180	7830 \pm 90
GSC-3866	190–195	8310 \pm 100
GSC-3847	225–235	9440 \pm 100

* Grayday and Monkshood sediment dates were corrected for $^{13}\text{C}/^{14}\text{C}$ fractionation.

† Accelerator-mass spectrometer ^{14}C dates; all other dates are conventional dates of bulk samples.

some time between 5000 (Grayday) and 2000 (Monkshood) BP. Because the modern northern limit of pine in interior Yukon is ≈ 160 km to the southeast near Mayo and the highest pollen values occur in the youngest sediments, it is highly unlikely that lodgepole pine was present within the study area during the period of record; the pine curves will therefore not be discussed further in this paper.

2. *Shrubs and herbs*.—Shrub pollen dominates the records from all three sites. Birch (*Betula*) pollen predominates, especially early in the records when it frequently reaches values of 60–80%. All of the birch seeds recovered (Fig. 4) are from dwarf birches, either *B. nana* or *B. glandulosa*. The basal portion of a *B. glandulosa* leaf dating from 2900 BP was recovered from Grayday. Juniper (*Juniperus*) pollen occurs at consistently low values of 1–4% from ≈ 9600 to 8900 BP at Honeymoon and only sporadically at the other two sites. Similarly, pollen of soapberry (*Shepherdia cana-*

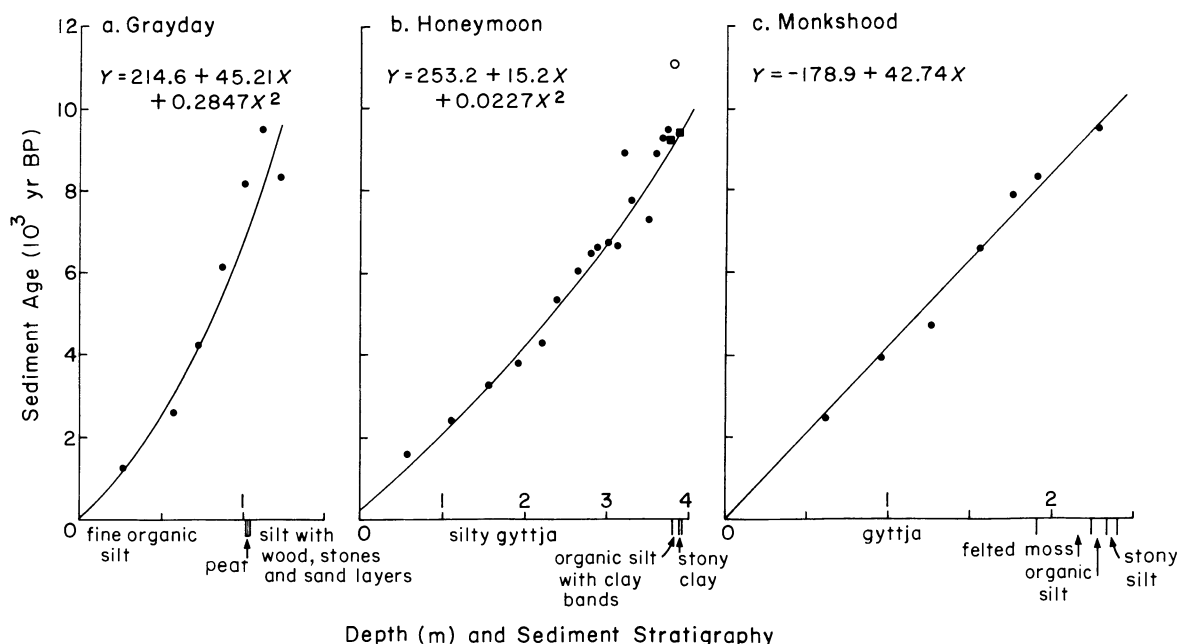


FIG. 3. Sediment stratigraphy and sediment age vs. depth curves. For (b), ○ represents a rejected conventional date (see Results: Chronology); the other symbols represent accepted conventional (●) or AMS (accelerator-mass spectrometer) (■) dates.

densis) occurs at consistently low values between ≈ 9600 and 8000 BP at Honeymoon and infrequently at Grayday and Monkshood between 10 000 and 7000 BP. Willow (*Salix*) pollen is a characteristic feature of all three sites, but percentages vary little with only a slight tendency to higher values between 10 000 and 7000 BP. The pollen percentages of heaths (*Ericaceae*) also show little variation at each of the sites. The only heath macrofossils recovered were seeds of the subshrub crowberry (*Empetrum*).

Sedge (*Cyperaceae*) is the most abundant herb pollen type. Percentages of pollen for sedge (Fig. 4) are constant at Grayday and Honeymoon, but at Monkshood there is a peak of sedge pollen in sediment composed of felted aquatic moss remains dating from 9700 to 8100 BP. Macrofossils of sedges are abundant at Grayday but infrequent at the other two sites. Pollen of grasses (*Gramineae*) and sages (*Artemisia*) occurs in most samples at values $< 10\%$ each. At Grayday and Monkshood spores of horsetails (*Equisetum*) are abundant between $\approx 10\,000$ and 7800 BP and then decline, increasing again at Grayday at 1500 BP. The curve for horsetails shows little variation at Honeymoon.

Other herbs are most abundant at Grayday and Monkshood from 10 000 to 7800 BP. At Grayday, pollen of the carnation family (*Caryophyllaceae*) is most prominent, whereas at Monkshood the bulk of other

herb pollen is derived from sorrels (*Rumex/Oxyria*), ferns (*Dryopteris* type), and various types from the rose (*Rosaceae*) family. At Honeymoon, other herbs are slightly more abundant between ≈ 9600 and 8500 BP, the most important being a variety of types from the rose family.

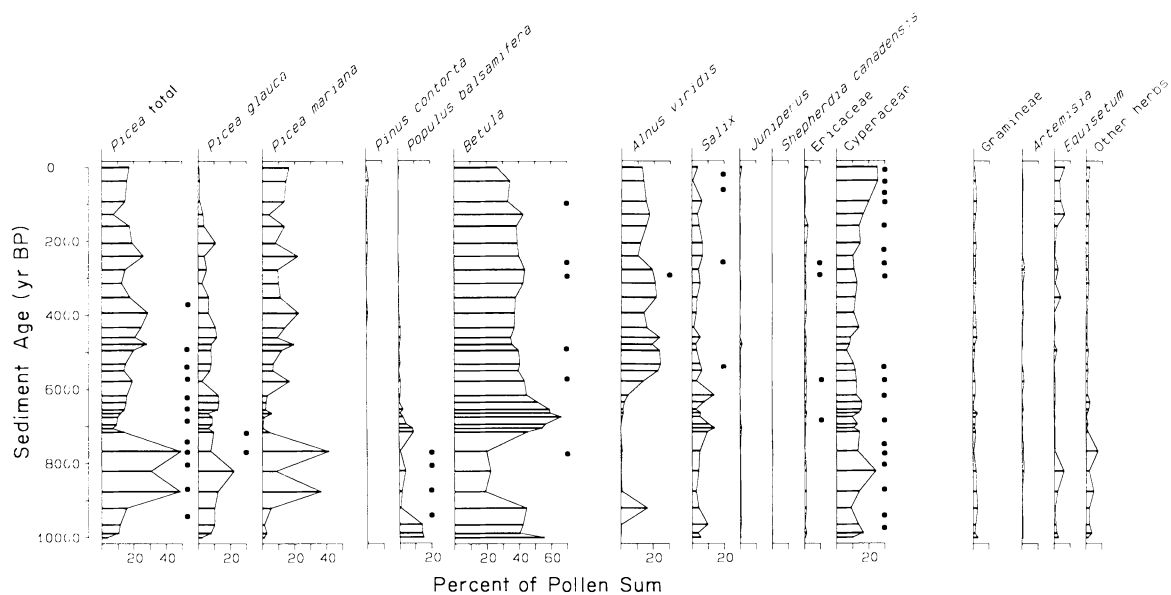
Pollen accumulation rates (PARs)

Diagrams of pollen accumulation rates (PARs) for major taxa were constructed for Honeymoon (Fig. 5) and Monkshood (Fig. 6). The Monkshood diagram spans only the most recent 8000 yr. Sediment prior to this differs greatly in composition (Fig. 3), and therefore in its pollen-trapping characteristics; it contains fewer pollen grains of all types. A diagram was not made for Grayday because of difficulties with the suspension of exotic pollen used to spike the samples.

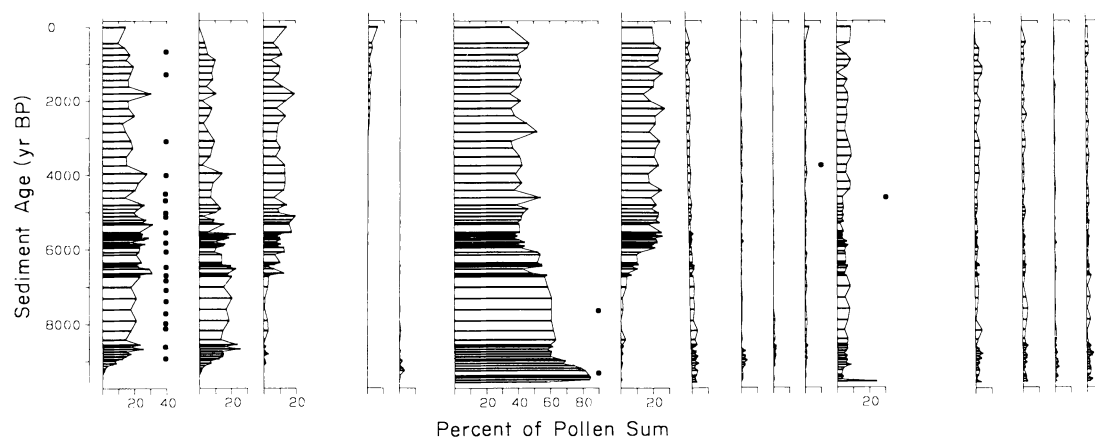
Trends in PAR curves for Honeymoon (Fig. 5) and Monkshood (Fig. 6) correspond closely with trends in percentage curves (Fig. 4). Total PARs are low at both sites but are generally twice as great at Honeymoon ($4000\text{--}8000\text{ grains}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$) than at Monkshood ($2000\text{--}4000\text{ grains}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$). At both sites PARs of all taxa decline after 2000 BP. At Honeymoon, which has a conical basin, this decline may be explained by a combination of decreased sediment focussing (Davis et al. 1984) and reduced compaction of the sediment,

FIG. 4. Pollen percentage diagrams for the sites studied. Dots indicate the presence of plant macrofossils: needles for *Picea* total, ovulate cones for *P. glauca*, terminal bud scales for *Populus balsamifera*, seeds (nutlets) for *Betula* (all of the dwarf birch type), ovulate cone bracts for *Alnus viridis*, *Empetrum* seeds for *Ericaceae*, and fruits for *Cyperaceae*.

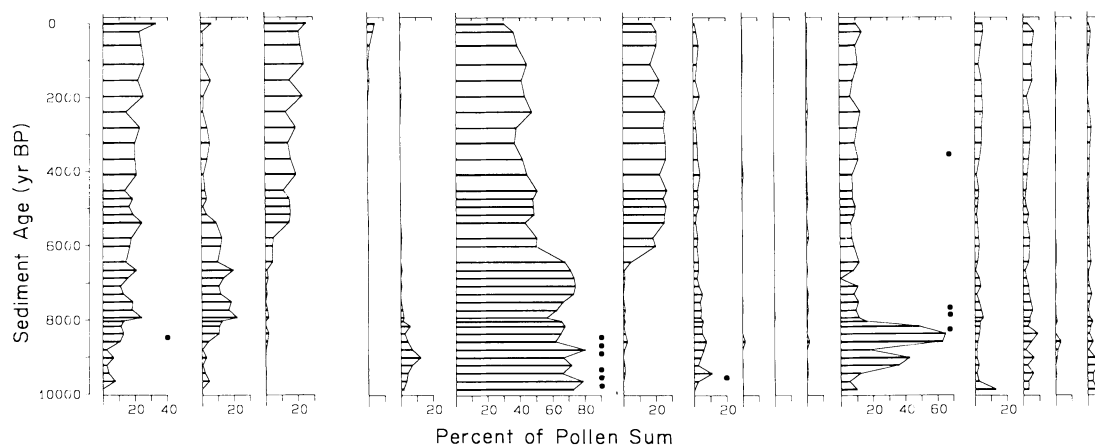
GRAYDAY POND



HONEYMOON POND



MONKSHOOD POND



HONEYMOON POND

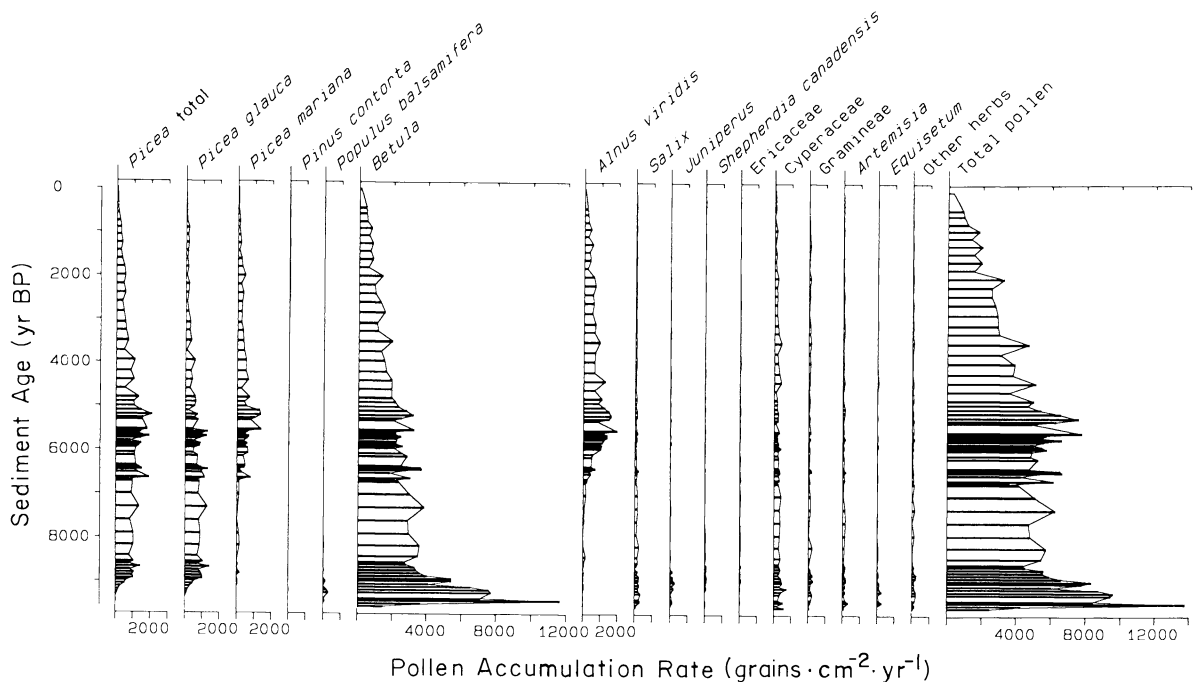


FIG. 5. Pollen accumulation rate (PAR) diagram for Honeymoon Pond. Note scale changes.

whereas only the latter explanation likely applies to Monkshood, which has a relatively flat-bottomed basin so that sediment focussing has probably not been an important phenomenon affecting sedimentation rates, a conclusion supported by the fact that the curve of radiocarbon ages vs. depths for Monkshood is best modelled by a linear regression (Fig. 3). Alternatively, the recent declines in PARs of all taxa may reflect the effects of colder climates on pollen production during Neoglacial times.

Spruce summary

Because this paper focusses on the history of spruce, we have summarized the spruce pollen data, both relative and PAR, and macrofossil data for the three sites in Fig. 7. When plotted as concentrations, rather than as presence/absence data as in Fig. 4, the macrofossil data show clearly the local presence of spruce between 9400 and 5000 BP at Grayday and between 8900 and 5000 BP at Honeymoon. Macrofossils of all types, except mosses, were uncommon in the sediments of Monkshood. The initial increase of white spruce, followed by its eventual decline as black spruce increased, is reflected in both the percentage and PAR curves.

DISCUSSION AND CONCLUSIONS

Our results provide clear evidence for the establishment of trees at 10 000 BP, or shortly thereafter, at all three sites that are presently in tundra. Balsam poplar

was the first tree present. Edwards and Dunwiddie (1985) studied the dispersal of pollen from groves of balsam poplar on the North Slope of Alaska and found that little pollen travels beyond 30 m, as recorded in moss polsters. The balsam poplar pollen found at our sites therefore probably means that the species was present locally. This conclusion from the pollen data is confirmed for Grayday by the recovery of bud scales of balsam poplar. A period of peak abundance of poplar centered around 10 000 BP is a common feature of pollen diagrams from Alaska, Yukon Territory, and adjacent Northwest Territories (Ritchie 1984a, 1987). Anderson et al. (1988) reviewed the spatial distribution and dating of sites containing the poplar zone. They concluded that poplar probably did not form extensive woodlands or scrub forests in eastern Beringia but rather was probably "restricted to gallery forests or localized groves." This conclusion seems applicable to our study area where the duration and values of balsam poplar abundance vary greatly between sites. Also, the predominance of birch pollen, which the macrofossils indicate is derived from dwarf birches, suggests an open landscape. We conclude that balsam poplar was more abundant in groves and gallery forests near our sites between 10 000 and 7000 yr ago, but it did not form a continuous forest.

Between 9400 and 8900 BP, the pollen percentage, PAR, and macrofossil data (Fig. 7) indicate that white spruce populations expanded and soon dominated the forest as balsam poplar declined in abundance. What

MONKSHOOD POND

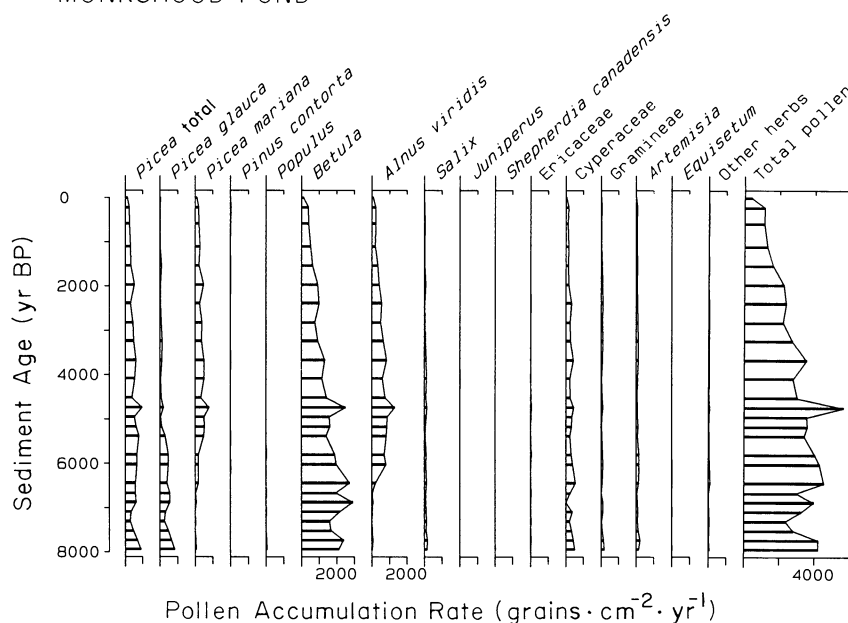


FIG. 6. Pollen accumulation rate (PAR) diagram for Monkshood Pond. Note changes in scale.

was the nature of this white spruce forest? Studies of modern pollen spectra from lake sediments from northern Alaska indicate that the 10% isopoll for total spruce pollen corresponds with tree line, between the 10 and 20% isopolls the vegetation is either open spruce woodlands or forest-tundra, and areas with $\geq 20\%$ total spruce pollen support high tree densities and a nearly continuous forest cover (Anderson and Brubaker 1986). In modern pollen assemblages from near the arctic tree line in the Mackenzie Delta region of northwest Canada, 5–15% spruce pollen occurs in samples from tundra, 11–17% in forest-tundra, and 20–30% in forest (Ritchie 1974, MacDonald and Ritchie 1986). Furthermore, in both study areas, forest-tundra samples contain significantly lower amounts of sedge pollen than tundra samples. For our sites, the percentage data of 15–25% spruce coupled with high percentages of dwarf birch pollen and moderate percentages of sedge at all sites suggests that the region supported either white spruce woodland, i.e., open forests in which $> 50\%$ of the landscape is covered by trees, or forest-tundra, i.e., an extensive cover of open spruce forest with low densities of trees covering $< 50\%$ of the landscape and areas between trees dominated by dwarf birches, similar to that illustrated in Fig. 2f of Ritchie (1974).

The PAR values are useful in resolving this question of interpretation. PARs for total spruce during the period of white spruce predominance range between 1000 and 3000 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ at Honeymoon and between 500 and 1000 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ at Monkshood (Fig. 7). In comparison, PARs for spruce from two sites in northwestern Alaska presently in forest-tundra typ-

ically range from 100 to 250 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ (Anderson 1985, 1988). In the central Brooks Range of Alaska, PARs for spruce at Ruppert Lake, which is today within boreal forest, range from 200 to 1500 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ during the past 5000 yr (Brubaker et al. 1983) and in the east-central Brooks Range at Screaming Yellowlegs Pond, which lies within open forests of white spruce, PARs for spruce generally range from 500 to 1500 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ (Edwards et al. 1985). In the northern Yukon at Lateral Pond, which is situated in open forests of black spruce and is the closest site to ours with PARs, spruce PARs range between 300 and 425 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ (Ritchie 1982). In the southern Yukon where high aridity maintains open forests of white spruce, trembling aspen (*Populus tremuloides*), and lodgepole pine, PARs for white spruce generally fall between 100 and 500 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ in recent sediments (Cwynar 1988). To the northeast of our study area in the Mackenzie Delta area, PARs for spruce at M-Lake, which is within open spruce woodland ≈ 40 km south of tree line, range between 125 and 500 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ (Ritchie 1977) and at nearby Twin Tamarack, which is surrounded by open black spruce forest, they fall between 100 and 200 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ (Ritchie 1985). In the Lower Mackenzie River Basin, at Sweet Little Lake, which lies within open woodlands of black and white spruce, PARs for spruce range from 250 to 800 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ (Ritchie 1984b). At Wild Spear Lake in northern Alberta where black spruce predominates and white spruce is confined to scattered populations on knolls, PARs for white spruce are < 40 $\text{grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ and between

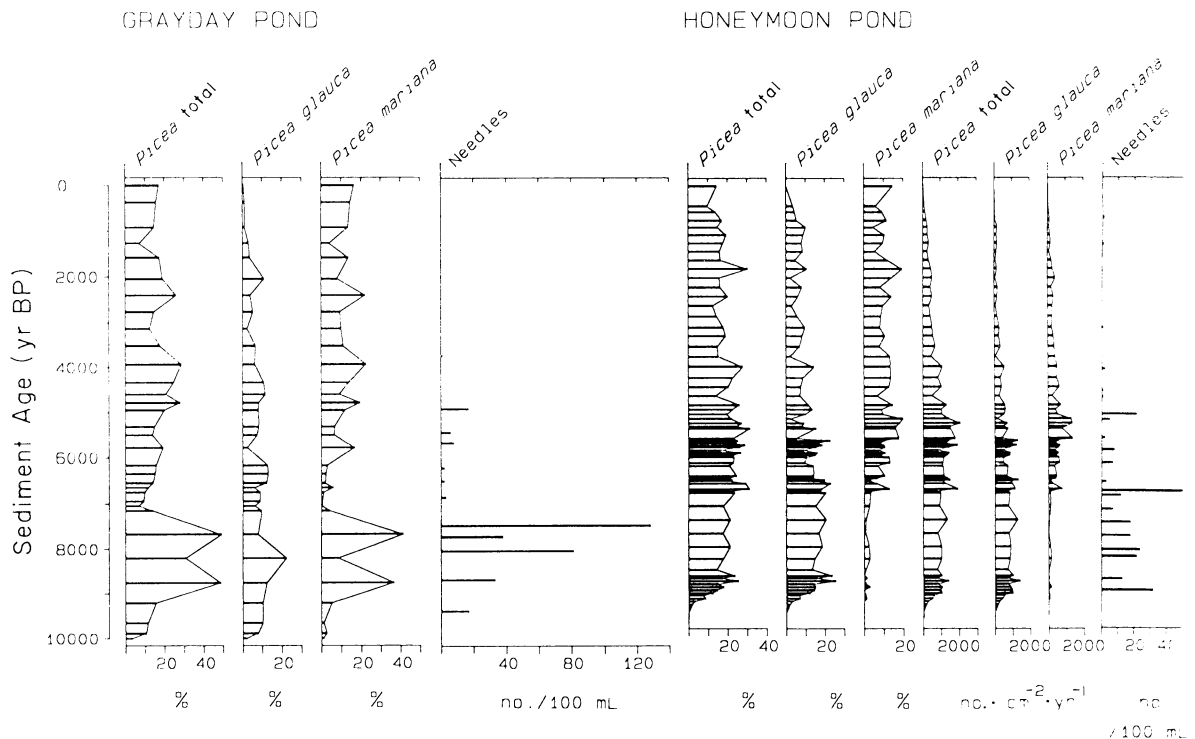


FIG. 7. Summary diagram for spruce data (pollen percentages and influx rates, and macrofossil concentrations).

500 and 1000 grains \cdot cm $^{-2}$ \cdot yr $^{-1}$ for black spruce (MacDonald 1987). The PARs for total spruce pollen at Honeymoon and Monkshood during the period of white spruce predominance are high (1000–3000 grains \cdot cm $^{-2}$ \cdot yr $^{-1}$ and 500–1000 grains \cdot cm $^{-2}$ \cdot yr $^{-1}$, respectively), leading us to conclude that extensive forests of white spruce woodland, rather than forest-tundra, covered the study area between 9400 and 6500 BP.

We believe that the high concentrations of spruce needles (Fig. 7) during this period support this interpretation, although no comparable macrofossil data have been reported from Alaska, Yukon, or the adjacent Northwest Territories. Furthermore, pollen of juniper and soapberry, both of which are common understory shrubs of open white spruce forests in the southwest Yukon today (Douglas 1974) and both of which appear to be absent from our study area, is most abundant at our sites during the period of white spruce predominance.

At \approx 6500 BP, black spruce populations began to increase as white spruce populations decreased, leading to the development of white and black spruce woodlands. PAR values for black spruce at Honeymoon and Monkshood up to 5000 yr ago are comparable to those of white spruce during the early Holocene woodland phase. This, plus the continued presence of spruce macrofossils, suggests that black spruce had well-established woodland populations near our sites. At 5000 BP the spruce woodlands began to decline, abruptly at

first, judging from the scarcity of macrofossils and decline in spruce PARs, followed by a long period of gradual decline to the present state. The low PARs are difficult to interpret in sediments younger than 2000 yr because of problems of sediment focussing and compaction. The caveat of Anderson and Brubaker (1986) that "the specific pollen frequencies that characterize each vegetation type vary from area to area" is especially applicable to our study because unlike the latitudinal zonation from forest to tundra, the tundra region of our study area is bounded by forest both to the south and north so that higher than usual percentages of tree pollen may be expected. Thus, although black spruce percentages in recent sediments are higher than those from some sites in forest-tundra and boreal forest (Ritchie 1974, Anderson and Brubaker 1986, MacDonald and Ritchie, 1986), the lack of spruce macrofossils and rarity of black spruce on the modern landscape clearly indicate that these high percentages cannot be interpreted as representing forest. The forests to the south and north of the study area likely supply most of the black spruce pollen in recent sediments.

To answer the first two questions we posed at the outset, it appears that the region was once forested, initially by groves of balsam poplar more extensive than the few isolated stands now present, then by white spruce woodlands. At 6500 BP, populations of black spruce and green alder increased as black and white spruce woodlands developed and persisted until 5000

MONKSHOOD POINT

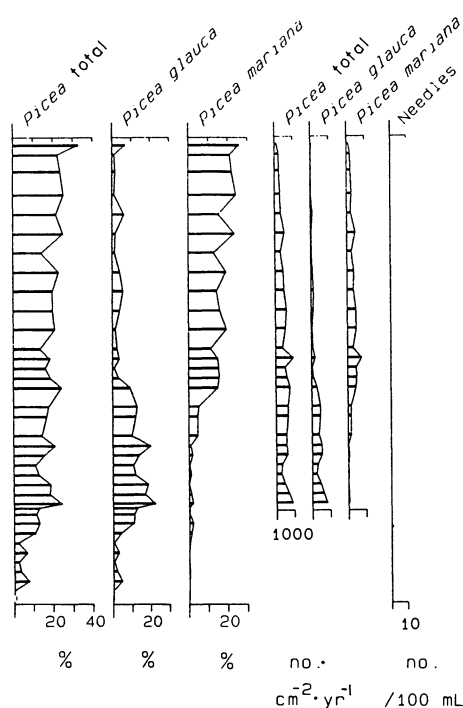


FIG. 7. Continued.

BP, when forests began to give way to shrub tundra. The groves of white spruce present in the region today are therefore probably relict populations which have survived in locally favorable habitats.

If black spruce was more abundant than white spruce in the spruce woodland prior to 5000 BP, then the problem remains as to why there are not more relict stands of black spruce today. The answer probably involves the types of sites on which the two species typically occur. Black spruce grows on wet and cool north-facing slopes and valley bottoms. These sites should be more sensitive to changes in macroclimate (lower insolation and temperature) than the drier and warmer sites on south-facing slopes on which white spruce grows. Although some white spruce habitat might convert to black spruce habitat as climate changed, the overall effect of lower insolation and colder conditions would be to eliminate black spruce populations first; white spruce is usually the species found beyond tree line (Payette 1983, Spear 1983).

The third question of whether or not changes in the forest limit are associated with changes in understory communities is more difficult to answer because of the "bluntness" of pollen analysis in "arctic" environments (Colinvaux 1964) and the relatively low diversity of shrubby and herbaceous types recovered from our sites. Nevertheless, when spruce woodlands begin to decline at 5000 BP, there are no significant changes in the kinds or abundance of associated shrub and herb pollen, either among those taxa plotted on Fig. 4 or

those which are not, such as *Sphagnum*. The only indication of a change is that sedge pollen increases slightly at both Grayday and Honeymoon. It appears from our data that shrub and herb populations may have behaved independently of changes in poplar and spruce populations.

In summary, black and white spruce have shown individualistic responses in their distribution and abundance within the mountains of the central Yukon, as have other species. The prediction of the Astronomical Theory of climate change that at high northern latitudes summer insolation was greatest during the first half of the Holocene (past 10 000 yr of geologic time) is supported by our finding that forests of poplar and spruce occurred at our sites, which lie in shrub tundra, between 10 000 and 5000 BP. There was no unified community response to the decline of black and white spruce at 5000 BP as might have been expected if the physiognomic boundary of tree line had a dramatic effect on microclimate and hence acted on all species more equally and severely than regional climate.

ACKNOWLEDGMENTS

We thank A. Christmas, M. Lacy, E. Leung, and J. Wood for assistance with coring and H. Rodd for assistance with computer graphics. B. Hansen assisted with the pollen analysis. P. Ovenden drafted several of the figures. W. Blake, Jr. and the Geological Survey of Canada kindly provided us with numerous radiocarbon dates. We thank O. L. Hughes for his insights into the glacial history of the study region. This research was supported by an operating grant to L. C. Cwynar from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

- Anderson, P. M. 1985. Late Quaternary vegetational change in the Kotzebue Sound area, northwestern Alaska. *Quaternary Research* 24:307-321.
- . 1988. Late Quaternary records from the Kobuk and Noatak River drainages, northwestern Alaska. *Quaternary Research* 29:263-276.
- Anderson, P. M., and L. B. Brubaker. 1986. Modern pollen assemblages from northern Alaska. *Review of Palaeobotany and Palynology* 46:273-291.
- Anderson, P. M., R. E. Reanier, and L. B. Brubaker. 1988. Late Quaternary vegetational history of the Black River region in northeastern Alaska. *Canadian Journal of Earth Sciences* 25:84-94.
- Berger, A. 1981. Astronomical theory of paleoclimates. Pages 501-526 in A. Berger, editor. *Climatic variations and variability: facts and theories*. Reidel, London, England.
- Birks, H. J. B. 1976. Late-Wisconsinan vegetational history at Wolf Creek, central Minnesota. *Ecological Monographs* 46:395-429.
- Brubaker, L. B., H. L. Garfinkel, and M. E. Edwards. 1983. A late Wisconsin and Holocene vegetation history from the central Brooks Range: implications for Alaskan palaeoecology. *Quaternary Research* 20:194-214.
- COHMAP. 1988. Climate change of the last 18,000 years: observations and model simulations. *Science* 241:1043-1052.
- Colinvaux, P. A. 1967. Quaternary vegetation history of arctic Alaska. Pages 207-231 in D. M. Hopkins, editor. *The Bering land bridge*. Stanford University Press, Stanford, California, USA.
- Cwynar, L. C. 1988. Late Quaternary vegetational history of

- Kettlehole Pond, southwestern Yukon. *Canadian Journal of Forest Research* **18**:1270–1279.
- Cwynar, L. C., E. Burden, and J. H. McAndrews. 1979. An inexpensive sieving method for concentrating pollen and spores from fine-grained sediments. *Canadian Journal of Earth Sciences* **16**:1115–1120.
- Davis, M. B., R. E. Moeller, and M. S. (J.) Ford. 1984. Sediment focusing and pollen influx. Pages 261–293 in E. Y. Haworth and J. W. G. Lund, editors. *Lake sediments and environmental history: studies in paleolimnology and paleoecology in honour of Winifred Tutin*. University of Leicester Press, Leicester, England.
- Douglas, G. W. 1974. Montane vegetation of the Alsek River region, southwestern Yukon. *Canadian Journal of Botany* **52**:2505–2532.
- Edwards, M. E., P. M. Anderson, H. L. Garfinkel, and L. B. Brubaker. 1985. Late Wisconsin and Holocene vegetational history of the Upper Koyukuk region, Brooks Range, AK. *Canadian Journal of Botany* **63**:616–626.
- Edwards, M. E., and P. W. Dunwiddie. 1985. Dendrochronological and palynological observations on *Populus balsamifera* in northern Alaska, U.S.A. *Arctic and Alpine Research* **17**:271–278.
- Fægri, K., and J. Iversen. 1975. *Textbook of pollen analysis*. Third edition. Munksgaard International Publishers, Copenhagen, Denmark.
- Glaser, P. H. 1981. Transport and deposition of leaves and seeds on tundra: a late-glacial analog. *Arctic and Alpine Research* **13**:173–182.
- Hansen, B. C. S., and D. R. Engstrom. 1985. A comparison of numerical and qualitative methods of separating pollen of black and white spruce. *Canadian Journal of Botany* **63**:2159–2163.
- Hultén, E. 1968. *Flora of Alaska and neighboring territories: a manual of vascular plants*. Stanford University Press, Stanford, California, USA.
- Krebs, C. J. 1978. *Ecology: the experimental analysis of distribution and abundance*. Second edition. Harper & Row, New York, New York, USA.
- Kutzbach, J. E., and P. J. Guetter. 1986. The influence of changing orbital parameters and surface boundary conditions on climate simulations for the past 18,000 years. *Journal of the Atmospheric Sciences* **43**:1726–1759.
- Lowden, J. A., and W. Blake, Jr. 1968. Geological Survey of Canada radiocarbon dates. VII. Geological Survey of Canada Paper **68-2, Part B**.
- MacDonald, G. M. 1987. Postglacial vegetation history of the Mackenzie River Basin. *Quaternary Research* **28**:245–252.
- MacDonald, G. M., and J. C. Ritchie. 1986. Modern pollen spectra from the western interior of Canada and the interpretation of late Quaternary vegetation development. *New Phytologist* **103**:245–268.
- McAndrews, J. H. 1966. Postglacial history of prairie savanna, and forest in northwestern Minnesota. *Memoirs of the Torrey Botanical Club* **22**:1–72.
- Morisset, P., S. Payette, and J. Deshayé. 1983. The vascular flora of the Northern Québec-Labrador Peninsula: phytogeographical structure with respect to tree-line. Pages 141–151 in P. Morisset and S. Payette, editors. *Tree-line ecology. Proceedings of the Northern Québec Tree-line Conference*. Nordicana 47. Centre d'études nordiques, Université Laval, Québec, Canada.
- Payette, S., and L. Filion. 1985. White spruce expansion at the tree line and recent climate change. *Canadian Journal of Forest Research* **15**:241–251.
- Payette, S., L. Filion, L. Gauthier, and Y. Boutin. 1985. Secular climate change in old-growth tree-line vegetation of northern Québec. *Nature* **315**:135–138.
- Ritchie, J. C. 1974. Modern pollen assemblages near arctic treeline, Mackenzie Delta region, Northwest Territories. *Canadian Journal of Botany* **52**:381–396.
- . 1977. The modern and late-Quaternary vegetation of the Campbell-Dolomite uplands near Inuvik, N.W.T., Canada. *Ecological Monographs* **47**:401–423.
- . 1982. The modern and late-Quaternary vegetation of the Doll Creek area, north Yukon, Canada. *New Phytologist* **90**:563–603.
- . 1984a. The past and present vegetation of the far northwest of Canada. University of Toronto Press, Toronto, Canada.
- . 1984b. A Holocene pollen record of boreal forest history from the Travaillant Lake area, Lower Mackenzie River Basin. *Canadian Journal of Botany* **62**:1385–1392.
- . 1985. Late-Quaternary climatic and vegetational change in the lower Mackenzie basin, northwest Canada. *Ecology* **66**:612–621.
- . 1986. Climate change and vegetation response. *Vegetatio* **67**:65–74.
- . 1987. *Postglacial vegetation of Canada*. Cambridge University Press, Cambridge, England.
- Ritchie, J. C., and F. K. Hare. 1971. Late-Quaternary vegetation and climate near the arctic tree line of northwestern North America. *Quaternary Research* **1**:331–342.
- Rowe, J. S. 1972. Forest regions of Canada. *Canadian Forest Service Publication Number 1300*.
- Spear, R. W. 1983. Paleocological approaches to a study of treeline fluctuation in the Mackenzie Delta Region, Northwest Territories: preliminary results. Pages 61–72 in P. Morisset and S. Payette, editors. *Treeline ecology. Proceedings of the Northern Québec Tree-line Conference*. Nordicana 47. Centre d'études nordiques, Université Laval, Québec, Canada.
- Stockmarr, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores* **13**:615–621.
- Terasmae, J., and O. L. Hughes. 1966. Late-Wisconsinan chronology and history of vegetation in the Ogilvie Mountains, Yukon Territory, Canada. *Palaeobotanist* **15**:235–242.
- Woodward, F. I. 1987. *Climate and plant distribution*. Cambridge University Press, Cambridge, England.
- Wright, H. E., Jr. 1967. A square-rod piston sampler for lake sediments. *Journal of Sedimentary Petrology* **27**:957–976.