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A buried spruce forest provides evidence at the stand and landscape scale for the effects of environment on vegetation at the Pleistocene/Holocene boundary

KURT S. PREGITZER*, DAVID D. REED*, THEODORE J. BORNHORST†, DAVID R. FOSTER‡, GLENN D. MROZ*, JASON S. MCLACHLAN§, PETER E. LAKS*, DOUGLAS D. STOKKE¶, PATRICK E. MARTIN** and SHANNON E. BROWN*

**School of Forestry & Wood Products, †Department of Geological Engineering and Sciences, **Department of Social Sciences, Michigan Technological University, Houghton, MI 49931, USA; ‡Harvard Forest, Petersham, MA 01366, USA; §Department of Botany, Duke University, Durham, NC 27708, USA; and ¶USDA Forest Service, North-eastern Forest Experiment Station, Department of Forestry, Iowa State University, Ames, IA 50011, USA*

Summary

1 Due to a unique set of circumstances, we were able to excavate an entire spruce (*Picea*) forest in Michigan's Upper Peninsula, USA, which was buried in the early Holocene (9928 ± 133 uncalibrated ^{14}C years BP). Trees ranged from < 5 cm to > 50 cm in diameter, and dominants were approximately 9 m tall. The stand was multi-aged, with a maximum tree age of 145 years. Well-preserved stem cross-sections ($n = 140$) were recovered and the entire stand was mapped.

2 Stand reconstruction combined with pollen and sediment analysis revealed a pure spruce forest in the sandy lowlands surrounded by hills dominated by pine, oak and birch. These results are consistent with the idea that topography and substrate played an important role in determining forest composition during Holocene plant migrations.

3 Very rapid climate fluctuations were occurring 10 000 BP. The extensive spruce forests that once dominated much of interior North America were being replaced by subboreal and temperate conifer and hardwood species migrating northward. During this dynamic period in the Earth's history, patterns of plant community change are usually inferred from the study of pollen assemblages, and lack of detailed stand level information has prevented the direct comparison of the composition, age, structure and growth rates of Holocene forests with those that exist today.

4 Our findings that the age-class distribution, size, spatial distribution of trees and radial growth rates of white spruce (*Picea glauca*) can be remarkably similar between the two time periods suggest that forest population and growth processes responsible for today's advancing tree-lines appear to have been at work 10 000 years ago.

Keywords: buried forest, climate change, Holocene, Pleistocene, pollen, population processes, spruce, succession, Younger Dryas period

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Correspondence: Kurt S. Pregitzer, School of Forestry & Wood Products, Michigan Technological University, Houghton, MI 49931, USA (fax 906 487 2915; e-mail kspregit@mtu.edu).

Introduction

Historical records of past climate and biotic change are often used to predict the Earth's future. Studies on fossil pollen have demonstrated that 10 thousand years before present (BP), the vegetation of North America and Europe was undergoing the most rapid reorganization of the postglacial period in response to very rapid climate fluctuations (Brubaker 1975; Davis 1983; Cohmap Members 1988; Overpeck *et al.* 1991; Whitlock *et al.* 1993). Studies of trees buried in glacial drift have also been important in interpreting the glacial chronology of the northern hemisphere, reconstructing regional vegetation, and calibrating climate change (Kaiser 1993, 1994; Bjorck *et al.* 1996). However, population-level studies of Holocene forests using *in situ* trees have been limited because only a few fossil forests have ever been uncovered, and those trees have often been overrun by advancing glaciers.

To understand the factors controlling contemporary tree migration, ecologists study forests at high latitudes and elevations, where tree-lines are currently advancing. These studies demonstrate that seedling establishment is influenced by inter-annual to decadal fluctuations in climatic conditions, along with variable seed bed conditions, erratic seed production, long-distance seed dispersal, and lags associated with the time it takes individual mother-trees to reach reproductive maturity (Payette & Filion 1985; Payette *et al.* 1985; Brubaker 1986; Scott *et al.* 1987; Payette *et al.* 1989; Rochefort *et al.* 1994; Szeicz & Macdonald 1994, 1995). However, are the population processes responsible for today's advancing tree-lines similar to those responsible for tree migrations that occurred 10 000 years ago? In other words, do forests today have size- and age-class distributions, and radial growth rates, similar to those that were advancing during the Holocene? These are important questions because the answers provide a fundamental perspective on how useful it is to model and make predictions about the future from reconstructions of past patterns of climate and forest change.

Methods

HISTORY OF THE STUDY AREA

To avoid confusion when comparing our results with the form usually presented in earlier literature, dates are given as uncalibrated ^{14}C values in years BP.

Our study site was located in Marquette County in Michigan, USA (Fig. 1). The surrounding area consists of bedrock hills, covered in places with a thin layer of unconsolidated glacial drift. The glacier present over the area retreated north and by the beginning of the Younger Dryas period, approximately 10 600 BP (Bjorck *et al.* 1996), much of the present-day Lake Superior basin was deglaciated (Farrand & Drexler 1985). The glacier then re-advanced south, initiating the so-called Marquette re-advance (Drexler *et al.* 1983; Farrand & Drexler 1985; Larsen 1988) that coincides remarkably well in time with the initiation of the Younger Dryas (Farrand & Drexler 1985), a rapid and brief period of climate cooling in the northern hemisphere that punctuated climate warming in the early Holocene (Bjorck *et al.* 1996). Radiocarbon dates from our site (9928 ± 133 BP, see below) correspond closely with the termination of the Marquette re-advance (9849 ± 258 BP; Drexler *et al.* 1983), and at this time the glacier was standing just a few kilometres north of the study site (Hughes 1971; Drexler *et al.* 1983). The abrupt climate warming that coincided with the end of the Younger Dryas (Bjorck *et al.* 1996) resulted in rapid wasting of this glacier, including deglaciation of the entire present-day Lake Superior basin (Farrand & Drexler 1985; Larsen 1988). Fluvial sediments from the ablation of this ice were rapidly deposited in glacial drainage channels that developed south of the moraines associated with the termination of the Marquette re-advance. These drainage channels were low-lying areas between the bedrock hills and quickly became filled with sand and gravel deposits, which rapidly buried the standing spruce forest. It was not until sand-mining operations, approximately 10 000 years later, that they were uncovered.

The study area is an active sand-mining operation located near Gribben Lake on one of the glacial drainage channels filled by ablation of ice associated with the Marquette re-advance. The groundwater table is close to the present-day land surface, and without continual pumping the mining pit fills with water. A ditch along the southern perimeter and a series of discharge wells are needed to lower the water table and allow machines to remove sand from the pit. During the course of normal mining operations, an entire forest was discovered buried in the sand below the groundwater table. Once the sand had been excavated to near the buried soil layer, it was possible to examine the remnants of the ancient forest and study the forest structure directly by mapping and measuring each tree trunk.

FIELD METHODS

Trees, logs and forest floor samples were recovered from the bottom of the sand-mining pit. After measurement with a calliper, tree cross-sections were recovered by hand-excavating around the standing tree trunks just below the point where the top of each tree had been sheared away by the mining machines. After recovery, 140 cross-sections were returned to the laboratory. An additional 70 trees

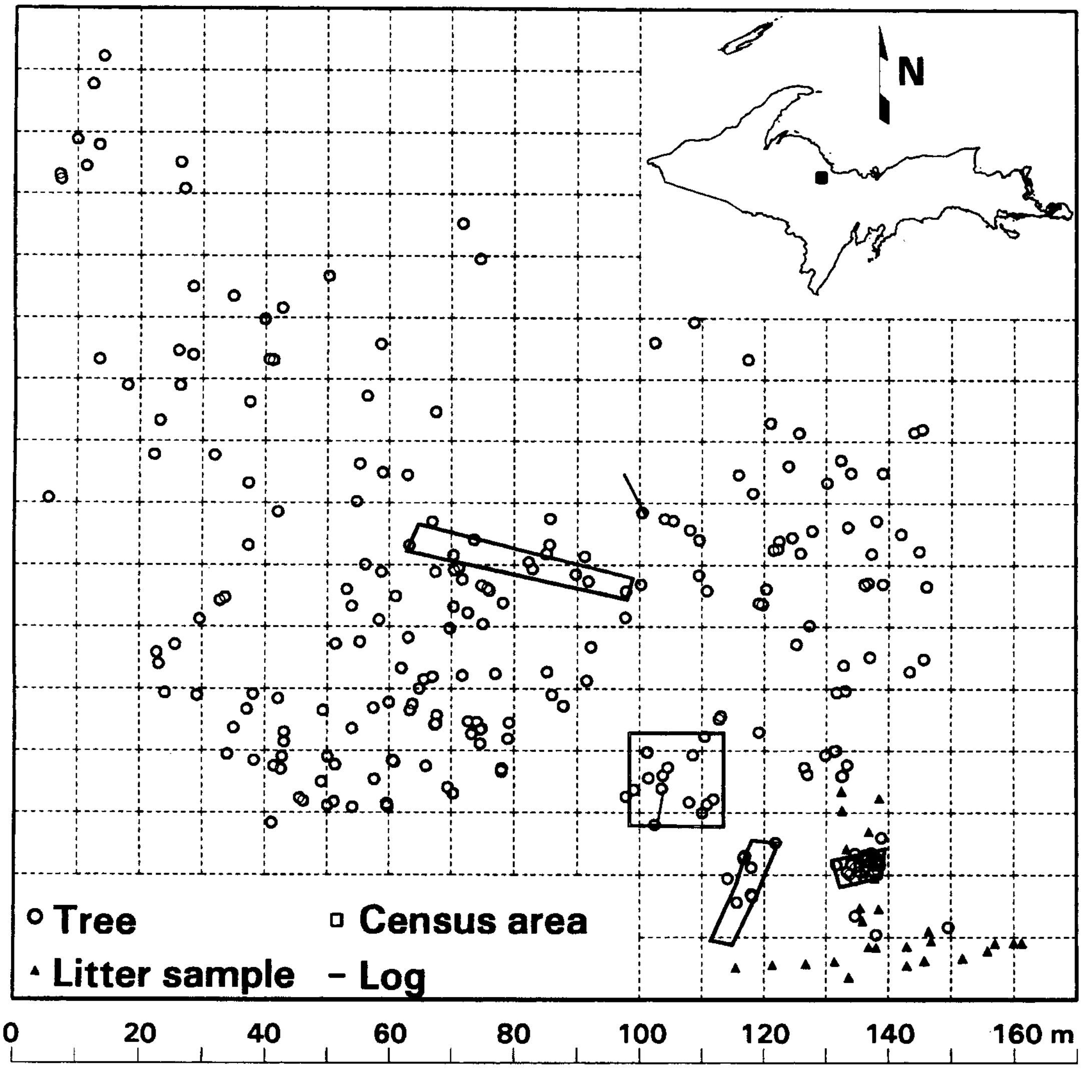

Fig. 1 Map showing the location of standing trees, areas excavated by hand (census area), two fallen logs, and forest floor samples from the Gribben buried forest site. Inset shows the site location within the Upper Peninsula of Michigan, USA.

were located and their diameters were measured in the field, but the rapidly flooding site prevented the collection of every tree discovered. A registered land surveyor measured the elevation and location of each tree cross-section at the point of diameter measurement.

Four polygonal areas (67–290 m^2 in size, 682 m^2 in total) were carefully and completely excavated by hand using shovels to ensure that an accurate census of buried trees was obtained. Height of the dominant trees was inferred from two trees (numbers 44 and 177) for which significant lengths were found buried horizontally in sand just above the forest floor. The root collar was identifiable on each. Tree 44 had a diameter of 26.0 cm at 1 m above the root collar and a diameter of 10.0 cm at 6 m above the root collar; tree 177 had a diameter of 40.2 cm at 1.0 m above the root collar and a diameter of 15.0 cm at 6.9 m above the root collar. These were the only two trees for which we had reliable taper information at more than one known height along the bole, including a measurement well into the crown, and where we could positively identify the root collar. Total tree height was estimated using two different tree taper curves applicable to white spruce (Gevorkiantz & Olsen 1955; D. Reed unpublished data).

The intact forest floor and the fluvial sediment above and below it were exposed in two perpendicular drainage ditches excavated with a backhoe. Twenty-nine intact soil monoliths (soil cores) were collected along the edge of the two ditches, and the locations and elevations of samples were then surveyed. The soil monoliths were excavated from > 10 cm above the original forest floor, approximately 25 cm into the underlying mineral soil, for physical and palynological analysis. A composite stratigraphic section was constructed from all visual observations and grain size data from 28 samples were plotted at the midpoint of the vertical distance of each sediment layer, with the intact forest floor serving as the reference location.

LABORATORY AND NUMERICAL METHODS

Subsamples were taken from all 140 tree cross-sections and examined microscopically using standard wood identification techniques (Panshin & de Zeeuw 1980). Subsamples of 89 cross-sections were sent to D. Stokke (USDA Forest Service, Ames, IA) for independent evaluation using light and scanning electron microscopy. Tangential surfaces of bulk specimens were examined with a stereoscope for the presence of fusiform rays. Safranin-stained hand sections of radial surfaces were observed with transmitted light microscopy. Some of the subsamples were also examined with a JEOL 5800 LV scanning electron microscope (SEM; JEOL Ltd, Tokyo, Japan). Wood samples were cut from frozen specimens, mounted on a metal stub with double-sided sticky tape, and sputter coated with a gold/palladium alloy prior to observation with the SEM. Samples were not chemically fixed in any way.

Accelerator mass spectrometer dates (Beta Analytic Inc., Miami, FL) were determined from the outer 20 rings of four different cross-sections identified as *Picea*. Calibrated ages were calculated following the methods of Stuiver & Reimer (1993) and Stuiver *et al.* (1998), to allow comparison with reports using different systems for the dates of Pleistocene and Holocene events (Table 1).

Eighteen of the sampled trees had > 125 annual rings at the point of measurement. Assuming that all trees died simultaneously at the time of burial, rings from individual years were matched in the sample trees by counting back from the outer-most ring after cross-dating had been used to confirm this assumption. Radial increment was measured to the nearest 0.01 mm along two axes and averaged by year for each tree. The average annual radial increment for each tree was then standardized to remove the age-dependent trend by first logarithmic differencing (Lane *et al.* 1993).

A minimum of 300 terrestrial pollen grains was counted from each of three soil monoliths spaced widely apart in the study area. The stratigraphic level at which each core was sampled for pollen corresponded to the discrete layer containing bryophytes and *Picea* needles that was present on the forest floor at the time of the outwash event. Sand layers above this horizon contained no pollen, which is consistent with rapid burial by glacial outwash. Sand and gravel below the forest floor contained only small amounts of degraded pollen.

Results

Standing trees were uncovered over an area of approximately 2.5 ha (Fig. 1). Soil monoliths could only be collected from the south-west corner of the study area because holes excavated elsewhere rapidly became flooded. With the top of the forest floor serving as the reference point, soil monoliths were collected at a mean elevation of 363.5 (± 0.06) m above sea level (a.s.l.). Sediment analysis revealed that the 'Gribben Forest' was killed by progressive flooding that preserved approximately 15 cm of intact forest floor composed of bryophytes, plant litter and a dense layer of needles from the dying spruce trees, beneath 15 cm of stratified silt and clay (Fig. 2). Subsequently, a more energetic braided fluvial environment buried the trees in a standing position and there is a build up of 7 m of sand and inter-bedded gravels to the modern land surface. Burial of the standing trees and the onset of anaerobic conditions must have occurred rapidly as many trees retained intact bark and fine lateral branches; bryophytes, as well as spruce cones, were well preserved in the forest floor layer.

All tree diameters were measured at a mean elevation of 364.0 (± 0.03) m a.s.l., 0.5 m above the top of the forest floor. All 140 individual trees sampled were identified as spruce (*Picea*) based on macroscopic and microscopic wood characteristics; species within the genus *Picea* cannot be consistently distinguished from one another on the basis of their wood anatomy. Accelerator mass spectrometer dates from the outer 20 growth rings of four trees averaged 9928 (± 133) uncalibrated ^{14}C BP (Table 1). Well-preserved cones, twigs and needles suggested that

Table 1 Uncalibrated and calibrated ^{14}C dates from the outer 20 rings of four different tree cross-sections identified as *Picea*. Calibrated ages were determined following Stuiver & Reimer (1993) and Stuiver *et al.* (1998)

Tree number	Laboratory identification	^{14}C age (uncalibrated) (^{14}C years BP ± SD)	Calibrated age (calendar years BP)
Tree 1	Beta-78156	9660 ± 60	11 155
Tree 66	Beta-91833	9830 ± 70	11 203
Tree 199	Beta-91834	9930 ± 70	11 258
Tree 16	Beta-91832	10 290 ± 90	12 103

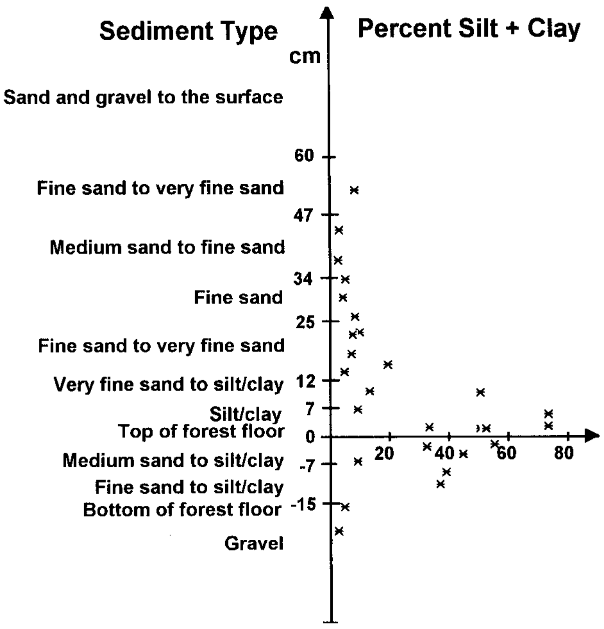

Fig. 2 Sediment type and percentage silt plus clay in systematic samples taken from two trenches opened in the south-eastern portion of the study site.

the forest was a pure stand of white spruce (*Picea glauca* [Moench] Voss). Size distribution of the sampled trees ranged from < 5 cm to > 50 cm diameter, with a concentration of stems between 10 and 25 cm (Fig. 3a). Tree density in the areas excavated by hand averaged 835 stems ha^{-1} (276–2700 trees ha^{-1}) and tree distribution was patchy (Fig. 1). Estimated basal areas ranged from 17.5 to 68.8 m^2 ha^{-1}. Dominant trees were approximately 9 m tall; estimated total heights were 9.2–9.6 m for tree 44 and 8.8–9.5 m for tree 177. The diameters of the two trees used to estimate height (26.0 and 40.2 cm) suggested they would fall within the dominant or codominant crown classes (Fig. 3a), imply-

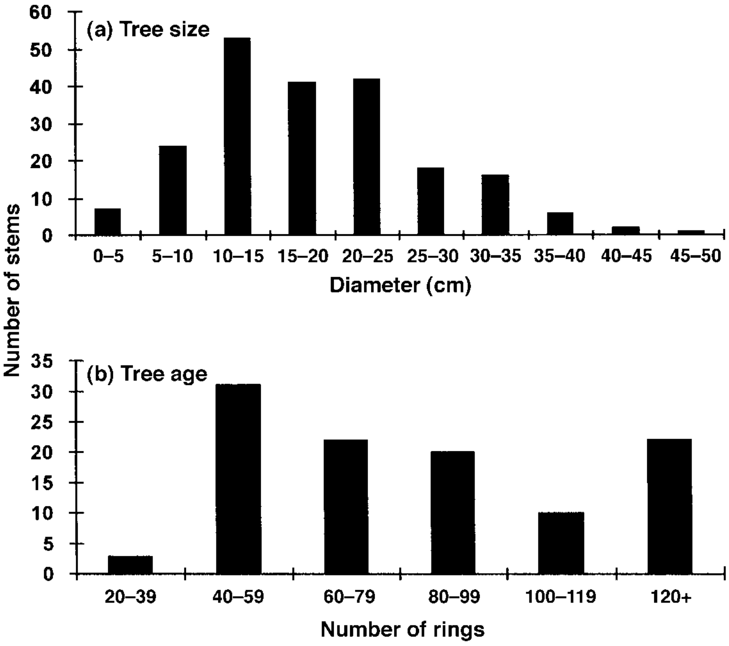

Fig. 3 Tree size and age-class distributions. Tree stem diameters were measured 0.5 m above the buried forest floor.

ing that their height calculated from the taper functions may be a reasonable estimate of dominant stand height. It was not possible to estimate the heights of dominant trees with greater precision, or to infer variability for this estimate of stand height. The stand was multi-aged, with a fairly even distribution of stems ranging from 40 to > 120 years old (maximum age of 145 years). Few trees were younger than 40 years (Fig. 3b).

A 125-year radial growth chronology was constructed for the 18 oldest trees using dendrochronology techniques. It showed rates of average radial growth ranging from 0.6 to 3.0 mm year^{-1}. Growth rates were fairly rapid and constant for the first 40 years and declined for the ensuing 80 years, as is expected in maturing trees (Fig. 4a). Ring-width indices showed no overall trend or evidence of the onset of the glacial flooding that killed the stand, but were characterized by a continually varying pattern of growth typical of natural stand and growth dynamics in a fluctuating climate (Fig. 4b). This is in contrast to the trees flooded, crushed and buried by the glacial advance associated with the Two Creeks Interstadial, which show extreme growth reductions in the outer annual rings in response to deteriorating growth conditions (Kaiser 1994).

Plant macrofossils from the forest floor were dominated by needles and cones of white spruce and bryophytes (*Drepanocladus uncinatum*, *Bryum* sp.), and suggested a poorly developed understorey of shrubs or herbs. In contrast, pollen assemblages from the forest floor were consistently more species diverse than either the sampled trees or macrofossils (Gribben Cores 16, 17, 23 in Fig. 5). Additional pol-

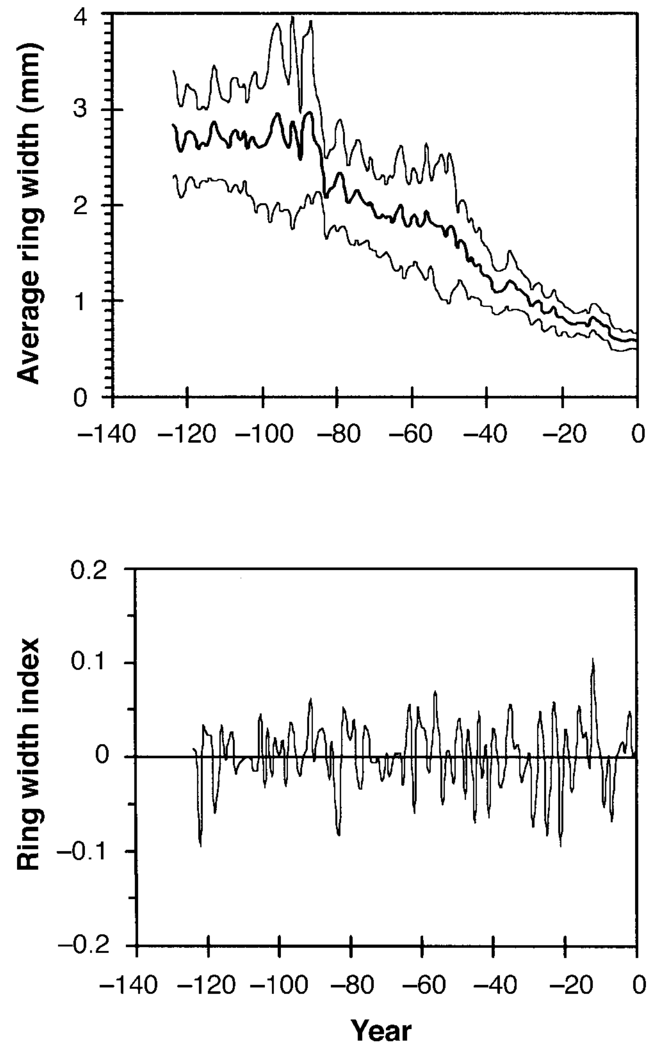

Fig. 4 Ring-width chronologies (125 years) for the 18 oldest spruce trees from the Gribben buried forest. Year zero is the year the trees were buried. Negative values represent the number of years prior to burial. (a) Average annual ring width (bold line), with corresponding upper and lower 95% confidence intervals. (b) Ring-width indices following standardization to remove an age trend (freely grown young trees typically have greater annual ring widths than older trees) and application of the bi-weight mean procedure.

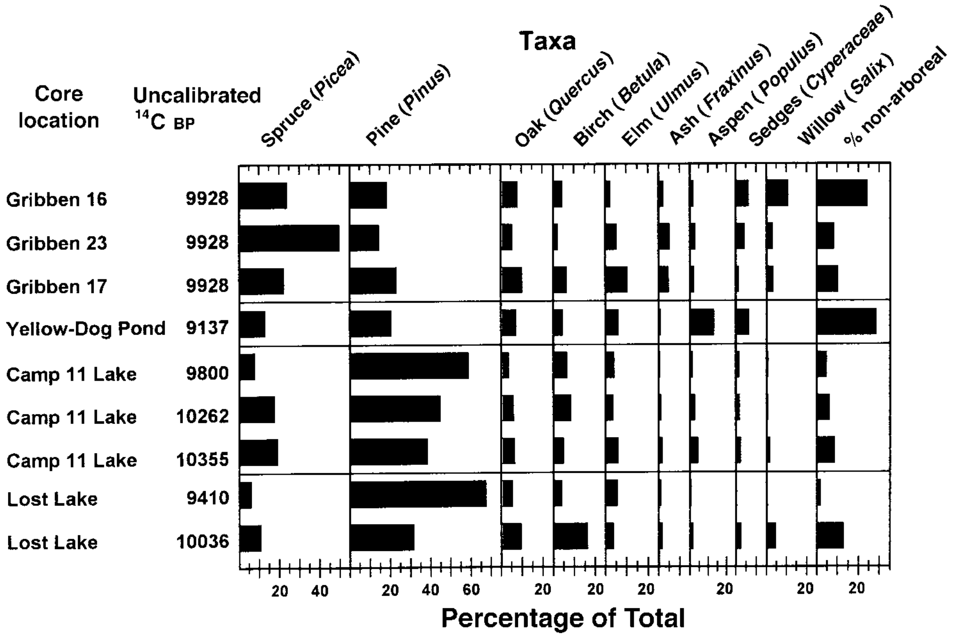

Fig. 5 Pollen assemblages from three Gribben soil monoliths and lake sediments collected 40 km north-west of the Gribben site by L. Brubaker (1975). Vegetation at both the Gribben and Yellow-Dog Pond sites grew on sandy substrate, while vegetation at the Camp 11 Lake and Lost Lake sites grew on glacial substrate with a greater moisture-holding capacity (Brubaker 1975).

len and spores for taxa represented at 1% or less included Cupressaceae, *Corylus*, *Carya*, *Ostrya-Carpinus*, *Shepherdia*, Chenopodiaceae, Tubuliflorae, *Ambrosia*, *Pteridium*, *Rumex*, Rosaceae, *Sarcobatus*, *Sphagnum*, *Monlete* spores, *Trilete* spores, *Lycopodium*, *Dennstaedtia*, *Lycopodium annotinum*, and *L. complanatum*. Damaged and unknown pollen made up < 5% of the total number of grains examined.

In order to understand forest composition in the landscape surrounding the study site, we compared the pollen assemblages for three Gribben soil cores with similar data collected by Brubaker (1975) in the 1970s from small lakes located 40 km north-east of the Gribben site (Fig. 5). Brubaker's Yellow-Dog Pond site was composed of sandy substrate like the Gribben soil, while vegetation at the Camp 11 Lake and Lost Lake sites grew on substrates with a greater moisture-holding capacity (Brubaker 1975). The pollen percentages for the Gribben site most closely matched Brubaker's Yellow-Dog Pond site. Her Camp 11 Lake and Lost Lake sites had much greater percentages of pine pollen (Fig. 5). Substrates with similar water-holding capacity therefore appear to have similar pollen assemblages at approximately the same time.

Discussion

We believe that the spruce trees that grew on this site were the first trees to colonize the newly exposed fluvial sediment following the initial retreat of ice into the Lake Superior basin. Brubaker's (1975) uncalibrated ^{14}C dates for basal lake sediments 40 km north-west of the Gribben site are 10 200 BP for Camp 11 Lake and 9100 BP for Yellow-Dog Pond, bracketing the mean Gribben date of 9928 ^{14}C BP. These radiocarbon dates, along with those of Hughes (1971), are all congruent with the chronology of glaciation south of the current Lake Superior basin before and after the burial of the Gribben Forest (Drexler *et al.* 1983; Farrand & Drexler 1985; Larsen 1988). Furthermore, we did not observe any significant soil horizon development other than the litter layer. Roots were therefore growing directly in the sand and gravel; the trees were open-grown and short, their boles were highly tapered, and their branches were held all the way to the ground.

In terms of age-class distribution, growth rate and stand structure, the postglacial spruce forest we excavated is strikingly similar to the expanding white spruce forest described by Payette & Filion (1985). Their forest is growing today near Hudson Bay, where spruce began to invade previously non-forested habitats around 1880. It is uneven-aged, with widely distributed and clustered age-class cohorts. The structure of this modern stand is variable and patchy, with open areas, dense patches of regeneration, and isolated individuals (Payette & Filion 1985). The age-class distributions and structures of the fossil spruce forests and contemporary forests are remarkably similar. Rates of radial growth are also similar, ranging from >4 mm year^{-1} to <1 mm year^{-1} (compare Fig. 4a with Payette & Filion 1985).

All the taxa represented in the pollen assemblages (Fig. 5) were present in the upper Midwest at the time the Gribben Forest was buried (Brubaker 1975; Davis 1983; Whitlock *et al.* 1993; Brugam *et al.* 1997). Trees such as pine and birch were absent from the buried spruce forest, but were evidently growing in the surrounding landscape (Fig. 5). This observation demonstrates that tree migration during the early Holocene was a patchy process in which pure stands of one genus developed, although other genera were well represented in both local and regional pollen records. Our data depict a landscape mosaic in which spruce forests dominated some low-lying and moist outwash areas, while a more diverse forest of pine, hardwoods and shrubs occupied portions of the surrounding uplands. These results are consistent with the idea that topography and substrate played an important role in determining forest composition during Holocene plant migrations (Brubaker 1975; Bernabo & Webb 1977; Graumlich & Davis 1993).

Examination of the Gribben Forest represents the first possibility for a detailed comparison of the structure, composition and growth characteristics of Holocene and modern forests. The age and structure of the stand, and the growth rates of the oldest spruce trees, are very similar to some forests growing today near the northern boreal tree-line. Important ecological processes shaping the structure and growth of the Gribben Forest are likely to have been seed dispersal, establishment and growth limitations on an infertile, newly deglaciated landscape. These same population processes operate today to control the establishment, growth and structure of stands at high elevations and latitudes (Payette & Filion 1985; Payette *et al.* 1985; Brubaker 1986; Scott *et al.* 1987; Payette *et al.* 1989; Rochefort *et al.* 1994; Szeicz & Macdonald 1994, 1995). Therefore, processes governing the response of forests to climate change have transcended the past 10 000 years to the point that we can find forests today that are remarkably similar to those that grew early in the Holocene. The Gribben Forest is a rich, new source of palaeoecological evidence concerning one of the most dynamic periods in the Earth's Quaternary history.

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