Marine palynology: potentials for onshore–offshore correlation of Pleistocene–Holocene records

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A review of marine pollen-spore distributions reveals regional variations in primary transport pathways. Fluvial transport prevails on the mountainous margins of the eastern Pacific and off major river deltas, including Arctic estuaries. Elsewhere, wind and sea ice are the main transport agents, and pollen concentration corresponds to dust influx. Redeposition of Quaternary palynomorphs is also important near emergent continental ice sheet centres where fine-grained sediment is being eroded. Pre-Quaternary palynomorphs can indicate sources of ice-rafted debris. Preservation and transport of pollen in marine sediments is not well understood. Laboratory processing with acetolysis shows damage of bisaccate grains, and copepod feeding experiments show some pollen damage of grains within the faecal pellet membranes. A multi-box model shows the relative importance of rivers, wind and ocean currents in pollen transport to shelves of Atlantic Canada: most pollen is wind-transported, but large storms may indirectly increase influx. In the Arctic, sea ice scouring and sediment transport are important in addition to northeasterly winds. These glacial processes would impact a third of the planet during glaciations. Pleistocene cores from NW Atlantic and Pacific Oceans show that glacial stage transport differed from that during Holocene and other interglacials because glacioeustatic lowstands exposed the continental shelves, and wind strength and direction changed following ice sheet growth. Pollen influxes and ice-volume records show variable leads and lags of palaeometerological events at glacial/interglacial boundaries, with a major decline in terrigenous organics after ~0.4 Ma (MIS 13–11).

INTRODUCTION

The application of classical Quaternary palynological methods (e.g. Faegri & Iversen, 1975) to the study of marine sediments had the huge benefit of providing continuous records of Pleistocene vegetation changes in mid-latitude regions (e.g. Heusser & Shackleton, 1979; Heusser, 1985; Heusser & Van der Geer, 1994; Heusser & Oppo, 2003), in contrast to the onshore sediments where ice sheets removed Quaternary peat and lake records, and where pollen preservation can be problematic in long basin sequences (e.g. Cooke, 1979). Marine pollen records can also be linked directly to the marine oxygen isotope stages (MIS) that provide a global millennial-scale chronology. Furthermore, application of palaeoecological transfer functions to the microfossils in the marine pollen samples provided quantitative proxy-data for seasonal changes in sea surface temperature, allowing examination of leads and lags in vegetation responses to Milankovitch orbital forcing parameters.

The importance of these marine palynostratigraphic and palaeoecological records also stimulated new studies of pollen-spore distributions in surface sediments of the temperate and tropical oceans, much of which is summarised by Traverse (1988). These studies led to qualitative models of marine pollen transport pathways, particularly off large deltas like the Orinoco, Rhine and Mississippi rivers (Traverse, 1994; Chmura *et al.*, 1999), where pollen distribution patterns suggested that rivers were the main transport agents. Until recently, however, much less was known about the palynology of arctic and subarctic marine regions, where unique sedimentary processes result from the dynamics of glaciers and sea ice, and where modern analogues of glacial MIS conditions might be found. Initial studies of the Arctic Ocean (Mudie, 1985; Matthiessen *et al.*, 2000) and circum-Arctic seas (Mudie & Short, 1985; Aksu & Mudie, 1985; Mudie, 1992; Rochon & De Vernal, l994) showed that palynology is particularly important for stratigraphic correlation and palaeoecological study of high latitude silled basins where preservation of calcareous and siliceous microfossils is poor. The potential of Arctic marine palynology can be judged by the fact about half the world's continental shelves (40×10^6 km^2) and all fiords were directly affected by Quaternary ice sheets and/or by winter sea ice (Figure 1).

Several studies have shown the value of palynology for onshore–offshore correlation of biofacies in cores from glaciated continental shelves (e.g. Vilks & Mudie, 1978; Scott *et al.*, 1984) and sub-arctic deep-sea environments (Heusser, 1983; De Vernal & Hillaire-Marcel, 1987). More recently, pollen studies have been combined with transfer-function reconstructions of decadal- to centennial-scale changes in Arctic sea ice cover (Levac *et al.*, 2001; Mudie *et al.*, in press). Palynomorphs are also useful for tracing pathways of organic carbon cycling in arctic marine environments (Short *et al.*, 1989; Stein & Stax, 1991) and pollen has been effectively used for back-tracking palaeowinds in the Canadian Arctic (Bourgeois *et al.*, 1985).

Quantitative environmental reconstruction, however, requires that pollen spectra in offshore deposits be related accurately to onshore vegetation at the time of deposition. There is a need to understand assemblage variations produced by transport processes and the hydrodynamics of depositional environments. Identification of the primary factors controlling transport and sedimentation of palynomorphs allows construction of deterministic process-response models (Mudie & McCarthy, 1994), and provides a base for development of stochastic models.

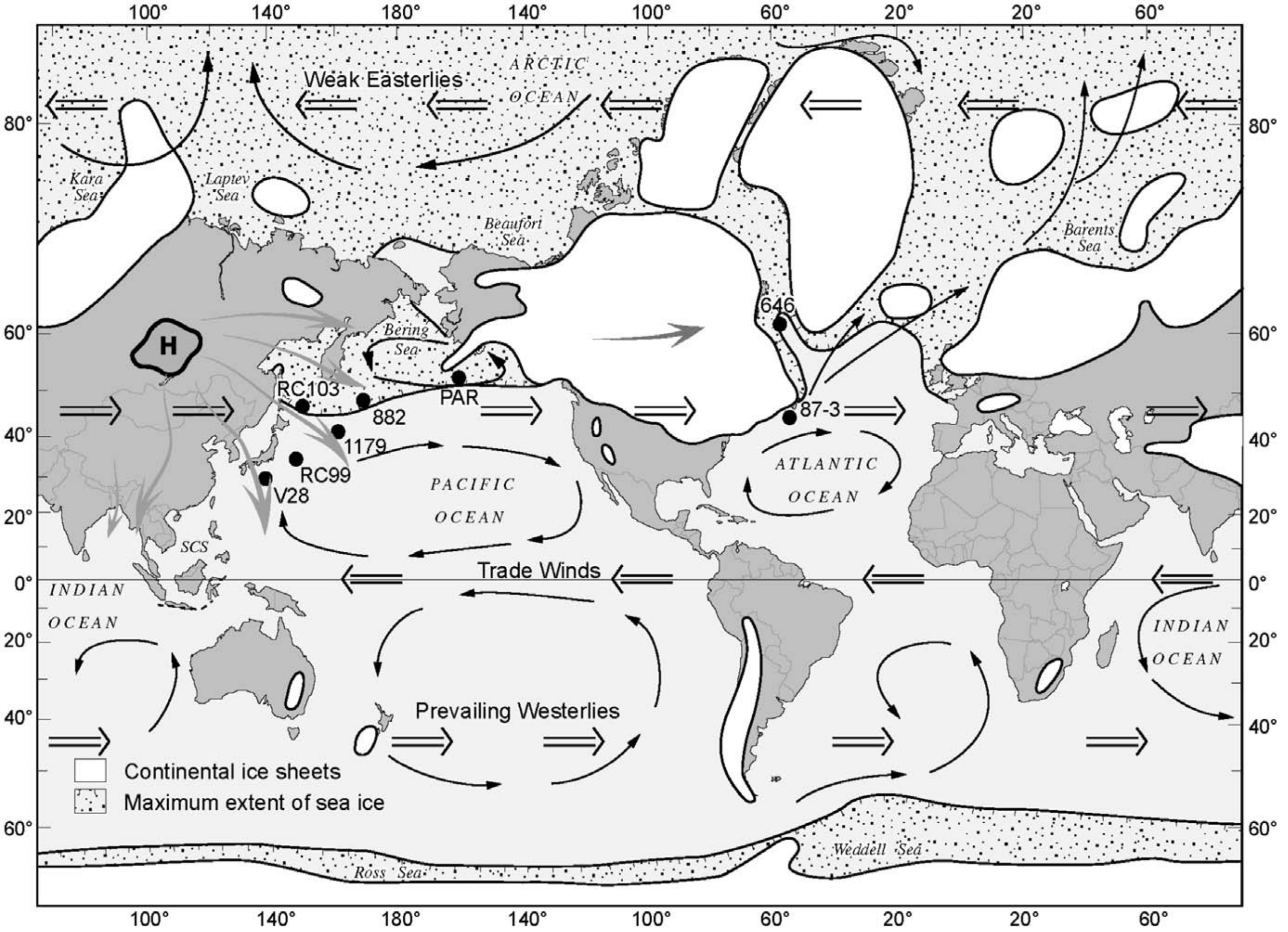

Figure 1. Global oceans, showing the correspondence between present-day prevailing winds and major ocean currents, position of maximum seasonal sea ice, key reference core sites and Last Glacial Maximum ice sheets.

In this paper, first we review previous studies on the palynology of late Quaternary glaciated marine environments. Subsequently, new data are presented that show the importance of laboratory processing methods for marine palynomorph assemblages and the role of zooplankton in pollen-transport processes. These data are then incorporated into a multi-box process-response model for fiord and glaciated shelf environments. Finally, the pollen records in selected Pleistocene cores are discussed in terms of insights they provide to general understanding of marine pollen transport pathways and to deposition of fine-grained organic sediment in the Atlantic and Pacific Oceans during the Quaternary glacial–interglacial oscillations.

REVIEW OF PREVIOUS STUDIES

Study of pollen transport in marine environments began in Europe with Hesselman (1919), who measured large influxes of wind-borne tree pollen to the eastern Baltic Sea, 30–50 km offshore. In this region, prevailing winds are westerly (onshore), and southerly cyclones are also common (Figure 1). Erdtman (e.g. 1921, 1954) also studied pollen and spores in marine sediments off Sweden, in the North Sea and along a trans-Atlantic transect at about 58°N Lat.. He concluded that wind and currents focus the deposition of buoyant conifer pollen-types along shorelines, but differential flotation is not a serious problem because of oxidation and redeposition of stranded subaerial pollen. In contrast, Faegri & Iversen (1975) found that *Pinus* is over-represented in marine deposits of eastern Sweden, while *Alnus* is over-represented in lagoon deposits. Erdtman (1954) found most pollen is deposited in the ocean within about 150 km of its source areas in Sweden, but small amounts of *Betula* and Gramineae pollen are transported across the subarctic North Atlantic by prevailing winds. Turon (1981) also concluded from *Picea* pollen distribution that westerly winds are the main sources of pollen input to Northeast Atlantic deep water. Later, it was shown that melt out of ice-rafted detritus may deposit recycled palynomorphs in glacial-stage sediments off Iceland and the Norwegian margin (Mudie, 1992), and in Heinrich layers off Newfoundland (Hiscott *et al.,* 2001).

Pollen in seabed samples was studied on traverses across Gdansk Bay (Lubliner-Mianowska, 1962) and summer pollen deposition was measured in bays near Stockholm (Praglowski, 1977). Pollen spectra in seabed and water samples closely matched the local vegetation, despite evidence of bottom current transport. It was concluded that long-distance transport was not a significant source of pollen in these subarctic bays. Redeposited pre-Quaternary pollen is easily recognised in the southern Baltic region (Iversen, 1936) and can be used to trace till provenance. In estuaries and fiords of the British Isles (Reid, 1975), pollen concentrations in silled lochs are high (>10 000 grains/g wet sediment), outnumbering dinocysts by a factor of >10. Further seaward, pollen:dinocyst ratios are <1.0, suggesting that most pollen is trapped in fiord basins. Offshore, tree pollen (60–75%) dominates in both glaciated and unglaciated regions of the North Sea (Chowdhury, 1982). Highest tree pollen percentages occur >60 km north of the Elbe River where *Pinus* is over-represented and *Alnus* is under-

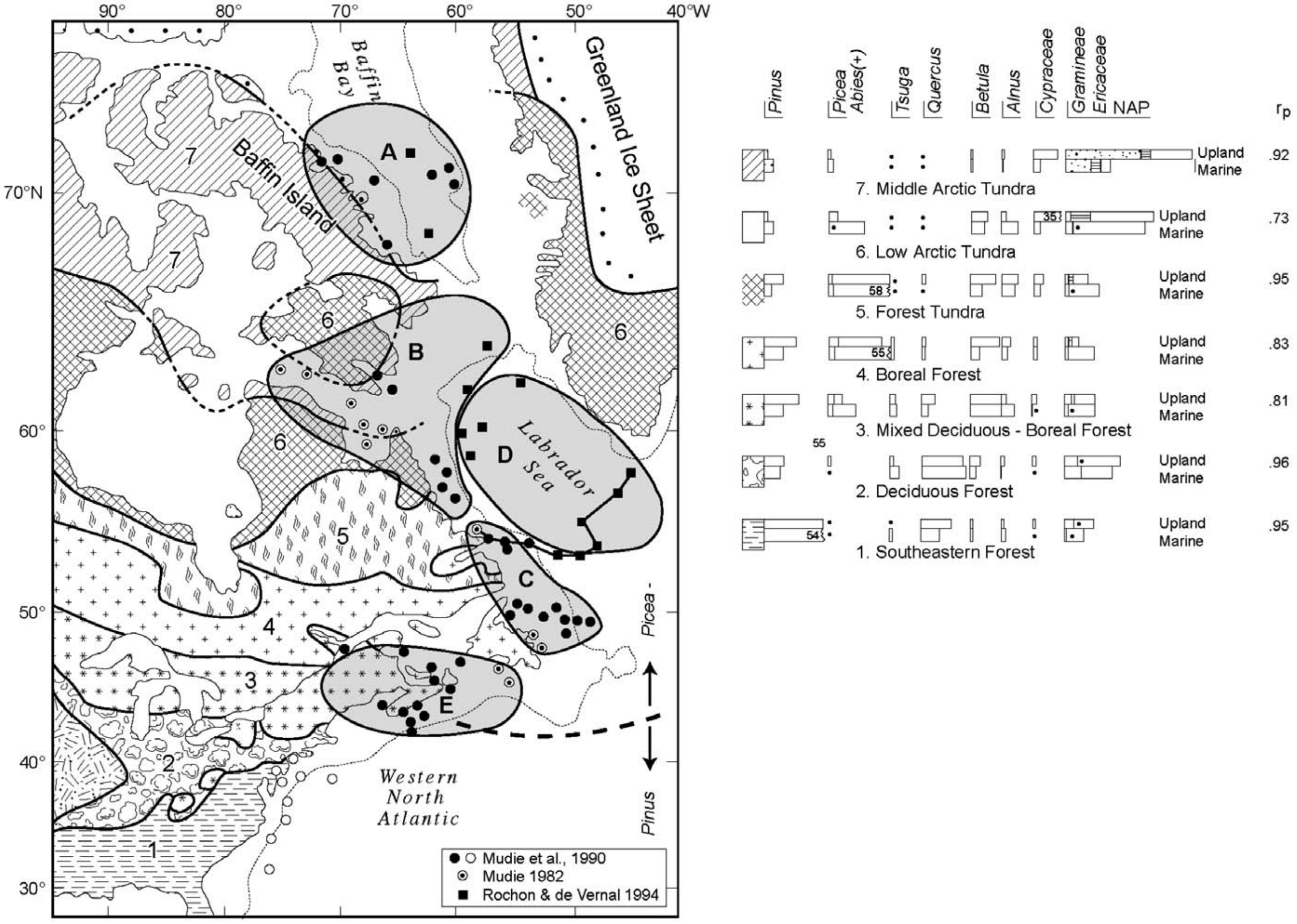

Figure 2. Vegetation zones of Eastern North America and corresponding surface pollen assemblages reported by Mudie (1982), Mudie *et al.* (1990) (large black and white circles) and by Rochon & De Vernal (1994) (squares). Shaded areas correspond to statistical factor assemblages: A = Herb tundra; B = *Sphagnum-Alnus* Forest tundra; C and D = *Picea* Boreal forest; E = *Betula*-AFQC mixed forest (AFQC = *Acer-Fagus-Quercus-Carya*). r_p = rank correlation coefficient.

represented relative to onshore vegetation. This distribution appears to reflect differential transport of *Pinus* in river water. Goodwin (1988) also suggested that the high percentage of *Alnus* in rivers and mudflats around the Frisian Islands resulted from flocculation of this pollen with the fluvial silt load.

After 1978, the attention of marine palynologists turned to eastern North America and the Northwest Atlantic Ocean. In this region, prevailing winds are westerly and predominantly offshore, but with strong southerly cyclonic storms in autumn (Figure 1). Initial studies of pollen-spore distributions on the eastern continental shelves and margins (Mudie, 1982; Mudie *et al.*, 1990) showed correlations of 0.73 to 0.96 between mean pollen-spore values of onshore vegetation zones and the offshore samples (Figure 2). Subsequently, Rochon & De Vernal (1994) established that there is a rapid decline in pollen concentrations on the shelf margin (31% decrease per 100 km), and a much slower decrease across the Labrador Sea. Nonetheless, distinctive pollen assemblages mark pelagic samples off the Tundra, Subarctic Tundra, and Boreal forest vegetation regions (Figure 2). In contrast, a complex pattern of pollen distribution occurs in the Gulf of St Lawrence below the St Lawrence estuary (De Vernal & Giroux, 1991), suggesting mixing from multiple sources.

Ecostratigraphic studies of pollen-spore assemblages in Holocene sediment cores from various bays of Nova Scotia (see Piper *et al.*, 1990), Lake Melville in central Labrador (Vilks & Mudie, 1983) and Baffin Island fiords (Mudie & Short, 1985; Short *et al.*, 1989) showed that the pollen-spore assemblages in coastal environments can be correlated closely with onshore pollen zonations. Holocene pollen records from adjacent continental shelf basins also showed good correlation with onshore reference sections (Vilks & Mudie, 1978; Scott *et al.*, 1984), but correlation was weaker for outer shelf cores off Newfoundland (Piper *et al.*, 1978) and the Baffin Island shelf (Praeg *et al.*, 1986). This difference seemed to reflect more iceberg scouring and/or deposition of ice-rafted detritus (IRD) in the Arctic and on subarctic shelf margins.

Palynostratigraphic studies of glacial marine sediments on the continental slopes off Labrador (De Vernal & Hillaire-Marcel, 1987), Baffin Bay and West Greenland (Aksu & Mudie, 1985), and of pelagic Labrador Sea sediments (De Vernal & Hillaire-Marcel, 1987; Aksu *et al.*, 1992) revealed that pollen-spore assemblages at the deep water sites only show the major features of the discontinuous onshore stratigraphies: glacial and interglacial intervals, interglacial climatic optima, and interstadial events during glacial stages. However, we will show that these palynostratigraphies can provide a unique continuous record of land–sea interactions for the past *ca.* 1 Ma. Correlation of temperate tree-pollen peaks with influxes of subarctic/temperate dinocysts and foraminifera can also be used for back-tracking of palaeowind directions in Labrador Sea (Aksu & Mudie, 1985; De Vernal & Hillaire-Marcel, 1987; Mudie & McCarthy, 1994).

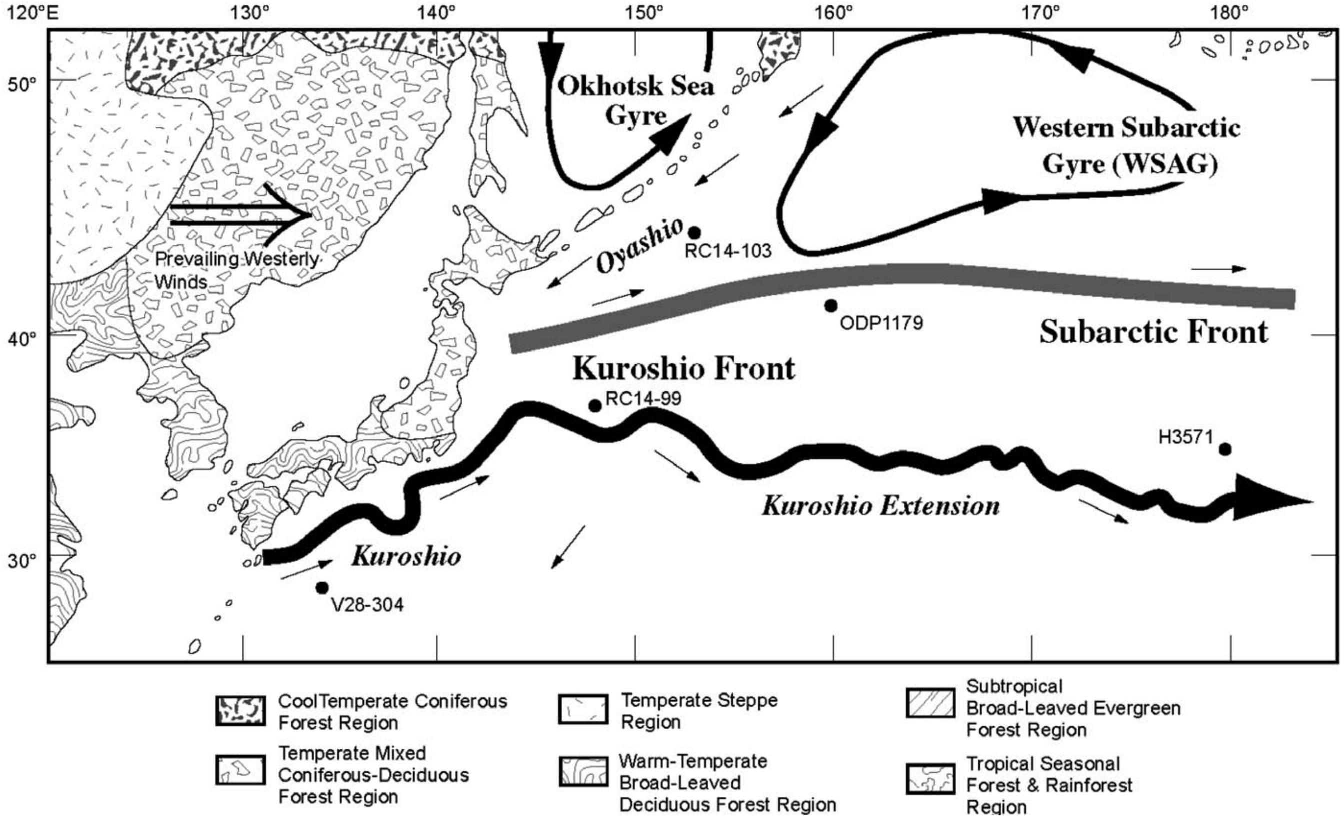

Figure 3. Location of deep-sea sites along a transect at mid-latitudes in the western North Pacific Ocean. Prevailing westerly winds and strong western boundary surface currents transport most of the pollen offshore. Surface circulation is modified from Kawahata & Ohshima (2002); vegetation from various sources, including Ren & Beug (2002).

South of the Grand Banks, glacial meltwater events may be evident as large influxes of Upper Carboniferous spores to the Fogo Seamounts (Alam *et al.,* 1983), Laurentian Fan (Heusser, 1983) and Sohm Abyssal plain (Giosan *et al.,* 2002). These Palaeozoic spores have been traced southwards (Needham *et al.,* 1969) to *ca.* 38°N Lat. in the path of the Western Boundary Undercurrent (WBUC), and Heusser & Balsam (1985) concluded that the offshore decrease of pollen in the western North Atlantic was due to the WBUC influence. This interpretation is subject to debate, however, in view of new studies on palynomorph transport in distal turbidites in the northwest Atlantic (*e.g.* Giosan *et al.,* 2002) and evidence of continental slope erosion by warm core rings at the edge of the Gulf Stream (McCarthy *et* al., 1990).

There have been few studies of aerial pollen transport in the Northwest Atlantic. Dyakowska (1948) found mainly *Pinus, Betula,* and tundra herb pollen (Cyperaceae, Gramineae) in impact traps off the west coast of Greenland. More recently, the importance of wind transport to the Labrador Sea and Baffin Bay was shown by impact trap and water samples (Mudie & Deonarine, 1983), snow samples (Lichti-Federovich, 1975; Bourgeois *et al.,* 1985) and ice cores (McAndrews, 1984; Short & Holdsworth, 1985). Transport of redeposited pollen by turbidity currents and other submarine mass transport mechanisms was discussed by McCarthy & Mudie (1998) and by McCarthy, Gostlin *et al.* (2004).

In contrast to the North Atlantic, most of the North Pacific coasts and shelves were not extensively glaciated during the last glacial stage (Figure 1). At present, sea ice in this ocean is seasonal and largely confined to the Sea of Okhotsk and regions north of Bering Strait. The earliest marine palynology studies were made on cores from western Bering Sea (Gorskova, 1952) and showed uniform assemblages of subarctic forest taxa similar to spectra for adjacent onshore vegetation. Palynomorphs in surface sediments from the Sea of Okhotsk (Figure 3) included ubiquitous *Pinus,* but other conifer pollen (*Abies* and *Picea*) were concentrated downwind from source areas, with northerly outliers suggesting secondary transport in ocean currents (Koreneva, 1966). *Alnus* and *Betula* were concentrated within 200 km of their boreal forest and forest tundra sources, and fern spores were preferentially deposited in river deltas. These distributions apparently primarily reflected the size and density of the palynomorphs, followed by sorting and redeposition with clastic sedimentary particles.

Subsequent studies were made in the northeastern Pacific Ocean, mostly on the unglaciated continental slope sites south of 53°N Lat., where abundance peaks of 5000–10 000 grains/cm^3 were found off rivers (Heusser & Balsam, 1977). Much smaller amounts (<50–100 grains/cm^3) were found in glacial marine sediments off the Queen Charlotte Islands (*ca.* 56°N) and southern Alaska (57–60°N). Here, as in the North Sea, *Alnus* was under-represented in the marine sediments, possibly because of bedload deposition with median silt in the arctic rivers (Catto, 1985) or sediments of tidewater glaciers (Goodwin, 1988). High offshore concentrations of Polypodiaceae in Alaskan glacial marine sediments are attributed to ferns on disturbed glaciated terrains (Heusser & Balsam, 1977). It appears that large rivers are the main sources of marine pollen transport on the mountainous coast of the eastern North Pacific, with wind transport accounting for most of the influx off the low-relief Alaskan coast and the Aleutian Islands (C. Heusser, 1985). Colinveau (1964) also concluded that rivers were the main pollen transport agents to Kotzebue Sound near the Bering Strait, with peaks of reworked and allochthonous tree pollen indicating changes in sedimentary regimes.

A multivariate statistical study of glacial marine sediments from the southwestern Bering Sea, *ca.* 56°N Lat. (Sancetta *et al.,* 1985), showed that *Alnus* and *Betula* pollen was common offshore during early MIS stages 3 (*ca.* 60 ka BP), stage 2 (*ca.* 30 ka BP) and in MIS 1, the Holocene. A similar chronology of pollen influx occurs in the northwest Atlantic Ocean at *ca.* 60°N (Mudie & Short, 1985) where it was attributed to long-distance aeolian transport, which is also indicated by influx of fine sand and silt (Aksu *et al.,* 1992). On the Patton Seamount, south of the Aleutian Trench, low Holocene pollen concentrations (<50 grains/cm^3) in core PAR87A (Figure 1) were also attributed to westerly wind transport (De Vernal & Pedersen, 1997) although the distinctive East Asian pollen marker *Cryptomeria* was not reported. Higher pollen influxes and reworked Tertiary palynomorphs marked the Late Glacial interval and were attributed to aeolian input and ice rafting from an extensive subaerial Alaskan shelf.

More recently, pollen transport to the deep sea has been extensively studied in sediments from the western North Pacific. The major biomes found today in East Asia, including Japan (Figure 3), are quite well represented in surface sediments in coastal and neritic environments. Diverse pollen assemblages, and moderately high concentrations, are found in proximal marine settings, e.g. ODP Sites 438 and 440 on the Japanese continental margin (Heusser & Morley, 1996), ODP Site 794 in the Sea of Japan (Heusser & Morley, 1996), and in the South China Sea (Sun *et al.,* 2000; Sun & Li, 1999; Katayama & Watanabe, 2003). Pollen transport to these sites can easily be attributed to prevailing westerly winds, with point sources of pollen at the mouths of rivers that drain the entire catchment, as predicted by the Neves effect of Traverse (1988). For instance, Katayama & Watanabe (2003) have shown seasonal contributions from both the Huanghe (Yellow River) and the Changjiang (Yangtze River) in the South China Sea. Wind is a particularly effective pollen transport mechanism in semi-arid environments, such as those in western China (Rea *et al.,* 1998; Ren & Beug, 2002).

The relationship between modern vegetation in East Asia and surface pollen assemblages at distal oceanic settings is obscured by more complex taphonomic factors. This is shown by the lack of differences between assemblages at three sites (Heusser & Morley, 1985, 1997) on a north–south transect off Japan: cores RC14-103, RC14-99 and V28-304 (Figure 3). Despite the great distance (~15.5° Lat.) between these sites, downwind of cool temperate mixed forest, warm temperate and subtropical broad-leaved evergreen forests, respectively, all the core-top assemblages are dominated by Pinaceae (*Pinus + Abies + Tsuga)* and *Alnus.* Pollen of *Quercus, Betula, Picea, Cryptomeria,* Cupressaceae and herbs, as well as fern spores are common throughout, but it appears that *Picea* and herb pollens are under-represented in RC14-103, given the steppe vegetation upwind in China and tundra up-current in Kamchatka, while pollen of the subtropical to warm-temperate tree *Cryptomeria* is over-represented. Pinaceae and *Betula* are also over-represented and *Quercus* is under-represented at V28-304, downwind and down-current of the subtropical forest.

Modern pollen transport to the sites beyond the continental margin appears to be a complex product of differential transport by wind and ocean currents. Katayama & Watanabe (2003), for instance, found that lateral transport near the seafloor carries terrigenous particles from the South China Sea to the Okinawa Trough. The Oyashio Current transports subpolar water south along the margin to Hokkaido, while the strong Kuroshio western boundary current of the North Pacific subtropical gyre transfers significant quantities of pollen northwards (Heusser & Morley, 1997). Both currents are deflected offshore around 40°N, transporting pollen to the abyssal North Pacific. Kawahata & Ohshima (2002) propose that the Kuroshio Current/Extension transports much of the terrigenous organic material to the Hess Rise (Figure 3), particularly during glacials.

Remote sites, like core H3571 on the Hess Rise (Kawahata & Ohshima, 2002), are characterised by very slow sedimentation, and pollen assemblages are sparse and weakly correlated with onshore vegetation. The *extremely* low pollen concentrations (~0.5 grains/g) in sediments deposited during MIS 1 at Site H3571 on the Hess Rise, for instance, are relatively rich in herb pollen, although grasslands are not common upwind or up-current. The presence of *Pinus, Quercus,* and *Cryptomeria* in recent sediments is more consistent with modern vegetation in East Asia. Kawahata & Ohshima (2002) argued that wind is not an important transport mechanism to the Hess Rise; however, westerly winds transport significant quantities of mineral dust to the mid-latitude western North Pacific Ocean (McCarthy, Findlay *et al.,* 2004; McCarthy, Gostlin *et al.,* 2004; Little, 2005).

There have been few studies of Quaternary marine sediments in the polar oceans because of their remote location and sparse vegetation. The semi-enclosed nature of the Arctic Ocean, however, makes this an interesting region to examine pollen transport pathways. About two-thirds of the Arctic surface water enters from the eastern North Atlantic, one-sixth from the Pacific through the Bering Strait, and the rest is from summer melting of snow and sea ice, and runoff from the Mackenzie River, and large Siberian rivers such as the Ob, Yenisei and Lena. Weak northeasterly winds dominate most of the year, interspersed by short intervals of southeasterly cyclones (Figure 1).

Most studies of the Arctic Ocean have been made in the summer-open water of the Beaufort Sea and Alaskan Shelf north of the Bering Strait, and on the Kara and Lena shelves north of Siberia. Nelson (1979) studied surface samples and a core from Colville Delta west of the Beaufort Sea, and compared the pollen spectra with samples onshore. Shrub tundra pollen (Gramineae, Cyperaceae and *Alnus*) dominate this western Alaskan Shelf, with 3–22% *Picea* pollen derived from long-distance wind transport. Off the Mackenzie Delta, where the landscape is covered with dwarf spruce, alder and herb tundra, *Picea* and *Alnus* dominate surface spectra both onshore and offshore across the 100 km-wide Beaufort Shelf (Figure 4a). There is an exponential decrease in pollen-spore concentrations from upper delta to outer Beaufort Shelf sites, but there is no clear pattern of pollen-spore species distribution. This absence of distinct gradients suggests considerable mixing of pollen from various sources, including redistribution by iceberg scouring (Matthiessen *et al.,* 2000), sea level transgression and thermokarst erosion processes (Solomon *et al.,* 2000). Absence of endemic Pacific Coast conifer tree pollen such as *Tsuga heterophylla* and *Metasequoia* shows that long-distance transport in surface currents is not important.

In the eastern Arctic, studies of the wide (200 km) shelf off the Lena River show that tree pollen dominates both onshore and offshore in this treeless tundra region (Naidina & Bauch, 1999). Pollen concentrations tend to decrease uniformly offshore across the Lena Shelf, with *Pinus* comprising >40% of the assemblages in the delta plume area. In the Ob and Yenisei deltas, pollen concentration is weakly correlated with surface salinity (Matthiessen *et al.,* 2000); the freshwater algae *Pediastrum* and desmids more clearly mark the river discharge plumes.

On the inner Barents Shelf, high pollen concentrations (>1000/cm^3/yr) in cores from bays of the White Sea correlate

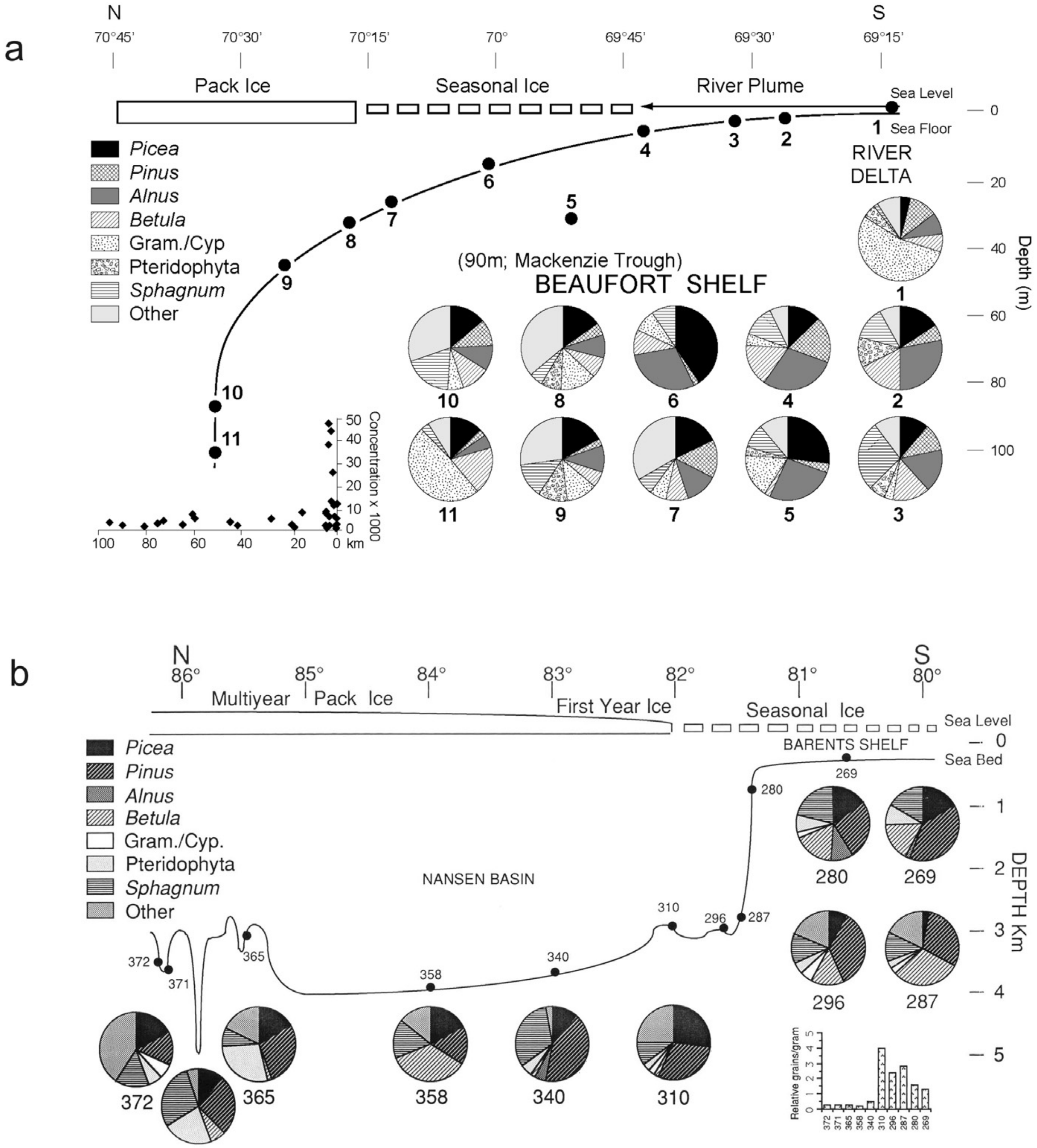

Figure 4. **a**, Schematic profiles of pollen distributions on the shelf off the Mackenzie Delta and across the Beaufort Sea, showing changes in pollen-spore concentrations in grains × $10^3.g^{-1}$ (line and bar graphs) and in pollen assemblages (pie graphs). **b**, Schematic profiles of pollen distributions from the Barents Shelf to Alpha Ridge, showing changes in pollen-spore concentrations in grains × $10^3.g^{-1}$ (line and bar graphs) and in pollen assemblages (pie graphs).

well with classical north European pollen zones, but cores from the Barents Shelf (Throndsen & Bjaerke, 1983; Brusewitz *et al.,* 1984) and Kara Sea (Kulikov & Khitrova, 1982) contained abundant reworked pre-Quaternary pollen and spores. Reworked Cretaceous spores obscured any zonation of Quaternary pollen on the outer shelf off Franz Josef Land (Kulikov & Khitrova, 1982). Surface sediments below the seasonally ice-covered Barents Shelf and multi-year ice in the Eastern Arctic (Figure 4b) contain very low Quaternary pollen concentrations, and pre-Quaternary palynomorphs are common beneath the Transpolar Drift. The seabed pollen-spore assemblages from the shelf and slope environments, however, are very similar to those of snow and water samples that contained only low numbers (6–30 grains/m^3) of modern forest-tundra pollen and spores. *Pinus* and *Picea* dominate most assemblages, but Gramineae (Poaceae) and Cyperaceae increase beneath the Transpolar Drift, perhaps transported from the Siberian Tundra. These data suggest that most pollen enters the deep basins of the Arctic Ocean by wind transport, melt-out of snow and young sea ice. Low Quaternary pollen concentrations beyond the continental slope (Figure 4b) probably reflect the heavy pack ice cover and influx of ice rafted detritus (IRD) from multiyear sea ice formed off river deltas on the Siberian coast.

Pollen, spores and dinocyst concentrations are very low in cores beneath permanent pack ice on the Canadian Polar Shelf (Hein & Mudie, 1991) and on the Alpha and Lomonosov Ridges in the central Arctic Ocean (Figure 4b; Mudie, 1985). These sites adjoin the High Arctic polar desert region and large rivers are absent. These data are consistent with the low pollen influx mostly <20 grains/l of melted snow) transported to the Canadian High Arctic by very long wind trajectories (Bourgeois *et al.,* 1985). It is also notable that the pre-Quaternary palynomorphs in the High Arctic region are predominantly Palaeozoic acritarchs, and they form an assemblage distinct from the Cretaceous-dominated assemblages found in the eastern Arctic Ocean (e.g. Bischof *et al.,* 1997).

In the southern Hemisphere, glaciated marine environments are mainly on the continental margin of Antarctica (Figure 1) and in the ocean basins adjoining New Zealand, Chile and Patagonia. Very strong southeasterly winds result from cold dry air flowing off the Antarctic ice sheets, and glaciers extend to the modern coasts of southwest New Zealand and South America. Off Tasmania, a slope core provided a continuous palynological record for MIS 5a–2, in contrast to the fragmentary onshore records (Colhoun *et al.,* 1994).

Despite the large extent of the southern Circumpolar Ocean, few marine palynology studies have been made. Koreneva (1966) found few pollen and spores in seabed samples beyond 50 km from the western Pacific continental margins, the assemblages being mostly wind-transported grains that poorly represented the onshore vegetation. Wind-transported pollen from Africa and South America comprises 1 to 40% of the pollen and spores in surface samples on Marion Island off West Antarctica *ca.* 47°S, 37.6°W (Scott & Van Zinderen Bakker, 1985), mostly low amounts of *Pinus.* Influxes of *Podocarpus* and *Nothofagus* to the Peru–Chile Trench may reflect fluvial transport from montane forests in Chile *ca.* 1000 km to the south, while high concentrations of *Ephedra* and Chenopodiacae pollen in southwest Atlantic cores suggest increased westerly wind transport during glacial stages (Groot & Groot, 1966; Stanley, 1966). Reworked palynomorphs in the Argentine Basin may reflect frequent melt-out of IRD from Weddell Sea icebergs where pre-Quaternary palynomorphs are abundant in glaciomarine muds and lodgement till (Kemp, 1972). In the Ross Sea, piston cores contained abundant palynomorphs in both glaciomarine muds and basal tills, with differences in palynomorph ages being related to ice drainage source areas (Truswell & Drewry, 1984). Laminated Holocene diatomites on the upwelling margin of the Kerguelen Plateau, however, contained only rare Quaternary terrigenous and marine palynomorphs (Labeyrie *et al.,* 1996). Onshore, moss polsters contained only 1–5 pollen grains, transported more than 3000 km by wind or birds' feet (Kappen & Straka, 1984).

In the South Atlantic Ocean, north of the Polar Front, pollen assemblages in 57 samples from the slope and rise off western Africa were used to reconstruct seasonal pathways of terrigenous input (Dupont & Wyputta, 2003; Shi *et al.,* 2001), and the vegetation history from MIS 6–1. Aeolian transport in strong easterly winds during austral fall and summer prevailed in most regions, and there was a good latitudinal correspondence between marine pollen assemblages and onshore vegetation. In the zone of westerly winds south of 25°S Lat., however, pollen input was very low (<10 grains/ml). In the tropics, river discharge prevailed off the Angolan Cuanza River, while aeolian input was the dominant transport path in the tropical regions off northwest Africa, augmented by fluvial input from the Congo and Niger Rivers (Dupont *et al.,* 1998; Hooghiemstra *et al.,* in press). As expected for the semi-enclosed Mediterranean and Black seas, several studies have shown excellent correspondence between marine and onshore pollen stratigraphies (e.g. Rossignol-Strick, 1995; Moreno *et al.,* 2005), and the importance of shifts in the monsoon winds was demonstrated both there and in cores from the tropical Arabian Sea (Prabhu *et al.,* 2004).

MATERIALS AND METHODS

Sampling and dating

As with traditional onshore Quaternary pollen studies, marine palynology samples need to be examined in the context of their depositional setting. In coastal, shelf and slope environments, high resolution seismostratigraphic profiles can be used to determine the presence of continuous late glacial and Holocene sedimentary sections (e.g. Scott *et al.,* 1984). In bathyal settings, seismic resolution is lower but the thickness of the Pleistocene and Holocene sections can usually be determined, and seabed features, such as drift deposits, debris flows and turbidity current channels and levees can also be seen and avoided. Careful examination of the lithology and smear-slide texture analysis can also be used to determine the presence of fine-grained turbidites (McCarthy & Mudie, 1998; McCarthy, Gostlin *et al.,* 2004). Appropriate *in situ* samples of fine-grained sediments, about 5–10 cm^3 volume, can then be taken for pollen analysis. Marine cores can be dated by conventional radiocarbon age determination of in-place molluscs, or by accelerator mass spectrometer dating of foraminifera in amounts as low as 1 mg. Pelagic marine sediments older than 75 ka are dated by the oxygen isotope records of foraminifera in the same samples, by magnetochronology and by the chronostratigraphic ranges of marine microfossils (coccoliths, foraminifera and radiolaria).

Pollen extraction

Use of the best method of laboratory processing for marine palynology is also important. It has been shown that use of acetolysis (acetic acid, followed by oxidation with a mixture of acetic anhydride and sulphuric acid), and use of bases (NaOH, KOH) for laboratory preparation of samples is very destructive to many thin-walled gonyaulacoid dinocysts (hystrichospheres) and to most protoperidinioid dinocysts (Marret, 1983; Hopkins & McCarthy, 2002). This bias is particularly important in glaciated arctic and subarctic marine environments where protoperidinioids are dominant (Mudie, 1992; Rochon & De Vernal, 1994; Mudie & Rochon, 2001).

Less is known about the preservation state of marine pollen, although Zonneveld *et al.* (2001) suggested that thin-walled grains like *Quercus* were better preserved in organic-rich marine sapropels than in inorganic marine sediments. Figure 5a shows the results of acetolysis treatment in addition to the recommended sieving, and HCl and HF treatments for processing of fine-grained marine mud (lutite) from the Scotia Shelf off southeast Canada (Mudie, 1982). The acetolysis treatment resulted in 30–50% reduction of *Picea, Pinus* and *Acer* pollen, with a reciprocal enrichment of thick-walled grains, including *Alnus, Betula,* Asteraceae, *Polypodium* and *Osmunda* ferns, and

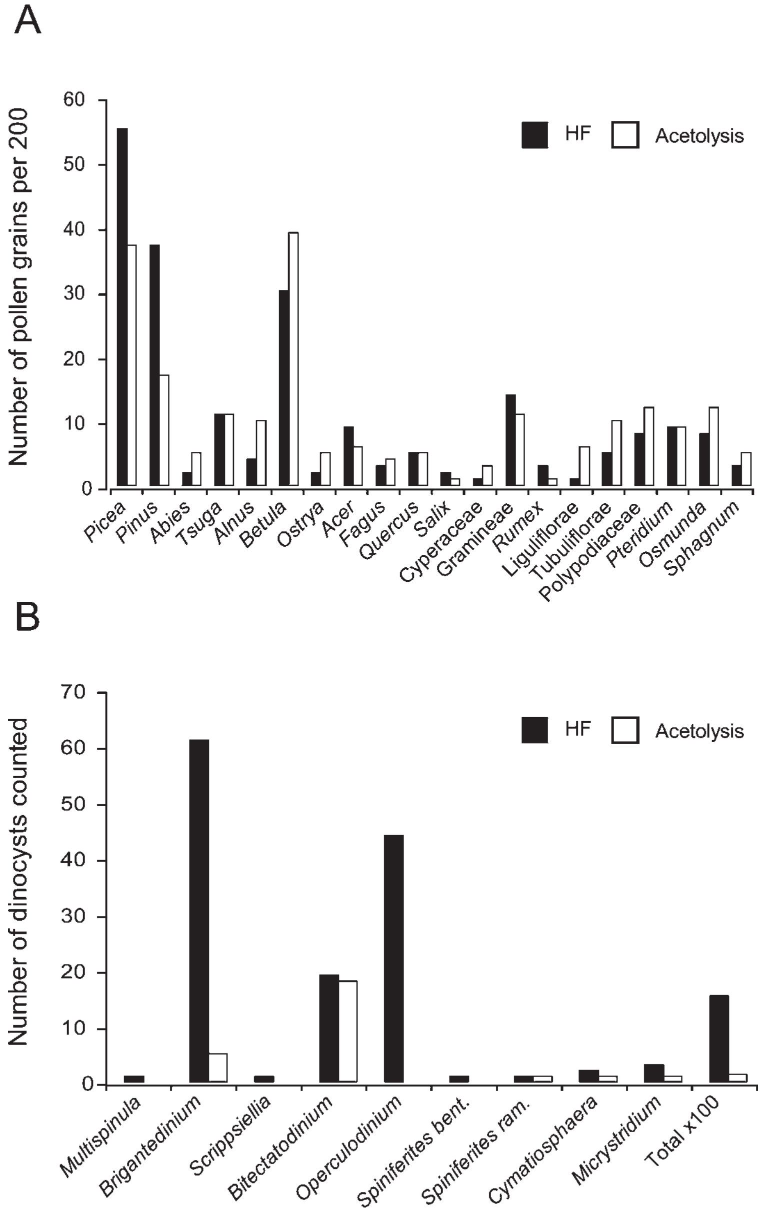

Figure 5. Results of experiments on chemical processing of shelf sediments with the acetolysis method and with only hydrofluoric acid (HF). **A**, Pollen. **B**, Dinocysts and acritarchs

Sphagnum moss spores. The extremely deleterious effect of acetolysis on thin-walled protoperidinioid dinocysts (*Brigantedinium* spp.) in aliquots of the same sample is shown in Figure 5b. Where pelagic pollen concentrations are very low, pollen can be further concentrated by use of dispersants and nylon sieves (Heusser & Stock, 1984), but routine use of sodium chlorate is not recommended. Heavy liquid separation requires great caution because small amounts of pollen are often decanted in the heavy liquid. Bourgeois *et al.* (1985) describe painstaking filtration methods required to recover fully the tiny amounts of pollen in snow.

RESULTS OF TRANSPORT-DEPOSITION STUDIES

The review of studies on pollen-spore distributions in glaciated marine environments shows that six elements govern the transport and deposition of fine-grained terrigenous organic material: winds, river water, ocean currents, sea ice, glacier ice, and erosion by water or ice. Other important processes may include redeposition by gravity flow or contour currents. Multiple box models can be used to construct deterministic process-response models that allow first-order evaluation of the main pollen-transport pathways for a given region (Mudie & McCarthy, 1994). This method was tested on the coast and shelf off Nova Scotia, which is a relatively shallow, passive continental margin dominated by storm waves, and can easily be applied to Arctic fiords or inland seas, such as the Great Lakes and the Black Sea (e.g. Mudie *et al.*, 2002).

The basic process-response model predicts that the annual pollen input (Is) to a given sink area (s^{1-n}) of mud accumulation can be calculated by equation Is = If + Ia – Im – Ir + Ii, where f, a, m, r and i are inputs from fluvial, aerial, marine tides, redeposition and ice rafting, respectively, in each compartment or sink of the multi-box model. The model is tested by measuring the annual pollen-loads in air (Ia), river (If) and marine water samples (Im), in sediments being eroded (Ir), and in sea ice (Ii), then comparing the sum of these inputs to the measured annual accumulation in the marine sediment (Is). Details of the method are given by Mudie & McCarthy (1994). The results for the Nova Scotian study are reproduced graphically here (Figure 6); the annual pollen influxes (Ia) for the 1987 flowering season at the head and centre of Halifax Inlet, Nova Scotia, are available on request. The multiple-box model assumes that, in

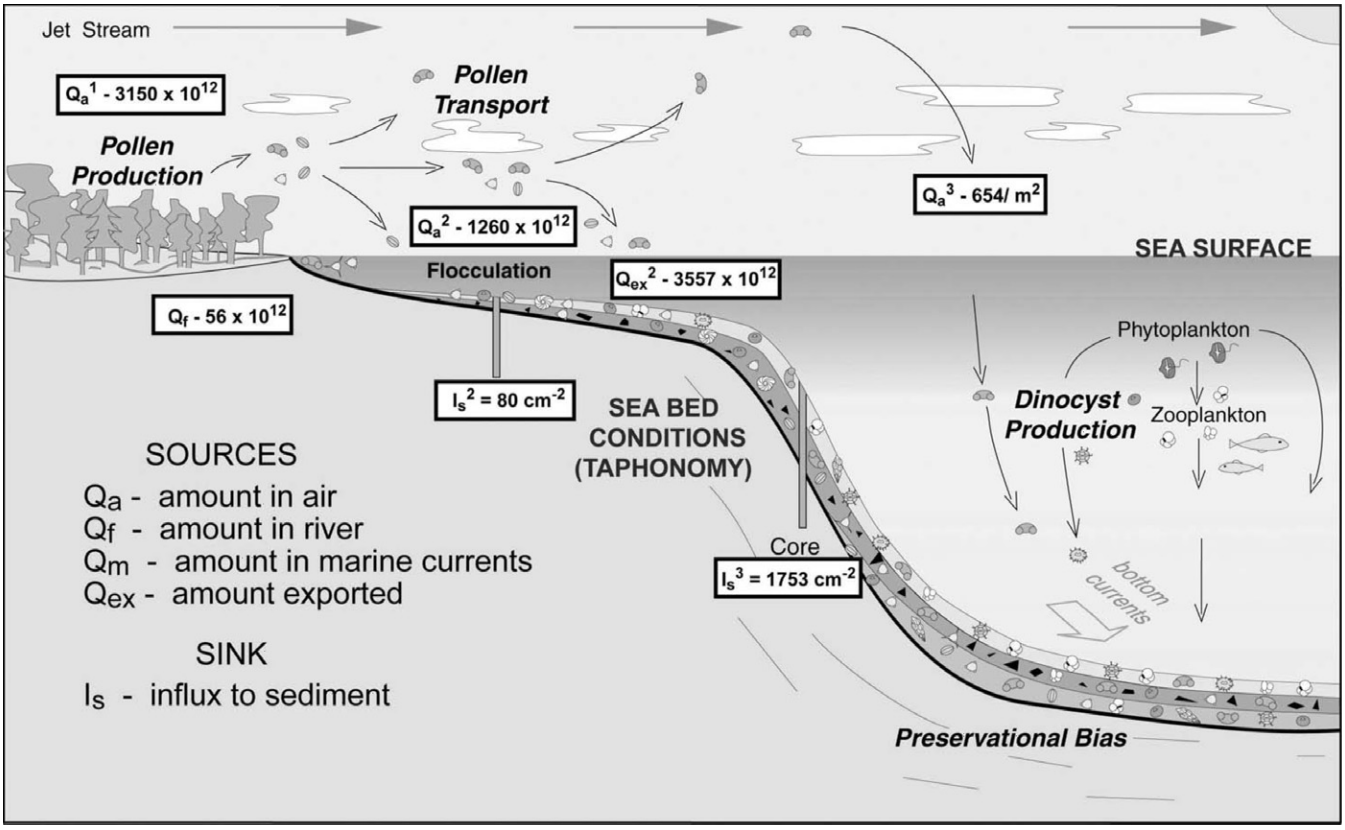

Figure 6. Pollen transport and deposition to the mid-latitude western North Atlantic Ocean, showing measured values for annual air (Qa^1) and river (Qf) pollen contents, and annual influxes to sediments after nearshore mixing (Is^2) and cross-shelf transport (Is^3). Qex is the amount exported from the nearshore by tidal exchange.

this boreal forest region, shoreline pollen inputs are relatively uniform for distances equal to the continental shelf width of about 200 km, and that tidal mixing of the pollen load in coastal inlets occurs within a few days/tidal cycles. It was also assumed that settling rates of individual pollen grains and spores (specific gravity *ca.* 0.5–1.5; diameter *ca.* 10–100 μm) are much higher under natural estuarine and continental shelf conditions where biological and physico-chemical processes will increase the particle sizes by flocculation, agglomeration and faecal pellet incorporation. This assumption is now supported by experiments on copepod consumption of *Pinus* pollen and settling rates of bisaccate pollen grains in seawater, which has a density of 1.02–1.09.

Two field experiments investigated the effect of plankton ingestion on palynomorph transport. First, sand-sized copepod faecal pellets were collected from a sediment trap in Halifax Inlet and the flocculent layer of a box core. Concentrations of palynomorphs in the pellets were much lower (10–30% for pollen; <5% for dinocysts) than in the fine sediment matrix from the trap and core samples. A high percentage of degraded grains suggested that pollen is damaged by plankton digestion, as reported for pollen in the guts of some insects (Stanley & Liskens, 1974). Alternatively, the zooplankton may carefully select the particle size they eat, rejecting larger, undamaged pollen grains. To test this, a copepod feeding experiment was conducted on the Scotian Shelf. The copepods rejected pine pollen as a food when it was mixed with diatoms, and only accepted the pollen when they were starved for 24 hours, then offered 'pure' pine pollen suspended in sterilised, filtered seawater. Most pine grains were subsequently excreted without apparent damage [Plate 1 (1 & 2)], in a tube-shaped pellet enveloped by a membrane. When disrupted from the pellet, however, the bisaccate grains showed numerous small tears [Plate 1 (3)], suggesting that the ingested grains were quite fragile.

The settling rate of *Pinus* and *Picea* pollen, the main pollen in North Atlantic marine sediments, was examined in a laboratory experiment. Large (5 g) samples of fresh *Pinus strobus* and *Picea rubens* pollen [specific gravity ~0.4–1.2 (Traverse, 1994)], were collected from windrows in Halifax Inlet and put into wide mouth beakers containing either distilled water (DW) or seawater (SW = 23‰). After two hours at 21°C, the solutions were stirred vigorously, then, after 19 hours of settling, samples (20 ml) were withdrawn from the surface and bottom of the beakers. It was found that both the DW and SW subsamples contained roughly equal volumes of floating and settled pollen. Light-microscope study showed that the settled grains had been agglomerated by phycomycete fungal hyphae [Plate 1 (4 & 5)] and rod-shaped bacteria. In contrast, floating grains remained single and appeared to contain air bubbles or oil bodies [Plate 1 (5)]. This fraction remained suspended throughout the 18-month laboratory experiment (see also Traverse, 1988), despite efforts to sink the grains by adding detergent or by physical damage through ultrasonification. These observations tend to support Erdtman's (1954) finding that differential floatation of winnowed buoyant pollen grains is not a serious bias in coastal areas because of oxidation and redistribution of pollen stranded on the shoreline.

The Nova Scotian shelf is a storm-dominated environment (Piper *et al.,* 1983) and the possibility that pollen inputs are greatly increased during storm flooding events was examined in Halifax Inlet (Figure 7). Storm-deposited sandy layers in a 350-year-long core were dated using records of Pb-210, industrial soot particles, and weed pollen distributions. At a sample frequency of ~20 years, there is no strong correlation between pollen influx and either sand layers or 25–50-year

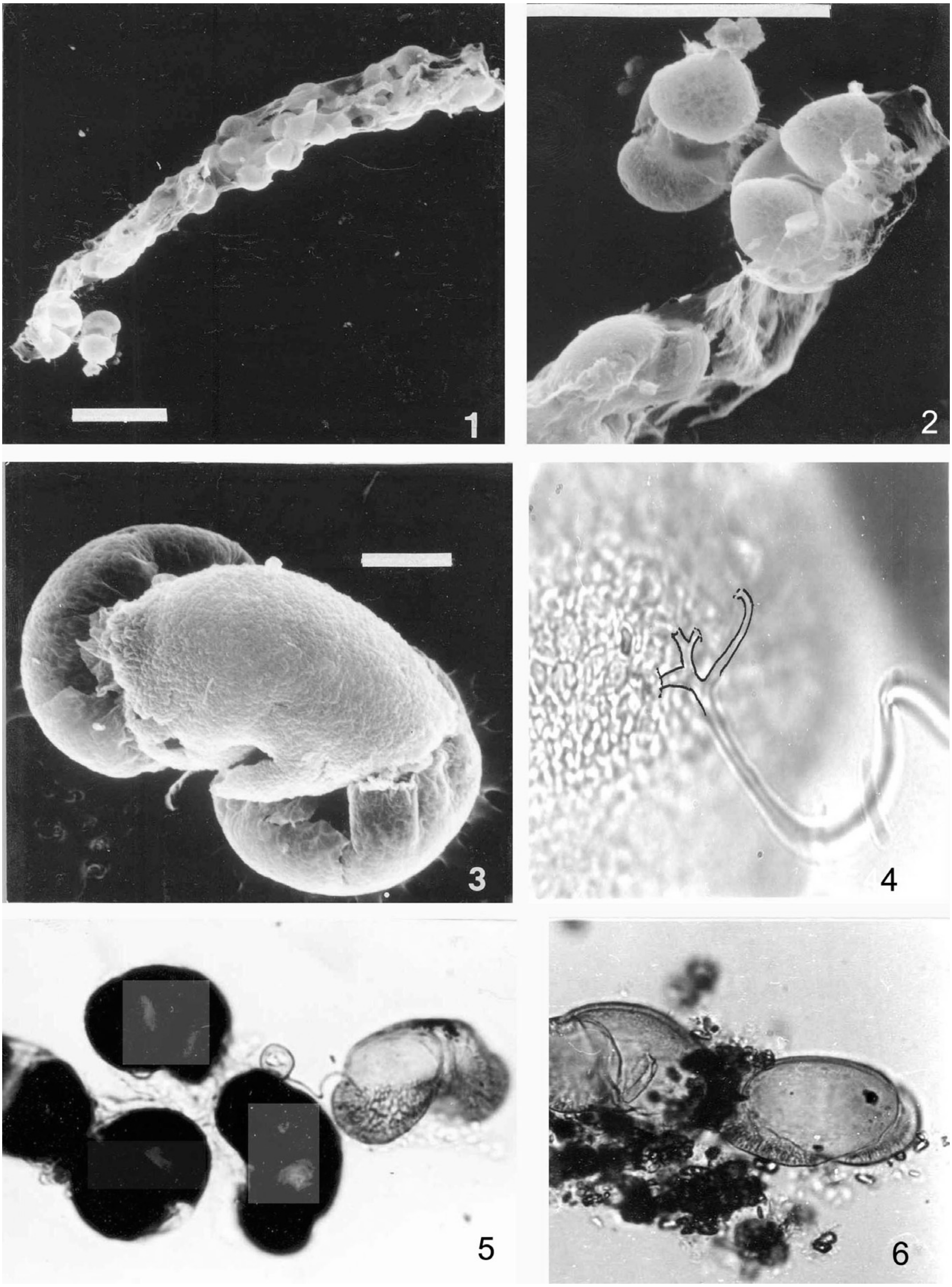

Plate 1. Scanning Electron Microscope (SEM) images and light microscope (LM) photos of pollen from copepod feeding experiments (**1–3**) and after one day in seawater. **1**, (SEM) copepod faecal pellet containing pine pollen. **2**, Details of torn end of pellet shown in (1) and extruded pollen grains. **3**, (SEM) Pinus grain, showing tears on bladders and cappa. **4**, (LM) Detail of fungal hypha attached to *Pinus* pollen. **5**, *Pinus* and *Picea* from seawater surface after 24 hours. **6**, Agglomerated grains from bottom sediment after 24 hours.

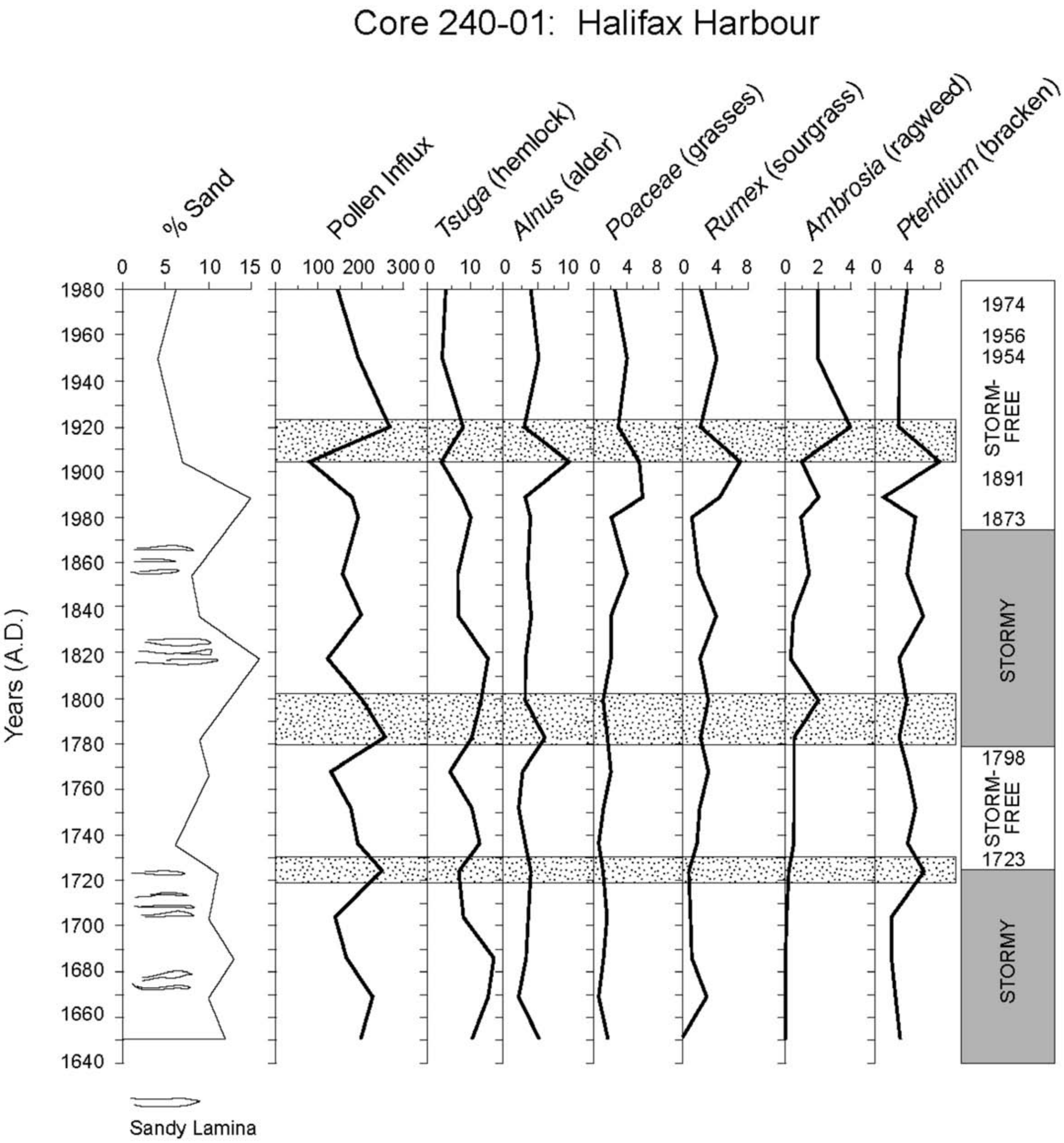

Figure 7. Pollen-spore content of storm layers in Core 240 from Halifax Inlet.

intervals of storminess. However, small peaks in pollen influx follow three of the hurricanes that occurred in 1723, 1798 and 1891. The first two occurred before the start of the major deforestation period (hemlock pollen decline) in 1820; therefore, the increased pollen influxes probably reflect the aftermath of major forest blow-downs rather than direct river transport.

GLACIAL–INTERGLACIAL VARIATIONS IN MARINE POLLEN TRANSPORT

In this section, we will use the information on modern pollen transport in an attempt to interpret glacial/interglacial differences in pollen transport. For simplicity, we limit our discussion to mid-latitudes in the western North Atlantic and western North Pacific where prevailing westerly winds transport pollen offshore, and use data from Quaternary pelagic sediments off Atlantic Canada and East Asia. As shown earlier, the major biomes found today in these regions are quite well represented in surface sediments of coastal and neritic environments, and shelf pollen assemblages record the same vegetation changes that mark the latest Quaternary glacial–interglacial fluctuations in lake, wetland, and loess settings of East Asia (Sun *et al.*, 1997; Zheng, 2000; Yuan *et al.*, 2000). Here we focus on possible use of long, almost continuous deep-sea records for reconstructing Quaternary palaeovegetation and palaeoclimate in view of the evidence that taphonomic problems can greatly skew marine pollen-spore assemblages in mid-ocean sediments.

In the Northwest Atlantic, two pelagic sites have been studied in detail (Piper *et al.*, 1994; Aksu *et al.*, 1992). On the J-Anomaly Ridge, south of the Grand Banks of Newfoundland, a 1 Ma record of clastic sediment and pollen influx at Site 87-3 (Figure 8) shows that both inorganic and organic particle influxes are more abundant before MIS 11 or 10 (~0.4–0.35 Ma), after which the pollen influx almost disappears until MIS 5e (Piper *et al.*, 1994). In contrast, during the past 0.4 Ma, there is a greater influx of Cambro-Ordovician acritarchs, probably sourced from melt out of icebergs from Baffin Bay and Hudson Strait. North of the Grand Banks, the Heinrich layers in Core MD95-23 are also enriched in reworked palynomorphs and magnetic minerals (Hiscott *et al.*, 2001).

On the West Greenland Rise, the 0.9 Ma record (Aksu *et al.*, 1992) for ODP site 646 shows a broadly similar sequence of palynological and sedimentary events (Figure 9). Here Heinrich sediments are absent and the input of Cambro–Ordo-

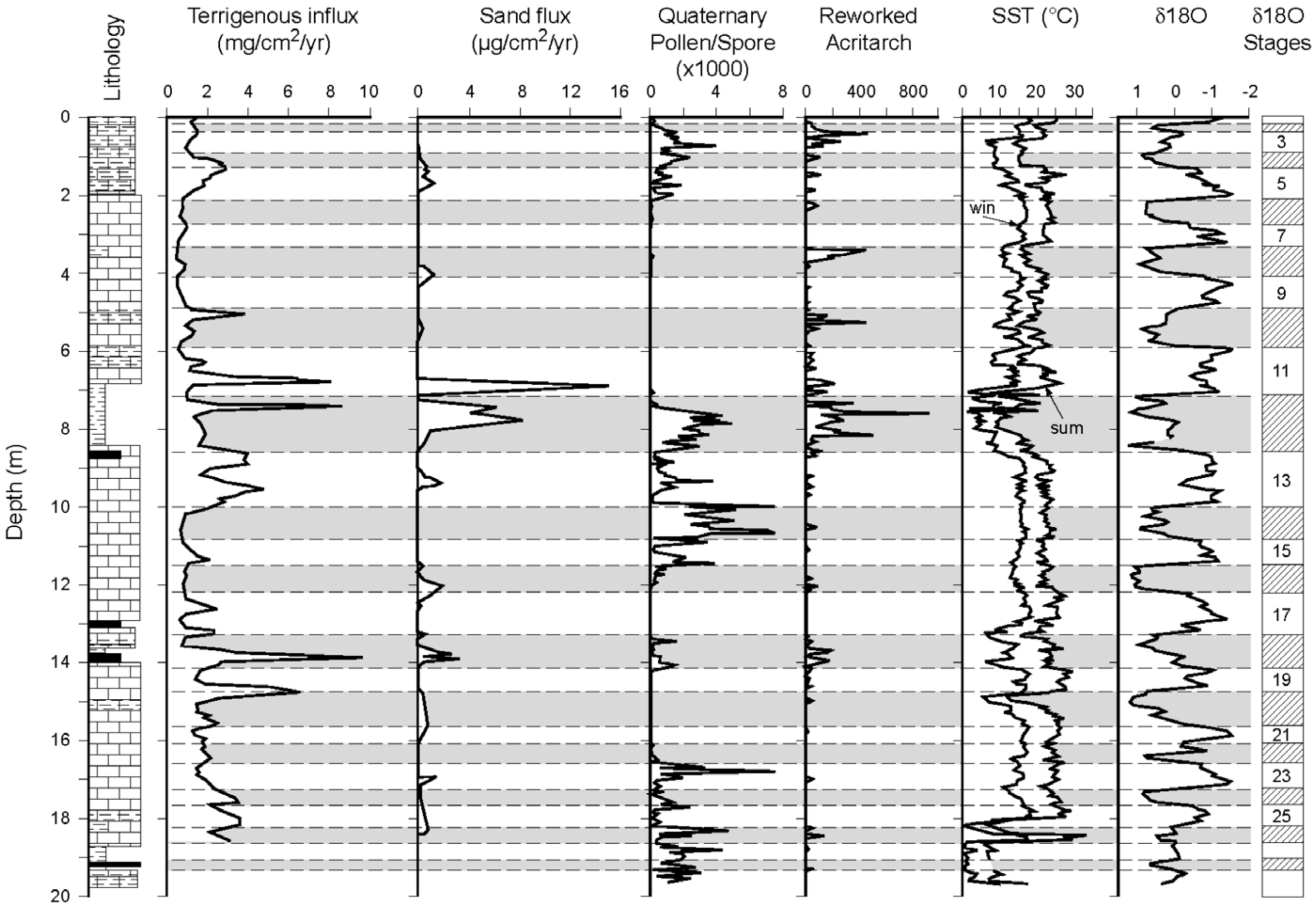

Figure 8. 1 Ma record from Core 87-03, NW Atlantic Ocean, J-Anomaly Ridge, showing correlation between pollen and clastic sediment flux, the oxygen isotope record, and estimated changes in seasonal SST (from Piper *et al.*, 1994).

vician acritarchs is very low, as expected from the absence of Baffin Bay icebergs. In contrast, peaks of Mesozoic pollen and spores mark the Early to Middle Pleistocene glacial stages, suggesting transport from the eastern Arctic in the East Greenland Current (cf. Bischof *et al*, 1997). High pollen influxes are mainly confined to interglacial stages or the glacial–interglacial transitions, although exceptions are evident for MIS 4, 8, 14 and 22. Despite this variability, it is notable that at both NW Atlantic sites 87-3 and 646, there is a major decline in terrigenous organics after ~0.4 Ma (MIS 13–11) when the 40 ka dominant orbital beat switched to ~100 ka.

Glacial–interglacial variations in pollen transport to the abyssal western North Pacific are illustrated by data the sediment cores on a transect near 35°N (Figure 1). Excellent chronological control for the late Quaternary was provided by oxygen isotope data from foraminiferal tests in core H3571 (Kawahata & Ohshima, 2002) and V28-304 (Heusser & Morley, 1997). Core RC14-99, which is below the CCD, could be correlated with V28-304 (Heusser & Morley, 1997). Chronological control was not as good at ODP Site 1179; here analysis of Plio-Pleistocene sediments relied on the magnetochronology, which is primarily useful before 780 ka (McCarthy, Findlay *et al.*, 2004; McCarthy, Gostlin *et al.*, 2004; Little, 2005).

Figure 10 shows the relative abundance of pollen over the past ~250 ka (MIS 6 to 1) in the more proximal cores V28-304 and RC14-99. Percentages of *Picea, Betula,* and herb pollen generally increase in both cores during stadials (MIS 2, 4, 6; also 5b and 5d), recording the expansion of boreal and steppe elements at mid latitudes in East Asia during these cool/dry intervals. Interglacials and interstadials (MIS 1, 3, and 5a, c and e) are characterised by higher percentages of *Cryptomeria* and *Quercus* that record expansion of temperate to subtropical forests during warm, humid intervals. However, Pinaceae (*Pinus, Abies* + *Tsuga*) percentages are more difficult to interpret: they are higher for interglacials/interstadials in V28-304 but increase during the stadials of RC14-99, presumably reflecting the exceptional adaptation of pine pollen for long-distance transport. This over-representation is especially marked in interglacial sediments of V28-304, which is upwind and up-current of the subtropical forest biome where Pinaceae are not common. Heusser & Morley (1997) used counts of 300 grains for pollen sums and Heusser (1990) noted that pollen concentrations ranged from ~100 grains/g in V28-304 to 2500 grains/g in the more proximal core RC14-99.

The correspondence between East Asian vegetation and pollen assemblages at Hess Rise site H3571 (Kawahata & Ohshima, 2002) is much weaker than in cores RC14-99 and V28-304. Figure 11 shows these data replotted as relative abundances, excluding *Alnus.* The pollen sums are very low: 15–140, averaging 55 pollen + spores, excluding *Alnus* and omitting sums <10. The only reliable indicator of stadial conditions in core H3571 is pollen concentration that averages one to two orders of magnitude greater in MIS 2, 4 and 6 than during MIS 3 or 5. The relative pollen abundances can be completely misleading. % *Picea,* for instance, is much higher during MIS 5 than MIS 6, 4 or 2, while % *Quercus* is equally high for glacial MIS 2 and 6 as during the warmer MIS 3 or 5.

Pollen concentrations in sediments deposited during glacials over the last 3.5 Ma are also several orders of magnitude higher at ODP Site 1179, about 1650 km off Hokkaido (McCarthy,

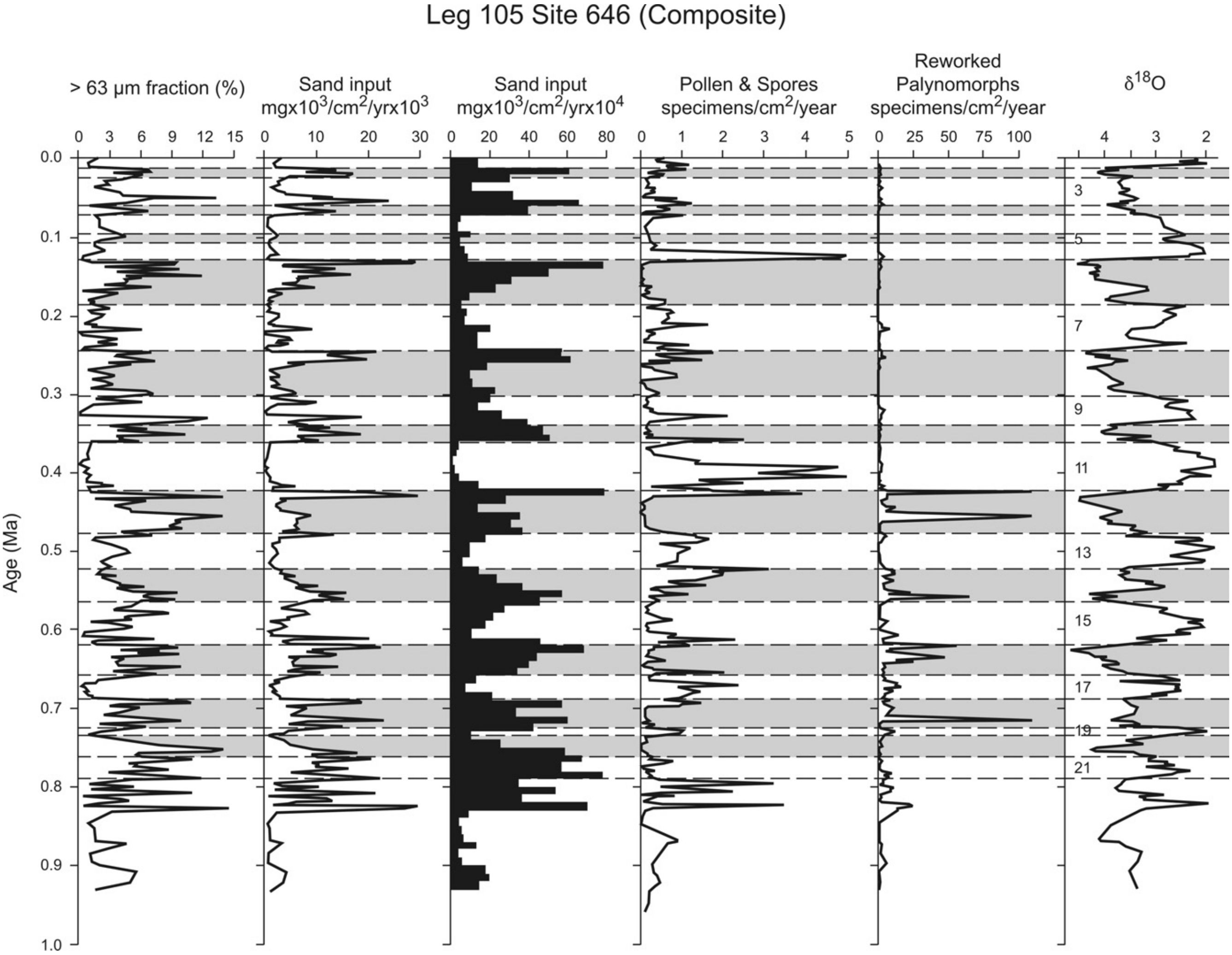

Figure 9. 0.9 Ma record from NE Labrador Sea, showing correlation between pollen and clastic sediment flux, oxygen isotope record, and estimated changes in seasonal SST (Aksu *et al.*, 1992).

Findlay *et al.*, 2004; McCarthy, Gostlin *et al.*, 2004; Little, 2005). There is no oxygen isotope chronology for this site, which is well below the modern CCD, but percentages of boreal and steppe taxa in the pollen peaks record cool, arid glacial conditions at times of high pollen flux (Figure 12). These glacial-stage pollen peaks appear to correlate with grain size peaks and very low magnetic susceptibility values in the Lingtai sequence on the Chinese loess plateau, thereby recording strengthened westerly winds. At Site 1179, the increased wind strength during late Cenozoic stadials corresponds to the winnowing of loess deposits and transport of coarse quartz further offshore (McCarthy, Findlay *et al.*, 2004; McCarthy, Gostlin *et al.*, 2004). The relatively high flux of humid/warm tree pollen indicators (e.g. Cryptomeria/Cupressaceae, *Fagus, and Carya*) may record transport of pollen from the south, either via the Kuroshio Current, cyclones or after resuspension from erosion of older interglacial sediments on continental margins.

DISCUSSION

The literature review of pollen-transport processes in marine environments reveals six main elements: wind, river water, ocean currents, sea ice, glacier ice, and erosion by water or ice. It is well known that the growth of ice sheets in the Northern Hemisphere affected atmospheric and oceanic circulation (CLIMAP, 1976; COHMAP, 1988), hence the importance of winds and currents as transport paths**.** During glacial stages, and on tectonically unstable margins, other processes may include erosion or redeposition by gravity flow, contour currents and ice rafting. The review shows that there are large regional variations in the dominance of these agents in modern high latitude regions, and it explains the major differences in emphasis that have placed on the relative importance of wind and river transport by different authors (e.g. Groot & Groot, 1966; Mudie, 1982; Traverse, 1988; Mudie & McCarthy, 1994).

As a generality, it can be said that during interglacial stages, the dominant pollen transport at any marine site is determined primarily by the direction and strength of the prevailing winds. The prevailing winds in turn drive the underlying ocean circulation, particularly outside the ice-covered polar oceans where long-distance transport as IRD becomes an important pathway, usually discernible by the presence of reworked pre-Quaternary palynomorphs. In the tropical and temperate regions with reliable rainfall, rivers may also be more important pollen transport pathways to marine environments. Locally, in the cold desert regions of the Sub-Arctic region, very large rivers, with headwaters many degrees of Latitude south of the Polar Circle, may keep Arctic estuaries and seas open in summer, and over-ride the wind transport signal that prevails over the most of the polar desert.

Mudie & McCarthy (1994) have demonstrated that the close correspondence between and eastern North American vegetation zones and surface pollen assemblages in coastal and neritic sediments of the western North Atlantic, where westerly winds prevail, can act as analogues of interglacial stages,. When

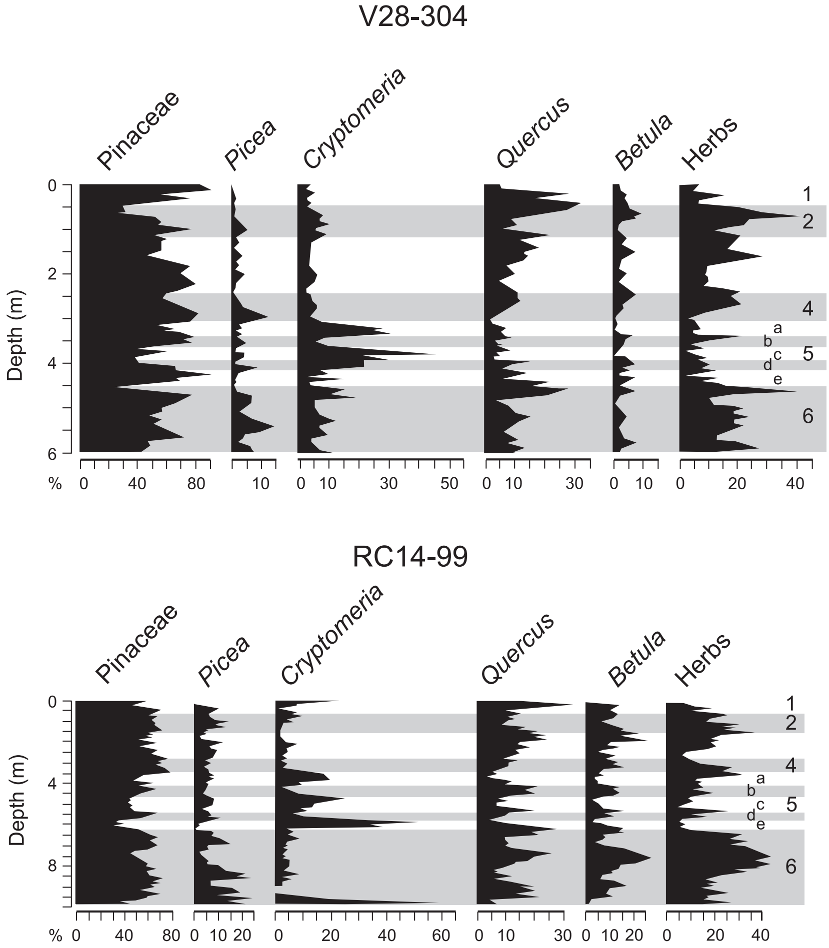

Figure 10. Relative abundances of major pollen taxa in cores V28-304 and RC14-99 (modified from Heusser & Morley, 1997) that are relatively close to East Asia/Japan, showing assemblages that reflect onshore glacial–interglacial vegetation changes quite well, despite biases of over-representation by more buoyant pollen taxa.

pollen is processed with HCl and HF, differential preservation has been demonstrated not to be a significant factor in Quaternary sediments in this region, except in areas of extreme oxidation (Hopkins & McCarthy, 2002). Pollen concentration and diversity in surface sediments decreases with distance from the shoreline, as pollen and embryophyte spores settle through the air and water column. Because of differential adaptation to long-distance transport in wind and water, however, the relative abundance of buoyant anemophilous pollen, particularly bisaccate grains like *Pinus* and *Picea,* and spores with intact exines, generally increases with distance from shore. Denser grains with thick exines, such as *Betula* and

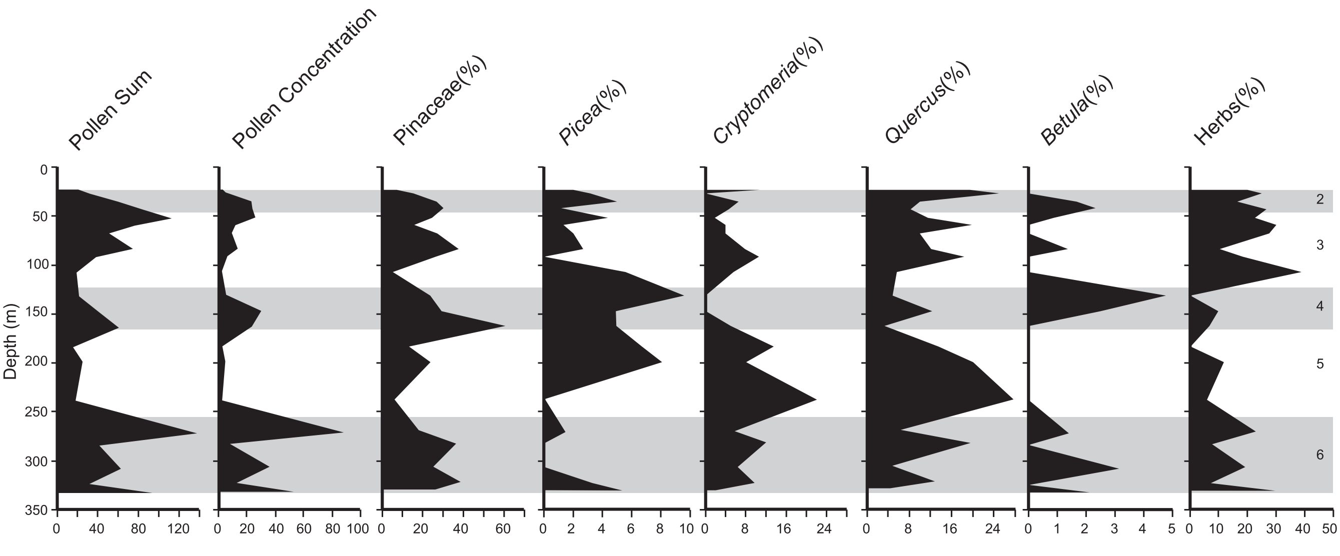

Figure 11. Relative abundances of major pollen taxa in core H3571 (redrafted from Kawahata & Ohshima, 2002), several hundred kilometres from East Asia/Japan, showing weak correlation with glacial–interglacial changes in vegetation during MIS 6 to 1, probably because of recycling from exposed shelves.

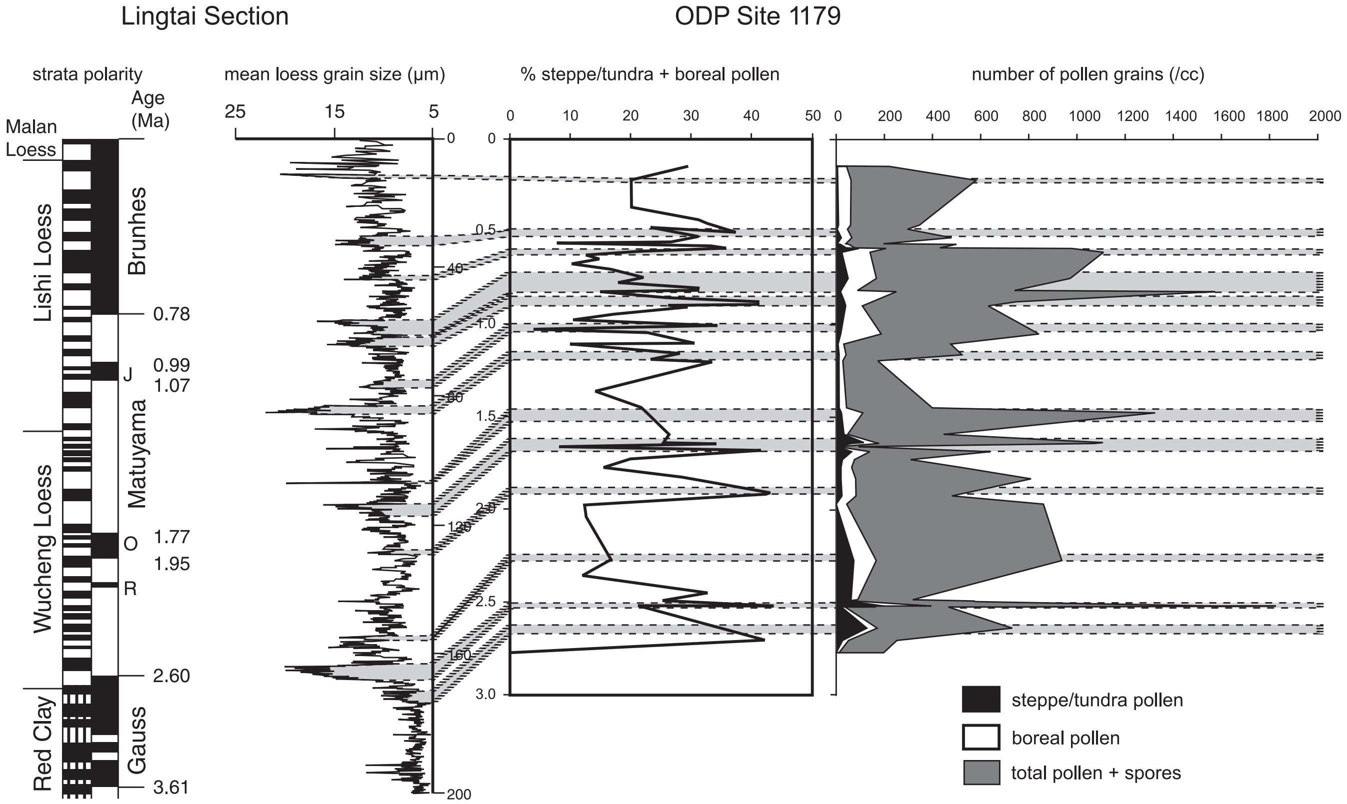

Figure 12. Correlation between coarse grain size in Chinese loess at Ling Tai (An, 2000) and peak pollen abundances at ODP Site 1179, showing periodic increased wind strength and winnowed dust-sized particles, and offshore deposition (McCarthy, Findlay *et al.*, 2004). Boreal forest and steppe and/or tundra biome expansion in response to glaciations is recorded by increased % *Picea, Larix, Alnus, Betula* and herb pollen.

Carya, are greatly under-represented, particularly beyond the shelf break (McCarthy & Mudie, 1998; McCarthy *et al.*, 2003). Our copepod and faecal pellet experiments show that zooplankton feeding is not the major pathway of deposition suggested by Chmura *et al.* (1999), but that agglomeration and flocculation are important.

During the late Wisconsinan glacial stages, pollen assemblages in neritic sediments of the Northwest Atlantic correlate relatively poorly with reconstructions of vegetation onshore (Mudie & McCarthy, 1994). This partly reflects the replacement of prevailing westerly surface winds by anticyclonic winds around the Laurentide Ice Sheet that transported dust toward interior North America (Broccoli & Manabe, 1987). The regional pollen load was also prevented from raining out onto the ice sheet and periglacial tundra by the cold air around the ice sheet (Richard, 1977). Most of the regional pollen rain therefore accumulated well south of the glacier margin.

In deep sea settings of the western North Atlantic, pollen assemblages are also skewed by resuspension of pollen from continental margins exposed during lowstands (McCarthy & Mudie, 1998). This source of terrigenous organic matter explains the huge increase in pollen flux to deep-sea environments when much of eastern North America was glaciated and seasonal sea ice extended southwards to about 50°N. Even as far south as Portugal (~40°N), pollen and spores were transported onto the Iberia Abyssal Plain by turbidites (McCarthy, Gostlin *et al.*, 2004). In the passive margin setting of the western North Atlantic, wide continental rises are built from coalescing aprons of mass wasted material and pollen can be entrained by bottom water currents (Figure 13); hence 'recycled' pollen dominates deep-sea sediments in parts of the North Atlantic Ocean. This, together with the high concentrations of pre-Quaternary palynomorphs, precludes their use for detailed vegetation–climate reconstruction during glacial intervals. However, the correspondence between pollen and clastic sediment influx can be used to infer probable sources of ice rafted debris or Heinrich layers (Figure 13), and their relationship to changes in sea surface temperature. It is also notable that the magnitude of pollen influx decreases greatly at the mid-Pleistocene switch in dominance of orbital climate forcing factors (MIS 13–11), at the time of major reorganisation of ocean currents and Northern Hemisphere ice sheet expansion.

No large ice sheets developed in East Asia during Quaternary glacials, but the intensification of both winter monsoons and prevailing westerly winds increased the aeolian flux of terrigenous material to the western North Pacific (Rea, 1994; Rea *et al.*, 1998; An, 2000; Kawahata *et al.*, 2000; Nilson & Lehmkuhl, 2001). The progressive aridification of East Asia, as a result of continued uplift of the Tibetan Plateau (Raymo & Ruddiman, 1992; Rea *et al.*, 1998) also promoted the expansion of desert and steppe biomes in China (Sun *et al.*, 1997). During glacials, stronger westerly winds and intensified monsoons (Rea, 1994; An, 2000) deflated unarmoured loess (Pye, 1995), winnowing the fines and increasing the mean grain size of sediments on the loess plateau. This offshore transport was facilitated by the progressive aridification around the ice sheets. High concentrations of pollen relatively rich in herbs, *Picea, Betula* and *Larix* (Figure 11) thus correlate with coarse grain sizes in loess sequences (McCarthy, Findlay *et al.*, 2004; Little, 2005).

Although much terrigenous material is trapped in the Pacific active margin setting, where narrow shelves and steep slopes are bounded by deep trenches, fine particles can be entrained in surface- and deep-water masses after resuspension from exposed shelves and oversteepened slopes. Southward migration of the Subarctic Front also altered the paths of the Oyashio

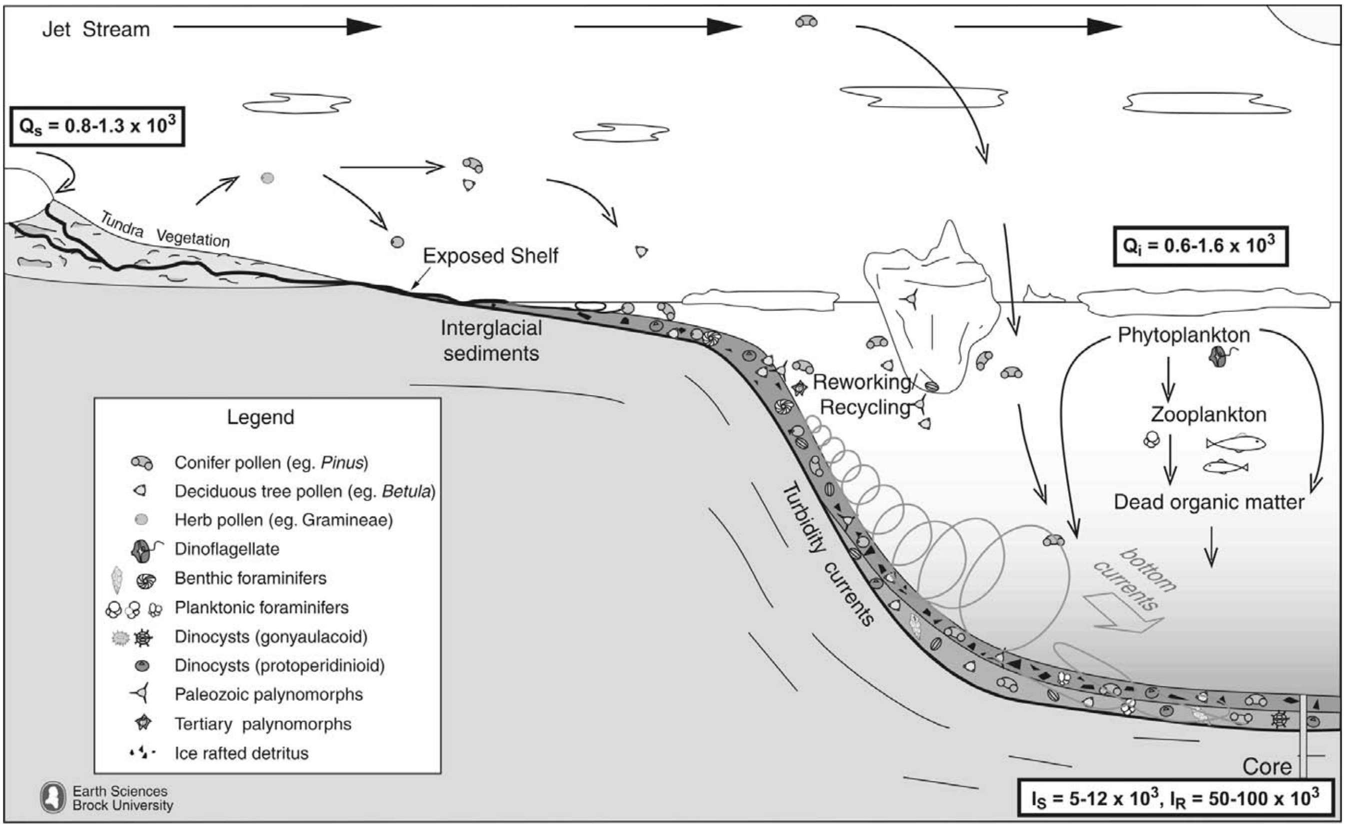

Figure 13. Pollen transport and deposition to the mid-latitude western North Atlantic during Pleistocene glacials. Compare with Figure 6, showing modern pollen transport dominantly by wind, rivers, and ocean currents, measured source values (in grains$^{-m^2 \cdot yr}$) for snow (Qs) and sea ice (Qi) are very low compared to annual influxes of Quaternary pollen-spores (Is) and reworked palynomorphs (Ir) at Site 646 during MIS 4, indicating the increased importance of erosion and redeposition by gravity flow during glacial stages.

and Kuroshio Currents (Ujiié & Ujiié, 1999; Ujiié, 2003; Yasuda, I., 2003). Kawahata & Ohshima (2002) attributed the higher influx and diversity of pollen deposited during stadials to recycling from exposed shelves and enhanced current transport. The very low interglacial pollen flux to the Hess Rise largely appears to be from chance transport: only *Cryptomeria* pollen reliably indicates Kuroshio Current transport from the South China Sea. At present, westerly winds transfer large quantities of mineral dust as well as pollen and spores to the mid-latitude western North Pacific Ocean, and stronger winds would have prevailed during glacials when polar–equatorial gradients were intensified (Figure 13). Rea (1994) estimated aeolian flux into the Northwest Pacific along the path of prevailing westerly winds at rates of 1000 mg/cm (ka)$^{-1}$, and we have shown (Figure 12) that wind from the loess plateaus was an important transport mechanism to ODP Site 1179 over the last 3.5 million years, particularly during glacials. Nakai *et al.* (1993) also found that silicates from the central North Pacific have identical REE values to Asian loess, supporting an aeolian origin for these sediments.

CONCLUSIONS

A review of studies on pollen-spore distributions in glaciated marine environments shows that six main elements appear to govern the transport and deposition of fine-grained terrigenous organic material. These elements are winds, river water, ocean currents, sea ice, glacier ice, and erosion by water or ice. Other important processes may include redeposition by gravity flow or contour currents. Regional variations in the dominance of the main agents can explain major differences that have been given to the importance of wind and river transport in the past.

Multiple box models can be used to construct deterministic process-response models that allow first-order evaluation of the main pollen-transport pathways for a given region. We show here that assumed rapid sinking of pollen in faecal pellets is not clearly justified, but flocculation and clumping by growth of marine microorganisms will deposit bisaccate grains within 12 hours in the absence of strong bottom currents.

Potential for successful reconstruction of past vegetation and climate using marine palynology depends on careful selection of sites in locations away from gravity flow deposits and on the western ocean margins in the Northern Hemisphere. Laboratory processing without acetolysis is a prerequisite for full recovery of marine pollen from sediment samples.

At suitable relatively nearshore marine locations, pollen assemblages can be successfully used for backtracking of wind circulation and/or sources of major organic carbon inputs. Further offshore, however, and in the polar regions of weak easterly winds, the potential for palaeometeorological and dust flux studies is complicated by excessively long wind transport pathways, and/or by resuspension deposition from exposed shelves and by ice transport.

ACKNOWLEDGEMENT

We are most grateful to cartographer Mike Lozon, Brock University, for his skillful drafting and great patience.

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