The importance of plant macrofossils in the reconstruction of Lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA

I have great pleasure in dedicating this paper to Herbert E. Wright Jr. It originated as a lecture given during a symposium held to celebrate his 80th birthday at Wengen, Switzerland on September 9th, 1997. Thirty-five years ago he initiated the use of plant macrofossils for the study of vegetation history in Minnesota, and he has been encouraging and stimulating their use and interpretation ever since.

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Abstract

Lateglacial and early Holocene (ca 14–9000 ^{14}C yr BP; 15–10,000 cal yr BP) pollen records are used to make vegetation and climate reconstructions that are the basis for inferring mechanisms of past climate change and for validating palaeoclimate model simulations. Therefore, it is important that reconstructions from pollen data are realistic and reliable. Two examples of the need for independent validation of pollen interpretations are considered here. First, Lateglacial-interstadial *Betula* pollen records in northern Scotland and western Norway have been interpreted frequently as reflecting the presence of tree-birch that has strongly influenced the resulting climate reconstructions. However, no associated tree-birch macrofossils have been found so far, and the local dwarf-shrub or open vegetation reconstructed from macrofossil evidence indicates climates too cold for tree-birch establishment. The low local pollen production resulted in the misleadingly high percentage representation of long-distance tree-birch pollen. Second, in the Minnesotan Lateglacial *Picea* zone, low pollen percentages from thermophilous deciduous trees could derive either from local occurrences of the tree taxa in the *Picea/Larix* forest or from long-distance dispersal from areas further south. The regionally consistent occurrence of low pollen percentages, even in sites with local tundra vegetation, and the lack of any corresponding macrofossil records support the hypothesis that the trees were not locally present. Macrofossils in the *Picea* zone represent tundra vegetation or *Picea/Larix* forest associated with typically boreal taxa, suggesting it was too cold for most thermophilous deciduous trees to grow. Any long-distance tree pollen is not masked by the low pollen production of tundra and *Picea* and *Larix* and therefore it is registered relatively strongly in the percentage pollen spectra.

Many Lateglacial pollen assemblages have no recognisable modern analogues and contain high representations of well-dispersed 'indicator' taxa such as *Betula* or *Artemisia*. The spectra could have been derived from vegetation types that do not occur today, perhaps responding to the different climate that resulted from the different balance of climate forcing functions then. However, the available contemporaneous plant-macrofossil assemblages can be readily interpreted in terms of modern vegetation communities, suggesting that the pollen assemblages could have been influenced by mixing of locally produced pollen with long-distance pollen from remote vegetation types that are then over-represented in situations with low local pollen production. In such situations, it is important to validate the climate reconstructions made from the pollen data with a macrofossil record.

1. Introduction

The rapid increase in computer capacity over recent decades has stimulated the collation of large data bases relating to past climatic changes, such as the World Data Center for Paleoclimatology, Boulder, Colorado. For example, pollen analytical data in the Northern Hemisphere have been compiled in the North American Pollen Data Base and in the European Pollen Data Base (Grimm, 1991; Jacobson, 1996). Pollen-data compilations can be synthesised geographically over selected time periods and have been used for the production of "isopollen maps" and migration maps (e.g. Davis, 1976; Huntley and Birks, 1983; Shuman et al., 2002), of climate/pollen response surfaces (e.g. Bartlein et al., 1986; Huntley, 1993), for making climate reconstructions (e.g. Huntley, 1994; Peyron et al., 1998), and for the reconstruction of vegetation biomes (e.g. Guiot et al., 1996; Prentice et al., 1996).

Vegetation provides important feedbacks to the climate system, particularly in terms of albedo (e.g. Foley et al., 1994; Kutzbach et al., 1996; Webb and Kutzbach, 1998). The scale at which past vegetation is reconstructed depends on the questions being asked and the use to which the reconstructions will be put. For example, the BIOME 6000 project aims to produce global biome vegetation maps for 6000 yr BP (Mid-Holocene) and 18,000 yr BP (Last Glacial Maximum, LGM) (Prentice and Webb, 1998), two maximally contrasting times when vegetation is thought to have been in equilibrium with climate, and which are favoured by palaeoclimate modellers for testing extremes of palaeoclimate on present-day models. Recently the results of biome reconstructions have been published (e.g. Williams et al. (2000) for Eastern North America; Tarasov et al. (2000) for northern Eurasia). Although vegetation types and their distribution that were different from today may have given rise to combinations of pollen types that do not have present-day analogues, biome reconstructions are unaffected (Prentice et al., 1996) as each taxon is assigned individually to a plant functional type that then contributes to the selection of the most likely biome (biomization) (Prentice et al., 1996). 'No-analogue' vegetation probably existed in the past because each species reacts to its environment individualistically (see Davis, 1989; Huntley, 1996) and 'no-analogue' biomes have been created to cope with this problem (Williams et al., 2001). Changes in environment may result in rapid increases or decreases of taxa that are already present and presumably in equilibrium with the previous climate, and a change in vegetation type may result (Tinner and Lotter, 2001; Shuman et al., 2002). However, vegetation may not be in equilibrium with climate as a result of migratory lags, particularly, at times of rapid climate change such as during the Lateglacial and early Holocene (Huntley (1996) and Huntley (2001)). The detection of disequilibrium depends on the geographical and temporal scales applied (see Davis, 1986; Williams et al., 2001 for a discussion). Tree birch (*Betula pubescens*) took about 600 years after the end of the Younger Dryas to reach Kråkenes at 62°N on the west coast of Norway (Birks and Ammann, 2000), and shorter lags of birch-tree response have been demonstrated during the Lateglacial in NW England (Marshall et al., 2002), but these lags would not be apparent if 1000 year time intervals are used for detecting vegetation and climate change as, for example, by Williams et al. (2001). Biomes are coarse–grained vegetation types and at the continental scale the past pollen records are seldom dense enough to produce other than broad-scale reconstructions through data interpolations. The global biome approach is not designed to reconstruct vegetation at the community scale (Prentice et al., 1992) or to track fine-scale spatial vegetation differentiation during times of climate change (Birks, 1994).

The Lateglacial and early Holocene period (broadly 15,000–10,000 cal yr BP) is a period of large and rapid climatic changes covering the transition from glacial to interglacial conditions. These changes need to be quantified in order to produce synoptic climate reconstructions which will allow the testing of hypotheses and models about the causes and processes of the Lateglacial climatic changes, the forcing factors and feedbacks. Fine-scale palaeoclimate simulations made by regional climate models nested within global climate models (e.g. Renssen et al., 2001) are relevant in regions where climate gradients are strong, such as in the Norwegian Sea and Scandinavian area (Renssen and Isarin, 2001). If these simulations are to be validated, fine-scale climate reconstructions are needed, both spatially and temporally, from palaeoclimatic archives. It is thus important that climate reconstructions made from biological data should be accurate and precise, and they should preferably be validated by independent

climate reconstructions from other proxies (see Birks and Birks, 2003).

An important basic tool for climate reconstructions on land is pollen analysis (Birks, 1981). It was through pollen analysis that the Lateglacial of northwest Europe was characterised (e.g. Iversen, 1954), and it was against this background that studies of the Lateglacial in the marine and ice-core realms developed, and that Lateglacial correlates were searched for over the rest of the globe.

Lateglacial palaeoclimatic reconstructions from pollen data should critically consider the question—How should percentages (and influx) of tree pollen be interpreted in terms of local growth of the trees? Upon the answer hang vegetational and climate reconstructions that may be used subsequently as boundary conditions for or for testing simulations in GCMs. It is not an easy question to answer. Faced with uninterpretable Lateglacial pollen assemblages, pollen analysts have often resorted to the term 'no-analogue pollen assemblage', meaning that the assemblage cannot be matched with modern assemblages produced by known vegetation. In Eastern North America, 'no-analogue' pollen spectra are frequent 17–12,000 ^{14}C yr BP, being most abundant around 14,000 ^{14}C yr BP (Williams et al., 2001). Anderson et al. (1989) showed that the most 'no-analogue' assemblages were deposited during 14,000–9000 ^{14}C yr BP, the time of greatest climatic change, in Alaska and northwest Canada. This time period also coincides with the greatest occurrence of simulated unique or unusual climates in Alaska and in central North America (Bartlein, 1997) in accordance with the greatest deviation of climate boundary conditions (especially ice volume, atmospheric composition, and insolation) from present levels throughout the past 20,000 years (COHMAP members, 1988).

The occurrence of 'no-analogue' climates during this time has been used to explain the occurrence of 'no analogue' pollen assemblages, which have been interpreted in terms of vegetation types not found today. An example is the proposed 'mammoth steppe' biome reconstructed from i.a. high Gramineae and *Artemisia* pollen percentages in sites from Beringia, where quantities of bones from large grazing mammals have been recorded (Guthrie, 1990). Similarly, arid steppe has been proposed to have covered large parts of N. Europe during glacial and Lateglacial time, based also on high percentages of Gramineae and *Artemisia* pollen and the occurrence of pollen of some indicator 'steppe' taxa (Iversen, 1954 and many subsequent authors). Vegetational inferences made from both 'analogue' and 'no-analogue' pollen data and the palaeoclimate reconstructions made from them ought to be validated from independent evidence (e.g. Birks, 1993; Elias et al., 1997; Goetcheus and Birks, 2001; Birks and Birks, 2003). The reconstruction of past climate from pollen assemblages depends on their correct interpretation in terms of vegetation (i.e. local occurrence) and the interpretation of 'no analogue' assemblages in terms of climate is a critical consideration (Birks, 1981). Climate reconstructions made from pollen data can be so far-reaching that they ought to be tested by evidence independent of pollen analysis.

Caution should also be exercised when numerical comparisons of modern pollen assemblages with climate are used to make transfer functions (e.g. Birks and Birks, 2003), or response surfaces (Bartlein et al., 1986; see Huntley, 1996), or when mapped modern pollen percentages are correlated with climatic parameters on a broad geographical scale (e.g. Guiot, 1987). Such comparisons may then be used, for example, to estimate past or future pollen abundances from climate model output (Webb et al., 1987; Overpeck et al., 1991), to infer past climates from fossil pollen data (Huntley (1993) and Huntley (1994); Peyron et al., 1998), and to make comparisons between GCM simulations and pollen-inferred climates (e.g. Webb and Bartlein, 1988; Bartlein et al., 1998; Prentice et al., 1998; Webb et al., 1998). Such activities have generally considered pollen assemblages on a broad scale using only the predominant taxa. The straightforward representation of the local and regional vegetation by the pollen assemblages and thus their climatic signal are assumed (e.g. Huntley, 1996; Williams et al., 2001; Shuman et al., 2002). As well as the composition and distribution of vegetation, climate boundary conditions have varied independently in the past, controlled by changes in orbital parameters amplified or damped by feedbacks within the atmosphere–terrestrial–marine system

(Kutzbach and Guetter, 1986; COHMAP members, 1988; Kutzbach and Webb, 1991). For profitable use in modelling activities, palaeoclimate reconstructions from biological proxy data should be based on all available information to be as precise and accurate as possible.

An important aspect of the Lateglacial vegetational changes in northwest Europe is the spatial development of birch forest during the Lateglacial interstadial (Bølling/Allerød, Greenland Interstadial GI-1, Björck et al., 1998), and the extent of its destruction during the subsequent Younger Dryas stadial (Greenland Stadial GS-1) (Lowe et al., 1994). As tree birch has climatic restrictions on its growth, its presence or absence is important when making palaeoclimate reconstructions. In the North American Mid-West, the presence of pollen of thermophilous deciduous trees during the Lateglacial *Picea* pollen zone has been interpreted as reflecting the presence of small quantities of these taxa growing in spruce-dominated forest in a way unknown today (no analogue) in the modern boreal forest. As these trees require certain minimum temperatures and moisture for their growth (Thompson et al., 1999), their local presence would imply that these conditions occurred during the time of the *Picea* zone, which would then have important implications for refining attempts to model the melting of the Laurentide ice sheet (Marshall and Clarke, 1999). Simulated climate changes and gradients from pollen data are greatest along the southern margin of this ice sheet, but the simulation has not been adequately tested so far from palaeoclimatic data (Williams et al., 2001). However, a strong Lateglacial climatic gradient was reconstructed from fossil chironomid evidence at its southeastern margin in maritime Canada by Levesque et al. (1997).

One means of testing pollen analytical reconstructions is to use plant macrofossils from the same sites or areas. Being relatively large and heavy, macrofossils are usually not transported far from their sources (Birks (1973) and Birks (2001)) compared with many wind-dispersed pollen types. Therefore, if they are found in sediments, it is probable that the parent plants were growing locally at the site or at least not far away within the region. There are several situations in which pollen assemblages can give a false impression of local vegetation and vegetational change (Birks and Birks, 2000; Birks, 2001). Here I will discuss how plant macrofossils can be used to evaluate the local vegetation reconstructions from pollen data and hence climate inferences in the two Lateglacial situations mentioned above; the interstadial occurrence of birch trees in northern Scotland and western Norway, and the occurrence of thermophilous deciduous trees in the Lateglacial spruce forests of the American Mid-West, mainly in Minnesota.

2. The interpretation of interstadial birch pollen in northern Scotland and western Norway

The sites discussed are shown in Fig. 1. Pollen and plant macrofossil analyses from Abernethy Forest in Scotland (Fig. 2) (Birks and Mathewes, 1978) showed that virtually all of the low percentages and influx of *Betula* pollen in the interstadial sediments originated from *Betula nana*. One tree-type fruit could indicate a very sparse local occurrence of birch trees. If tree birch is present, macrofossils are usually plentiful, and this is the case in the early Holocene at Abernethy Forest. *Betula* pollen influx rapidly rose to higher values than in the interstadial. At first, macrofossils show that *B. nana* contributed to the *Betula* pollen, but it died out after ca 600 years, and all the *Betula* pollen was produced by tree birch. Interestingly, upon the arrival of *Pinus*, a high pollen producer, the percentages of *Betula* decreased (Birks and Mathewes, 1978), but it was still an important component of the local forest, as shown by the continued high influx and the occurrence of its macrofossils. *Pinus* pollen is well known for its long-distance dispersal, and the first rise of its curve reflects its immigration to the area at ca 7300 ^{14}C BP. The macrofossils show its local arrival some 150 years later when its pollen percentages were ca 50% (Birks and Mathewes, 1978) and its pollen influx was ca 2500 grains cm^{-2} yr^{-1}.
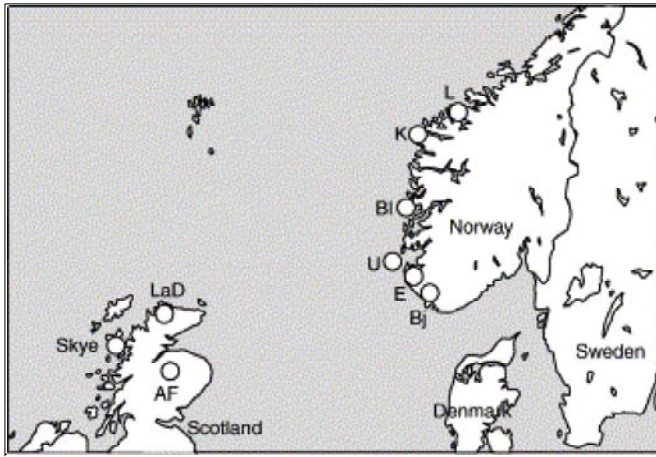
Fig. 1. Map of northern Scotland and western Norway showing Lateglacial sites discussed in the text. LaD=Lochan An Druim (Birks, 1984), AF=Abernethy Forest (Birks and Mathewes, 1978), Bj=Bjerkreim (Birks, unpublished), E=Eigebakken (van Dinter and Birks, unpublished), U=Utsira (Birks, 1993), Bl=Blomøy (Birks, 1993), K=Kråkenes (van Dinter and Birks, 1996), L=Lerstadvatn (Birks, unpublished).
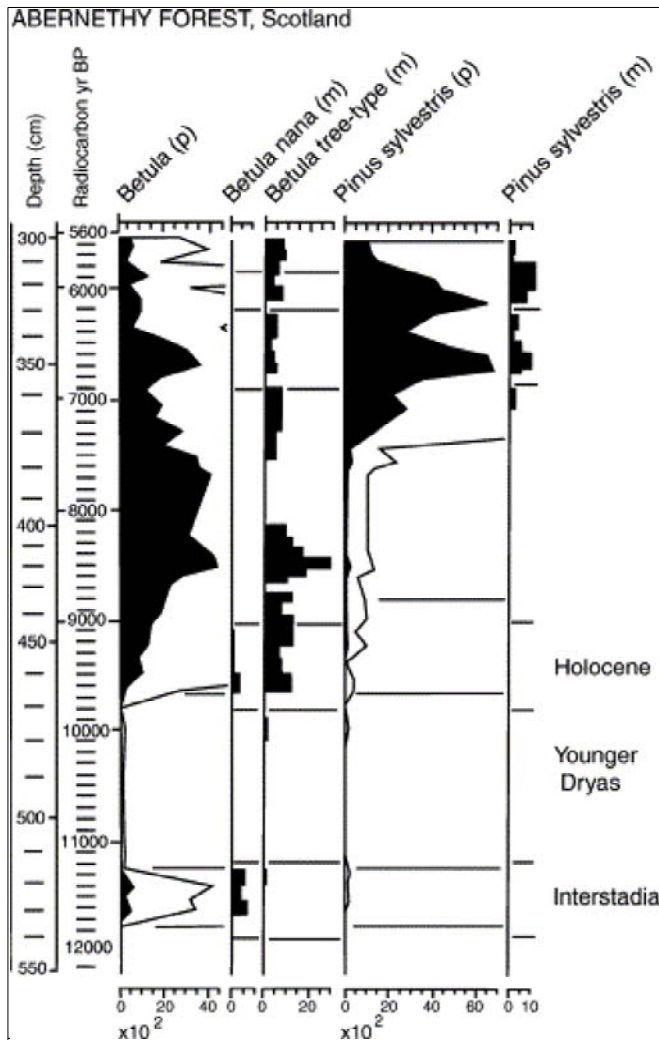

Fig. 2. Comparison of pollen (p) and macrofossil (m) influx of *Betula* and *Pinus* at Abernethy Forest, Scotland. Pollen influx is grains cm^{-2} y^{-1}; macrofossil influx is number 10^3 cm^{-2} y^{-1}. Redrawn from Birks and Mathewes (1978).

At the site of An Druim, near Eriboll in northwest Scotland (LaD in Fig. 1), a Lateglacial pollen percentage diagram shows about 5% *Betula* pollen in the interstadial (Fig. 3, zone AD-2, Allerød; Birks, 1984). However, influx estimates were very low, suggesting that birch was not locally present. Macrofossil analyses from the same core failed to record any birch

macrofossils in the interstadial, and in addition, the macrofossil assemblage could be interpreted as a local vegetation dominated by *Empetrum* and *Dryas* dwarf-shrub heath and snow-beds with *Salix herbacea* and *Polytrichum sexangulare*. Such an environment would not sustain tree-birch growth which requires a mean July temperature above 10°C. Following the relatively cool interstadial, the Younger Dryas (zone AD-3) was colder, causing the elimination of the dwarf-shrub heaths. In contrast, the early Holocene sediments at An Druim contained tree-birch fossils that were associated with high *Betula* pollen percentages and influx, and no fossils of the snow-bed species occurred. Temperatures rose rapidly at the start of the Holocene, quickly exceeding the tree-birch temperature limit and birch trees colonised the landscape as soon as they could migrate from their Younger Dryas refugia. A similar situation was reported by Huntley (1994) in the central Scottish mountains. Low percentages (5–10%) of *Betula* pollen in Lateglacial sediments at Morrone originated from distant sources. The rich plant macrofossil assemblage (including many bryophytes) represented a local vegetation mosaic of open treeless dwarf-shrub and moss heath, snowbed and mire communities around the site. Large amounts of hydroseral Cyperaceae pollen (and macrofossils) in the early Holocene masked the expected increase in percentages of *Betula* pollen, although the local presence of tree birch was attested by its macrofossils. Because it was so small, the site received a preponderance of local pollen, dominated by Cyperaceae and Gramineae. The range of modern pollen analogues for the Lateglacial pollen assemblages was so wide, covering steppe to arctic and alpine tundra, that the locally produced macrofossils were used to constrain the analogue matching. At this site, the pollen record was most unsatisfactory for reconstructing past vegetation and climate. However, the macrofossil record alone gave a very detailed picture of the local vegetation changes (Huntley, 1994).
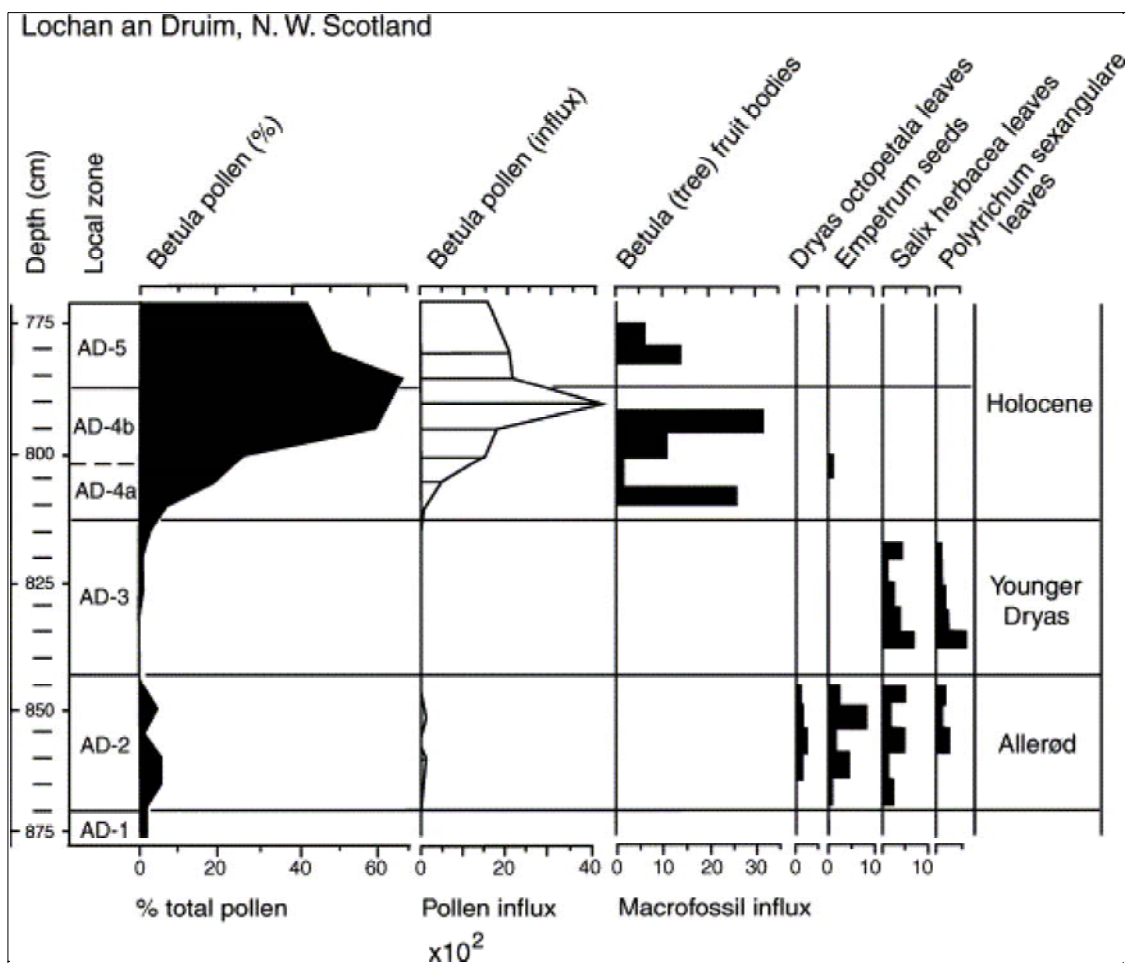

Fig. 3. Comparison of *Betula* pollen percentage and influx and macrofossil influx at Lochan An Druim, northwest Scotland, together with some prominent Lateglacial macrofossil taxa. Pollen influx is grains cm^{-2} y^{-1}; macrofossil influx is number 10^3 cm^{-2} y^{-1}. Redrawn from Birks (1984)

These Scottish results were somewhat surprising, as it had been assumed that the whole of the British Isles supported birch woodland during the interstadial, following the pattern described from Denmark, although there had been some indications of local and regional differentiation in the density of the interstadial woodland, e.g. from pollen studies on the Isle of Skye, western Scotland (H.J.B. Birks, 1973). The interstadial tree-*Betula* pollen at these northern sites was largely derived from its long-distance transport from further south. The fact that relatively high percentages are recorded is a result of the low pollen production by the local vegetation. A similar pattern of high modern pine pollen representation in tree-less vegetation was demonstrated as long ago as 1940 by Aario (1940) in Finland. Pollen diagrams and surface samples from Svalbard typically contain 20–50% tree pollen (e.g. Hyvärinen, 1970; van der Knaap (1987) and van der Knaap (1988)), and here it is obvious that this must be long-distance transported. A macrofossil study of a Holocene sequence on Svalbard (Birks, 1991) demonstrated the value of macrofossils for the reconstruction of the local vegetation whose pollen production was extremely low, both by the local representation of the plant remains, and the ability to identify them to species level. This study forms a model for Lateglacial studies where local tree presence inferred from pollen data is in question.

Macrofossil studies in the Lateglacial of western Norway have been reported by Birks (1993). At a site on the island of Utsira, near Stavanger (U in Fig. 1), the situation was similar to that at An Druim in north-west Scotland. In the interstadial (Bølling/Allerød; GI-1), macrofossil analyses showed that the low percentages and influx of *Betula* pollen (Paus, 1990) were long-distance transported and the local vegetation consisted of dwarf-shrub heath dominated by *Empetrum* and snow-beds and wet flushes with *Salix herbacea*. At Blomøy west of Bergen (Bl in Fig. 8), Mangerud (1970) recorded up to 30% *Betula* pollen in the interstadial, but macrofossil analyses revealed a Mid-alpine type of vegetation dominated by *S. herbacea* snow-beds and wet flushes around the site which had a very low local pollen production (Birks, 1993). The pollen records of *Betula* and *Salix* and the identification of several thermophilous herb-pollen types were taken to imply mean July temperatures of at least 10°C and up to 14°C at Utsira (Paus, 1990). The absence of macrofossils of tree birch and of any thermophilous herbs, combined with the vegetation analogue (based on macrofossils) of dwarf-shrub heaths and snowbeds equivalent to vegetation above the treeline in the west Norwegian mountains today implied that the birch and thermophilous herb pollen was derived by long-distance transport and that the original pollen estimates of mean July temperatures should be reduced by at least 2 and up to 6°C (Birks, 1993). The evidence of local vegetation provided by macrofossils in these Lateglacial situations emphasises strongly that climatic inferences should be drawn only from those species that can be proved to be growing near the site.

Subsequent macrofossil analyses at sites further north in Norway have extended the pattern shown by Birks (1993), for example, at Kråkenes, near Ålesund (K in Fig. 1) (H.H. Birks, unpublished). Here ca 10–15% *Betula* pollen in the interstadial was recorded (Larsen et al., 1984; Birks et al., 2000) whereas macrofossils showed that the local vegetation was closely analogous to Mid-alpine vegetation in western Norway today, with a mosaic of snow-beds and associated flushes, wind-exposed fell-fields, and some dwarf-shrub heath. A multidisciplinary study at this site (Birks et al., 1996; Birks and Wright, 2000), using evidence from pollen, plant macrofossils, chironomids, Coleoptera, and Cladocera, has confirmed the interstadial mean July temperature reconstruction at below 10°C, and closer to 6–7°C (Birks et al., 2000; Birks and Ammann, 2000; Brooks and Birks, 2001).

All these sites are at the Norwegian coast (Fig. 1). Macrofossil investigations further inland showed that *Betula nana* was prominent in the lowlands, and a dwarf-shrub interstadial vegetation replaced snow-beds in the Nordfjord area east of Kråkenes (Birks and van Dinter, 1997) and near Ålesund at Lerstadvatn (L in Fig. 1) (H.H. Birks, unpublished; see Kristiansen et al., 1988). It would appear that the strong oceanic-continental climate gradient eastwards along the Norwegian fjords today probably also operated in the Lateglacial interstadial. A mapped summary of all the Lateglacial pollen diagrams supported this view, with higher percentages of *Betula* pollen inland compared with the coast through the whole of southern

Norway (Birks, 1994). Regions with different percentages of *Betula* pollen were delimited, and the ecotones between them could be positioned, indicating the climatic gradients in the interstadial and the Younger Dryas. The high interstadial percentages of *Betula* pollen recorded in the south of Norway were interpreted as the presence of birch woodland.

A test of this reconstruction was made by macrofossil analysis of the Lateglacial site at Eigebakken, in south-western Norway (E in Fig. 1) (M. van Dinter and H.H. Birks, unpublished). Pollen had previously been analysed and interpreted by Paus (1989). He recorded up to 50% *Betula* pollen, and size measurements suggested that much of this may have originated from tree birch. Therefore, he reasonably concluded that a fairly closed birch woodland had developed during the interstadial. The macrofossil analyses produced many wingless birch fruits throughout the sequence. Numerical analyses of the shape of the fruit bodies (van Dinter and Birks, 1996) indicated that all the interstadial fruits originated from *B. nana*, and that tree birch was absent (Fig. 4). This conclusion was supported by finds of female catkin scales of *B. nana*, but none of *B. pubescens*. There was no record of *B. pubescens* at Eigebakken until the early Holocene (van Dinter and Birks, 1996). Therefore all the *B. pubescens* pollen recorded by Paus must have originated from further south. Tree birch has been proved to be present in the interstadial by macrofossil records in Denmark (e.g. Jensen, 1985; Bennike and Jensen, 1995), south Sweden (e.g. Liedberg Jönsson, 1988; Björck et al., 1996), and Britain (e.g. Godwin, 1975). However, the Eigebakken interstadial vegetation and also that at Bjerkreim further south still (Fig. 1) (Birks, unpublished) was dominated by *B. nana*. This has a relatively low pollen production (Andersen, 1980) and thus the long-distance transported tree-birch pollen obtained a substantial percentage representation. Similarly, the high summer temperatures reconstructed by Paus (1989) from records of thermophilous herb-pollen types at Eigebakken and elsewhere should also be regarded as unlikely, as these taxa could not have grown locally (Birks, 1993); the local mean July temperature was below the thermal requirement for tree-birch growth (i.e. less than 10°C). It is unlikely to have been above this limit, because tree-birch was present within 300–400 km. Its pioneer nature and the minimal competition from treeless vegetation should have allowed it to migrate to southern Norway within the ca 2000 years of the interstadial if the temperatures were high enough for it, as it did within a few centuries in the early Holocene. Independent confirmation of this temperature inference is provided by Coope et al. (1998). They mapped Lateglacial mean temperatures of the warmest month inferred from Coleoptera data from 14,500–9000 ^{14}C yr BP and showed that they were warmest at the west coast of southern Norway between 14,500 and 13,000 ^{14}C yr BP, at 9–11°C. This is too cool or at the limit for widespread tree-birch growth in an oceanic climate (Odland, 1996), although there could have been scattered colonies in sheltered habitats with stable microclimates (Stewart and Lister, 2001). Temperatures only exceeded the birch thermal limit at the start of the Holocene and it then spread rapidly. All the available evidence contradicts the assumption made by Kullman (2002) of temperatures high enough for the full- and Lateglacial survival of tree-*Betula, Pinus*, and *Picea* along or near the Norwegian west coast as there is a total lack of direct macrofossil evidence for such tree growth and local vegetation (and climate) reconstructions from macrofossils are analogous to those above or beyond treeline today.
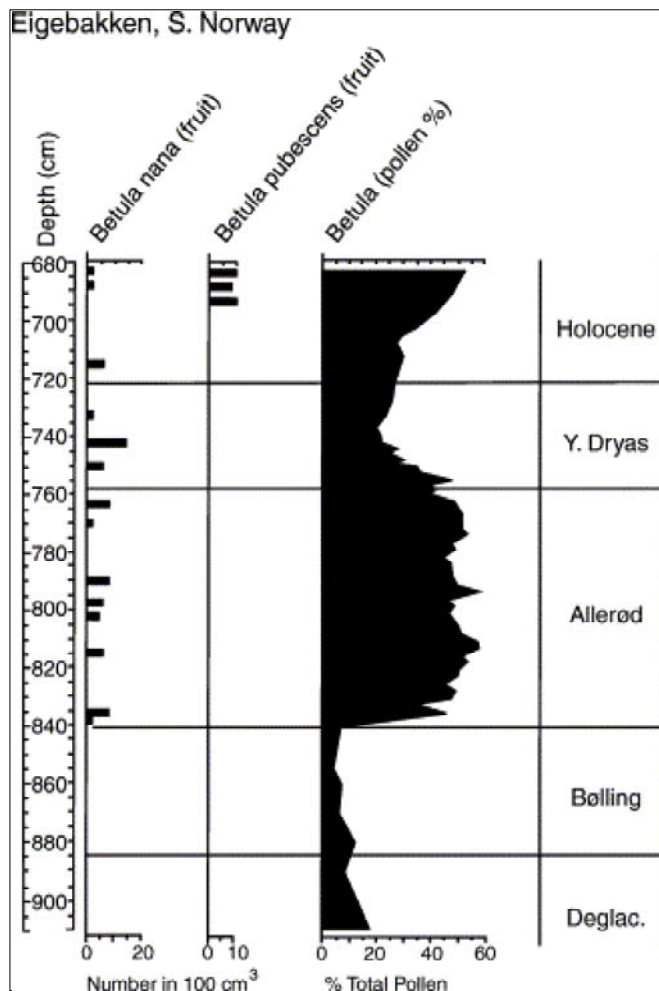
Fig. 4. Comparison of *Betula* pollen percentages and concentrations of *B. nana* and *B. pubescens* fruits (number in 100 cm³) in the Lateglacial sediments at Eigebakken, western Norway. Redrawn from van Dinter and Birks (1996).

These conclusions show that the pollen-based vegetation maps and ecotones of Birks (1994) and Paus (1995) are incorrect, and that the palaeoclimate estimates made from pollen results alone need to be revised. Further work is now needed in southern Norway to clarify the situation. However, the macrofossil results so far indicate that, where the local vegetation has a low pollen productivity, the influence of long-distance transported pollen, particularly in percentage terms, can be considerable and misleading. Thus the crucial importance of plant macrofossils in such situations is emphasised for the reconstruction of the local vegetation and subsequently its realistic interpretation in terms of past climate.

3. The interpretation of thermophilous-tree pollen in the Lateglacial *Picea* pollen zone of Minnesota, USA

The occurrence of small amounts of thermophilous-tree pollen in the Lateglacial pollen diagrams of the Mid-West USA (Fig. 5) is a long-standing problem of interpretation. The temporal occurrence of these taxa is illustrated along a north–south transect (see Fig. 5) in Fig. 6, and discussed by Wright (1971). Thermophilous-tree pollen is often accompanied by that of thermophilous herbs such as *Ambrosia* type, *Humulus lupulus*, and *Typha latifolia*. *Picea* pollen is dominant for varying periods before ca 10,000 ^{14}C yr BP (Fig. 6) depending on latitude (Fig. 5; see Cushing, 1967), and consistent percentages of *Larix* (that has a very low pollen representation; Davis and Goodlett, 1960; Davis, 1963) indicate that *Picea* and *Larix* were predominant in the Lateglacial forest south of the Laurentide ice sheet. In northern Minnesota the treeless tundra vegetation adjacent to the ice sheet was extensive, and the development of *Picea*-dominated forest was delayed by about 3000 years from the south to the

north of the state (Watts, 1967). The pollen diagrams contain pollen from two types of deciduous tree in the *Picea* zone. The first type includes boreal taxa that can co-exist with *Picea* spp. today, such as *Betula, Salix, Populus, Fraxinus nigra* type, and *Alnus*. The second group is generally more thermophilous and would only be expected at the southern margin of the boreal forest today, at the transition to temperate forest. It includes *Ulmus, Quercus, Ostrya–Carpinus, Tilia, Corylus, Fraxinus pennsylvanica* type, *Juglans* spp., *Celtis, Carya, Acer negundo*, and *A. saccharum*. The local occurrence of these taxa would imply relatively high summer temperatures and precipitation (Thompson et al., 1999).
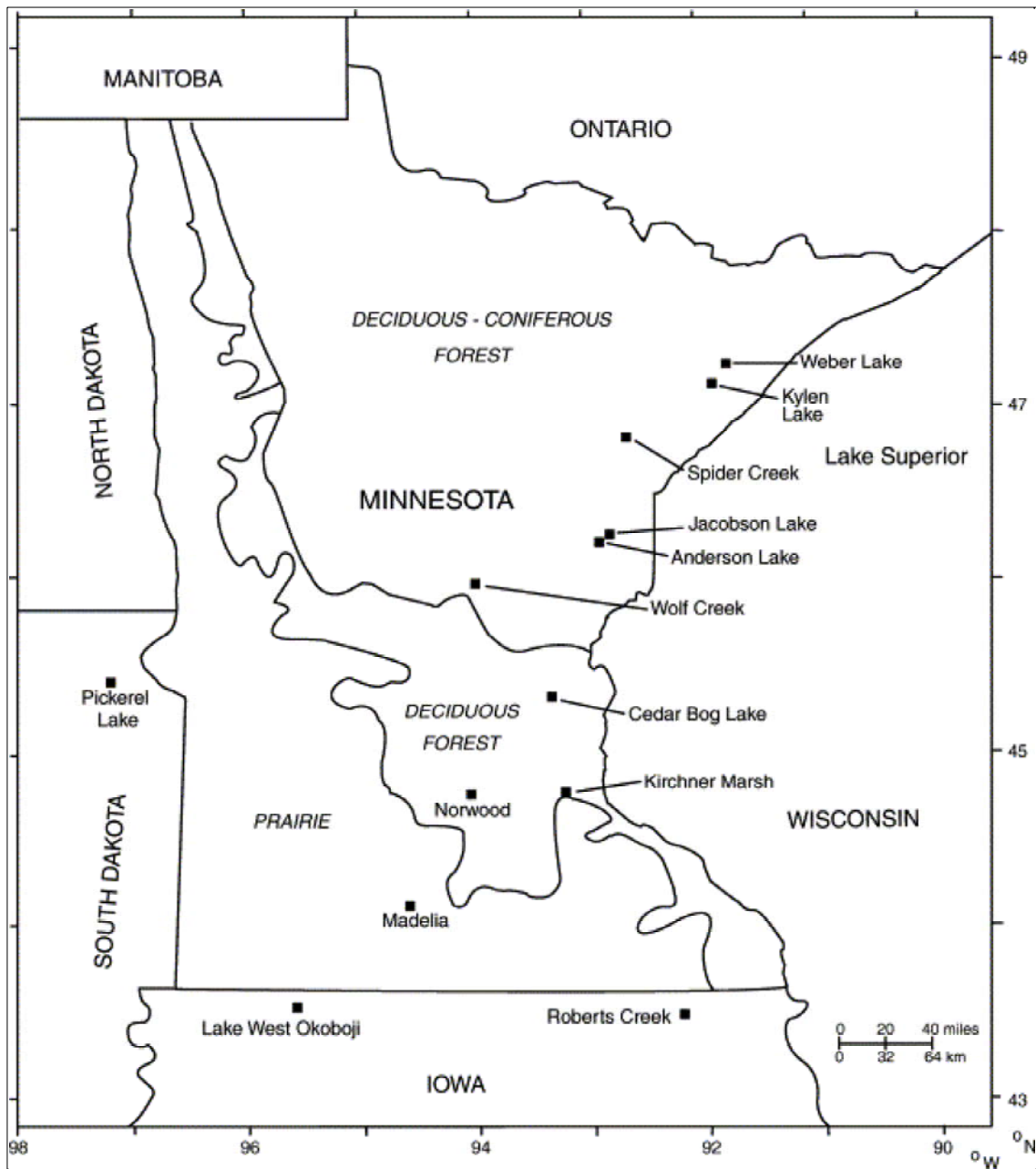

Fig. 5. Map of the Minnesota area, USA, showing the present vegetation and sites where macrofossil and pollen sequences are available and other sites in Fig. 6.
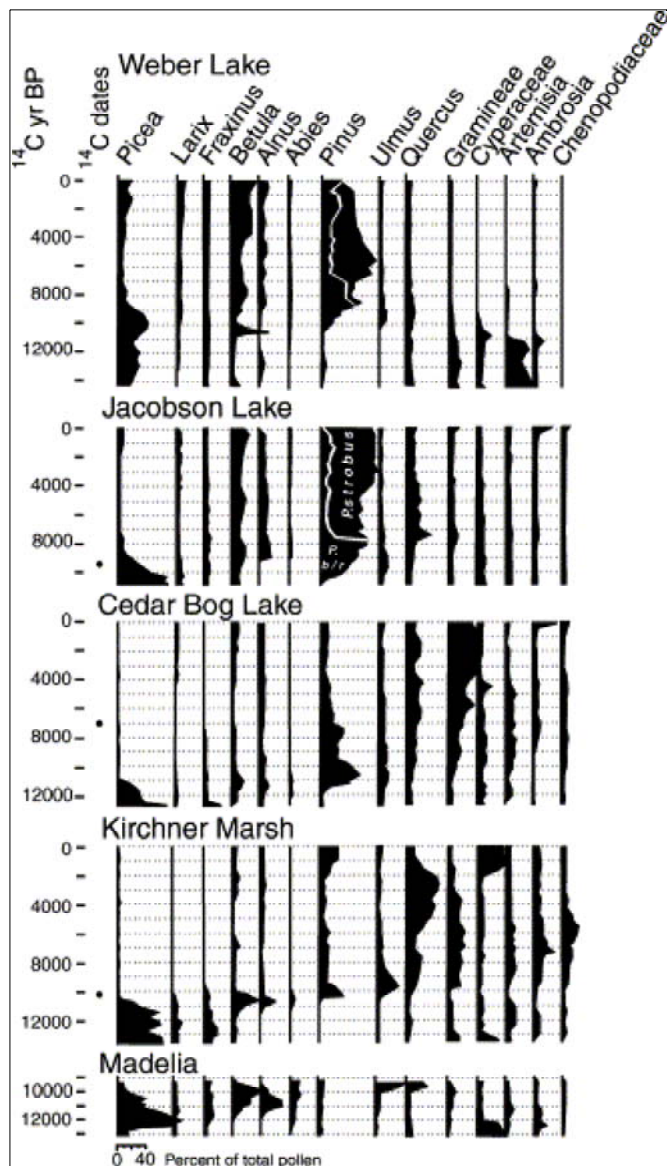
Fig. 6. Comparison of Lateglacial and Holocene pollen sequences along a north-south transect through Minnesota (sites in Fig. 5). Curves of *Ulmus* and *Quercus* represent the thermophilous deciduous tree taxa; curves of *Fraxinus, Betula,* and *Alnus* represent the deciduous boreal-forest taxa. Radiocarbon age scales and dates are shown; the Holocene starts at about 10,000 ^{14}C yr BP. Redrawn from Wright (1971).

Three explanatory hypotheses have been proposed (Wright, 1971). (1) The pollen is redeposited from interglacial sediments mixed into the till. This was effectively rejected by Cushing (1964). (2) The pollen was long-distance transported from the south. The pollen diagrams are dominated by *Picea* pollen, implying the dominance of *Picea* in the forest. *Picea* is relatively low pollen-producer, and *Pinus,* a high pollen-producer, was absent, so small quantities of thermophilous-tree pollen could show up as detectable percentages. (3) The thermophilous-trees were present in small scattered stands within the *Picea–Larix* forest.

One possible way to distinguish between hypotheses 2 and 3 is to determine the composition of the local and regional pollen rain using small lakes. According to recent models of pollen deposition and representation, if the thermophilous deciduous trees were growing locally in patches, their pollen percentages should vary in total and individually depending on their abundance and particularly on their closeness to the lake shores (see Davis, 2000). If the thermophilous deciduous tree pollen was regional, its proportion should not vary across the vegetational region. At present the sites available are unable to test these hypotheses, although, so far, no site has shown substantially higher percentages than the other sites that may reflect local presence. The thermophilous deciduous tree pollen assemblage occurs in low percentages

in all the Lateglacial *Picea* zones throughout Minnesota, with somewhat higher values in the south (Fig. 6), suggesting that the pollen is long-distance dispersed, probably from this direction.

Another possible way to distinguish between hypotheses 2 and 3 is through macrofossil analyses. The locations of macrofossil diagrams from the Minnesota region are shown in Fig. 5. In some of them, macrofossils of *Betula*, *Salix*, and *Populus* have been recorded from their *Picea* zones. The birch associated with the *Picea* zone is usually the shrub *B. glandulosa*, with tree birch only occurring after the transition to the *Pinus* zone (Holocene). In none of the Lateglacial sequences have macrofossils of thermophilous trees been recorded, except for a fossil of *Acer* in N.E. Iowa. Does this mean that the thermophilous-trees were absent? It is dangerous to argue from absence, especially from macrofossil evidence, as macrofossils, especially of tree taxa, may be produced in small numbers and have poor dispersal (e.g. Birks, 2001). Independent supporting evidence is necessary to propose absence with confidence.

Picea has a low pollen representation (although not as low as *Larix*) (Davis, 1963) which may not mask small amounts of long-distance pollen which is then represented by low but consistent percentages. This hypothesis is difficult to test with modern surface samples because modern boreal forest contains *Pinus* spp. whose high pollen representation tends to overwhelm taxa with small pollen quantities (Wright and Watts, 1969; Wright, 1971). However, the effect of the low representation of *Picea* pollen was dramatically shown at Longswamp, eastern USA, by Watts (1979). Here, the arrival of *Pinus* coincided with a substantial reduction in the percentages of *Picea* pollen, but the concentrations of *Picea* needles were unaffected, suggesting that its local abundance near the site was not actually modified by the arrival of *Pinus.* Therefore, it is quite probable that small quantities of pollen of anemophilous deciduous trees were transported and deposited beyond their area of growth, particularly in the turbulent atmospheric conditions associated with the proximity of the ice-sheet margin, and they were able to show up as detectable percentages in a *Picea*-dominated pollen assemblage. The extent of long-distance pollen transport has been demonstrated by McAndrews (1984) by pollen analyses from the ice core from Devon Island in the Canadian arctic. The pollen was derived from North America and the whole northern hemisphere.

Indirect evidence against the local occurrence of thermophilous trees is given by reconstructions of the local contemporary vegetation from macrofossil evidence. In the Lateglacial at Spider Creek (Baker, 1965), *Picea* pollen is dominant, and is associated with relatively high percentages of *Fraxinus* and *Quercus* pollen, and lesser values of *Betula, Alnus, Populus, Ulmus, Ostrya–Carpinus, Corylus, A. negundo, Tilia,* and *Carya* (Fig. 7). However, in the lower part of the sequence, the macrofossil analyses show no tree macrofossils at all, but large quantities of *Dryas integrifolia* and *Salix herbacea* plus other herbs of open tundra vegetation. Therefore, at this northern location close to the Laurentide ice sheet (Wright and Watts, 1969) (Fig. 5), the local vegetation was treeless tundra, and *all* the tree pollen was long-distance transported, thus showing that the thermophilous types are definitely capable of considerable long-distance transport. The Lateglacial/Holocene climatic warming is reflected by the expansion of aquatic plants and the local arrival of *Picea* and *Larix*, associated with a transitional peak of *Betula glandulosa* but no thermophilous-tree macrofossils. The *Picea* zone at Spider Creek thus consists of two parts. First there is a tundra phase following deglaciation where high percentages of *Picea* pollen result from long-distance transport into a tundra vegetation producing very low amounts of local pollen. Then, soon after the climatic amelioration indicated by the expansion of aquatic plants (Fig. 7), taken as the start of the Holocene, local *Picea* and *Larix* forest developed, attested by their macrofossils. The climate at Spider Creek was probably too cold for the growth of any trees during the Lateglacial. At the Holocene amelioration, *Picea* and *Larix* colonised. The tundra-forest ecotone was not far to the south; Jacobson Lake and Anderson Lake (Wright and Watts, 1969) (Fig. 5) contain abundant Lateglacial *Picea* and *Larix* macrofossils and these trees expanded as the ecotone crossed Spider Creek.
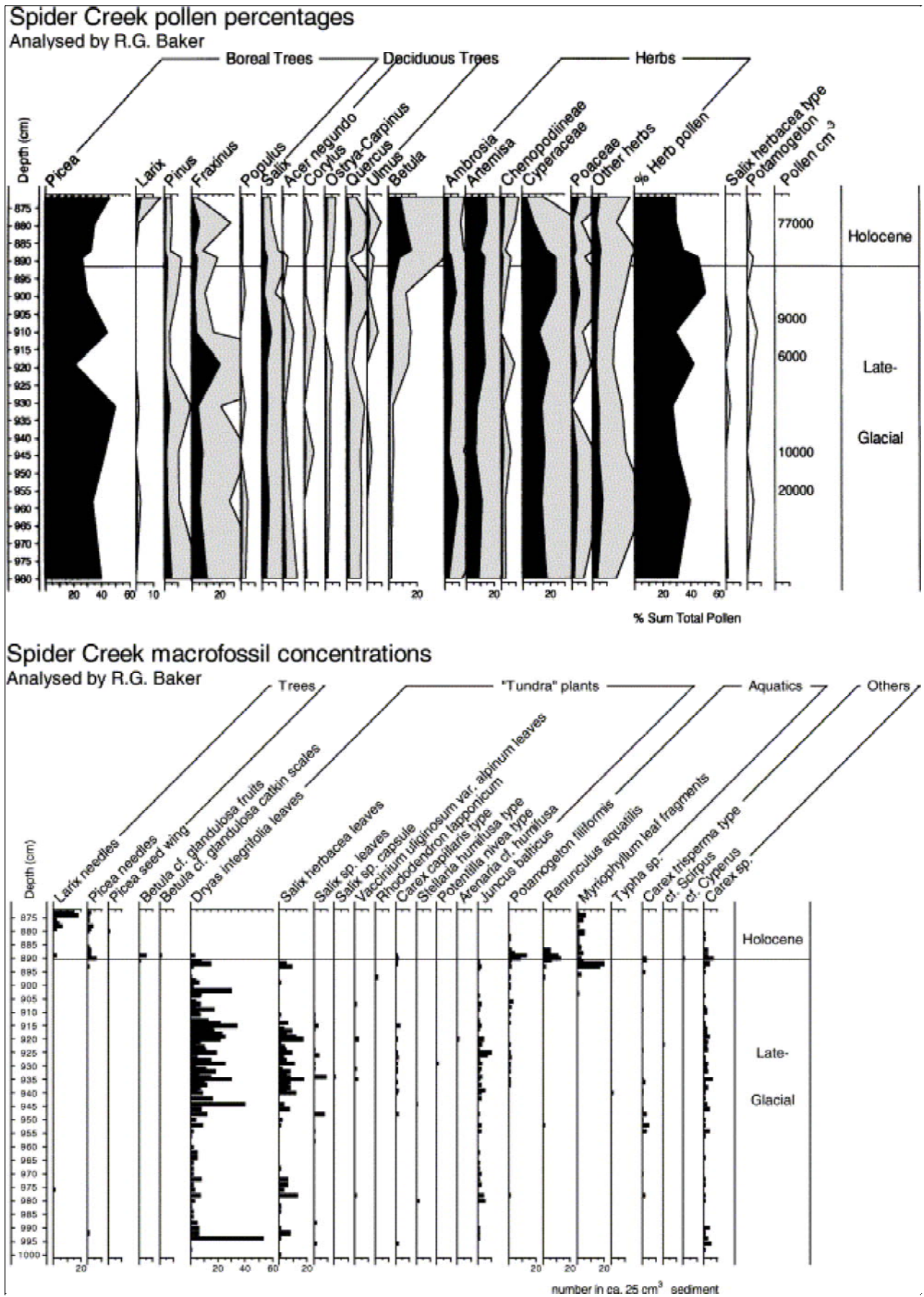
Fig. 7. Pollen percentages (sum of total pollen) and macrofossil concentrations in Lateglacial sediments at Spider Creek, Minnesota. Pollen curves are shown with a ×10 exaggeration. Redrawn from the data of Baker (1965) kindly provided by R.G. Baker.

The early Lateglacial and Holocene climate probably had greater seasonality (warmer summers; colder winters) and less precipitation than today's climate (Kutzbach and Webb,

1993; Shuman et al., 2002). This may help to explain the unexpected abundance of *Ambrosia*-type pollen in the Mid-West Lateglacial, as for growth and flowering *Ambrosia* requires days shorter than 14 h but warm temperatures (Grimm, 2001, and personal communication). The high Lateglacial *Artemisia* pollen values (Fig. 6) are likely to be derived from *A. frigida,* common in the northern Great Plains today. *Artemisia* species are seldom found as macrofossils, but those of *A. frigida* have been recorded in full-glacial sediments in N. Yukon (Zazula, 2002). It thrives in dry shallow soils and its and *Ambrosia*'s Lateglacial pollen abundances suggest that the *Picea* zone vegetation may have been open forest or a mosaic of forest and steppe related to soil moisture. The warm summers may have been suitable for the growth of several of the thermophilous deciduous trees, (e.g. *Quercus alba, Tilia americana, Ulmus americana*) which overlap marginal parts of the same climate space as *Picea mariana* and *P. glauca*, although their present geographical ranges scarcely overlap in the southern Great Lakes region (Thompson et al., 1999). However, most of them are moisture-demanding and will not tolerate the very cold Lateglacial winters predicted by climate models (Shuman et al., 2002). At Spider Creek, the concentrations of *Quercus* and other deciduous tree pollen increase along with that of all pollen taxa in the Holocene (Baker, 1965), possibly suggesting greater influx, and thus that deciduous trees were closer to the site than previously. However, chronology is inadequate for the calculation of pollen influx (grains cm^{-2} yr^{-1}) so, unfortunately, changes in sediment accumulation rate (a switch from silts to marl) cannot be excluded as a cause of the increased concentrations. In addition, one would expect *Pinus* pollen percentages to increase as *Pinus* expanded at the start of the Holocene in sites to the south before any expansion of the thermophilous deciduous trees, but *Pinus* percentages at Spider Creek are unchanged or lower in the early Holocene (Fig. 7).

A major problem in comparing vegetational changes from the Minnesota pollen diagrams is poor dating control. It is uncertain whether the rise of *Picea*, including its macrofossils, is of different age at Spider Creek and Jacobson Lake only some 50 km to the south. The date obtained from marl for the early Holocene *Betula* pollen peak at Spider Creek is anomalously old (Baker, 1965). At Jacobson Lake algal gyttja dated at the base and top of the *Picea* zone yielded the same dates of 10,400±300 ^{14}C yr BP. At neighbouring Anderson Lake, the end of the *Picea* zone was dated to 10,200 and 10,500±200 ^{14}C yr BP (Wright and Watts, 1969). Other dates for the *Picea/Pinus* transition, generally taken as the start of the Holocene in the Minnesota area, are all on whole sediment and cover a range 9700-ca 10,500 ^{14}C yr BP. (The dates on wood at Roberts Creek do not date the start of the Holocene (Baker et al., 1996)). The chronological problems are compounded by the existence of radiocarbon plateaux during this time period. However, relationships between the pollen curves over the region illustrate independent migration routes and fluid forest composition as taxa responded to climate changes at the start of the Holocene (Wright and Watts, 1969). Clearly, modern approaches to ^{14}C dating, preferably using AMS on terrestrial plant material, are needed to clarify the sequence of forest vegetation history in both time and space over this climatically and vegetationally sensitive area. A recent AMS date on terrestrial macrofossils from Devils Lake Wisconsin (Maher, 1982) indicates that the previous Lateglacial dates on bulk sediment are about 1000 years too old (E.C. Grimm, personal communication 2002). Such chronological inaccuracies have serious implications for syntheses of data and reconstructions of patterns of palaeoclimatic change (e.g. Shuman et al., 2002), and underline the critical importance of accurate chronology before sites can be meaningfully compared and patterns synthesised.

The vegetation sequence through the *Picea* zone shown at Spider Creek is supported by macrofossil evidence at other sites in the Minnesota region (Fig. 5). The most detailed pollen sequence associated with macrofossil data is that from Wolf Creek (Birks, 1976). The succession here resembles that at Spider Creek but with earlier timing. An initial "tundra" zone and the subsequent *Picea* zone contain numerous records of thermophilous tree-pollen taxa (Fig. 8). However, in spite of 20% *Picea* pollen in the "tundra" zone (pollen zone 1; macrofossil zones 1 and 2, Fig. 8), the macrofossils show that the vegetation was treeless with dwarf-shrubs and herbs of arctic affinities. Around 50% *Picea* pollen during the *Picea* zone (pollen zone 2; macrofossil zones 3 and 4, Fig. 8) was accompanied by macrofossils of *Picea*

glauca, P. mariana, and *Larix* and some herbs typical of boreal-forest understorey, but no deciduous-tree taxa (Birks, 1976). At the start of the *Pinus* zone at the opening of the Holocene, tree-*Betula* macrofossils became abundant and *Pinus banksiana* needles occurred. The pollen of the thermophilous trees continued to be recorded in low amounts, showing some expansion with climatic warming, but not to percentages that might be expected if they were growing locally. The synthesis of the Minnesota Lateglacial by Watts (1967) shows *Picea* and *Larix* macrofossils consistently associated with the *Picea* pollen zone, together with a characteristic set of pioneer aquatic taxa and woodland species, including typically *Cornus canadensis, Rubus* sp., and *Fragaria virginiana*, and, less frequently, other species of boreal forests. These assemblages suggest that the environment of the *Picea* zone was comparable to the modern boreal forest, and was therefore unlikely to have a climate suitable for most thermophilous trees, although the more northern and boreal deciduous species such as *F. nigra, Populus, Salix, Alnus,* and *Betula* may have grown in association with *Picea* and *Larix* (Wright, 1971). Macrofossils of some of these northern deciduous tree taxa have been recorded occasionally at some sites (Wright, 1971; Wolf Creek, Birks, 1976). The excavation of an early Holocene buried spruce forest in northern Michigan (Pregitzer et al., 2000) permitted a unique look at the forest composition. No other tree remains were associated with the *Picea* forest, but the pollen record suggested that the surrounding hills were dominated by *Pinus* forest with i.a. *Betula, Ulmus*, and *Quercus*, although no macrofossil evidence was obtained for these taxa. However, this is not surprising, as it is unlikely that any of their macrofossils would have been transported, deposited, and preserved in a *Picea* forest.
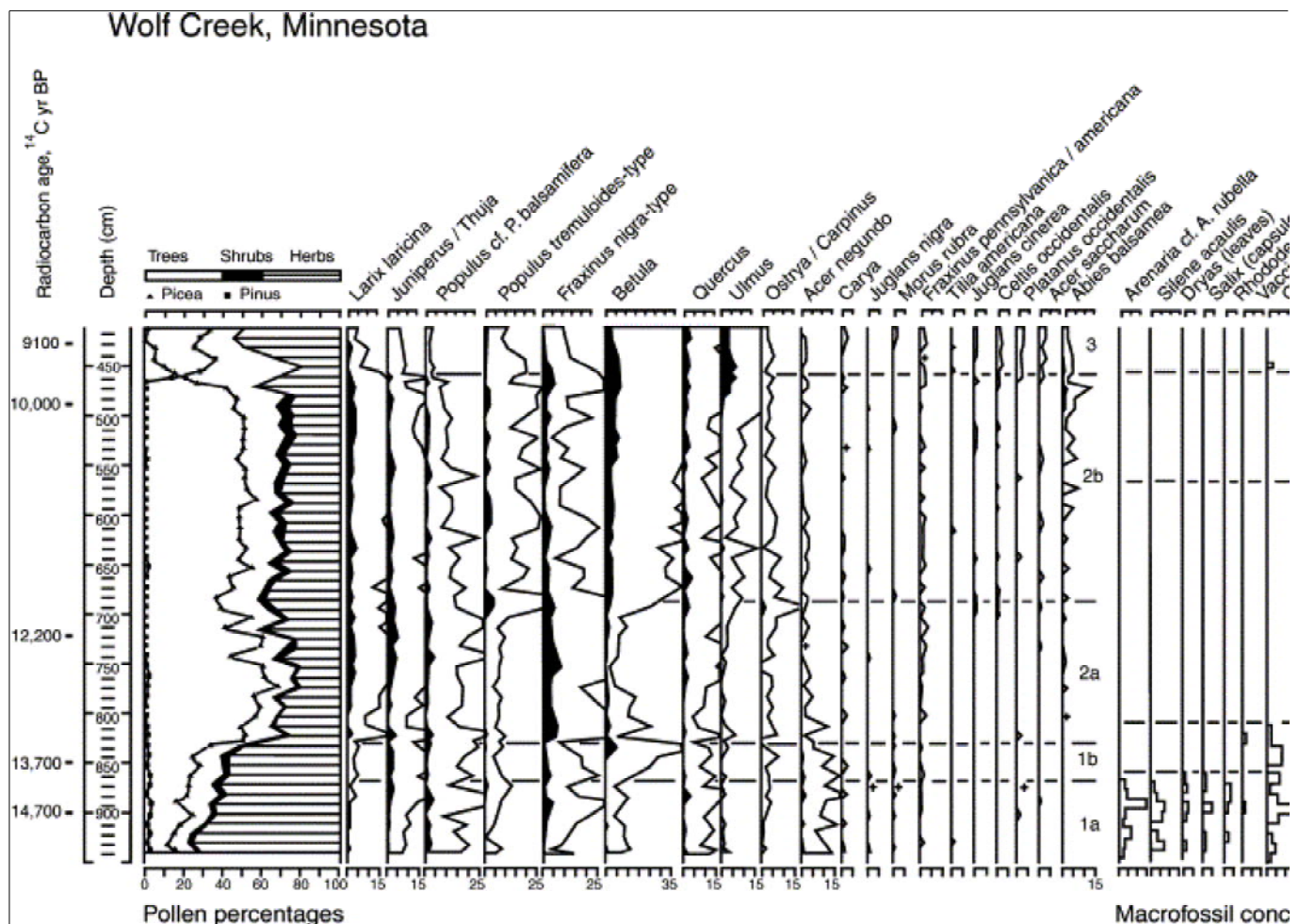

Fig. 8. Comparisons of selected pollen percentages and macrofossil concentrations in the Lateglacial sequence at Wolf Creek, Minnesota. Redrawn from Birks (1976).

This raises an important point. Before claiming absence of thermophilous trees because of absence of their macrofossils, we should consider if their remains could be expected to occur. A surface-sample study across the vegetation zones of Minnesota (Birks, 1973) recovered no

remains of thermophilous trees, even from lakes in deciduous forest. The absence of macrofossils of thermophilous trees in lake sediments may be due to low representation of their remains or to the difficulty of identifying them. The fruits or seeds of many are large and adapted to animal dispersal. Others are winged for wind dispersal, and have greater potential to be found in lakes, e.g. *Fraxinus, Ulmus, Acer*. Perhaps, unlike conifer seeds, they are not well preserved, or are released during autumn when foliage obstructs their wide dispersal. However, other vegetative parts are dispersed and can be potentially preserved, such as leaves, bud scales, bracts, twigs, etc. Leaves of deciduous trees can be preserved in certain sedimentary situations, as in small stream meanders, flood plains, and small overhung lakes and ponds (e.g. Chaney, 1924; Markussen, 1979; Spicer (1981) and Spicer (1989); Thomasson, 1991). However, identifiable leaves rarely survive in larger lakes. Bud scales are more resistant, and those of *Betula, Salix*, and *Pinus* are often recorded. *Populus* catkin scales are frequently found as they are easy to identify, and they can supplement the often poor record of *Populus* pollen. Vegetative parts of other taxa are recorded less frequently, but are nevertheless sometimes identifiable and can supply valuable information. For example, the only macrofossils of *Fagus* from the Holocene sediments of Hobschensee, Switzerland, were bud scales. These helped to distinguish periods of high *Fagus* pollen percentages that were locally produced from those that were produced by non-local *Fagus* trees at a higher altitude (Schneider and Tobolski, 1985). Bud scales of *Larix*, together with other parts, showed the local presence of *Larix* in the early Younger Dryas at Gerzensee, Switzerland (Tobolski and Ammann, 2000), whereas the pollen was not recorded. It is quite possible that analysts fail to recognise bud scales or other vegetative parts such as buds or twigs, but with increasing awareness and skill, these remains can potentially be recovered and identified. The difficulty of tracing a Holocene record of thermophilous deciduous trees has been demonstrated in western Norway (W. Eide, personal communication) where the occurrence of bud scales, leaves, etc. in Holocene lake sediments is sparse. Bud scales of some taxa (e.g. *Corylus*) are poorly preserved and bud scales of other taxa are hard to identify as fossils. It seems also that the trees have to be very close to the lake or the inflow stream for vegetative remains to be represented in lake sediments (e.g. Wainman and Mathewes, 1990), and that these macrofossils are only occasionally preserved in quantity in exceptionally favourable conditions.

Such a favourable site is Roberts Creek, N.E. Iowa (Baker et al., 1996). A series of organic deposits were analysed from the river floodplain and provided a detailed multiproxy record for the last 12,500 years. In the *Picea* zone, predating ca 9300 ^{14}C yr BP, *Picea* and *Larix* macrofossils are common, but the only macrofossil record of a thermophilous tree is of *Acer*. This suggests that the other thermophilous trees were genuinely absent in the *Picea* zone, although their pollen is recorded in the usual low percentages (Fig. 9). Evidence supporting the reconstruction of boreal conditions is provided by the plentiful macrofossil records of forest shrubs and herbs, aquatic and wetland taxa including bryophytes, and insect remains (Baker et al., 1996). Macrofossils of *U. americana* (bud scales), *Juglans cinerea, T. americana, Ostrya virginica* (leaves), *F. nigra, Carpinus caroliniana*, and *Quercus*, together with understorey taxa associated with deciduous forest, were recovered from the early Holocene sediments in association with much higher pollen percentages (Fig. 9). The alluvial taphonomy of the Roberts Creek deposits has favoured the deposition and preservation of a rich assemblage of macrofossil remains, and has provided a more detailed record of the vegetation than normally possible from a lake sediment. The contrast is shown by Lake West Okoboji, N.W. Iowa (Fig. 5) (Van Zant, 1979). Low but consistent percentages and influx of *Ulmus, Quercus, Corylus,* and *Ostrya–Carpinus* pollen occurred during the *Picea* pollen zone, where *Picea* macrofossils were common but no macrofossils of the thermophilous-tree taxa were recorded. *Ulmus* and *Quercus* pollen expanded rapidly at the opening of the Holocene (Van Zant, 1979) but unfortunately no macrofossils of them were found. A similar pollen sequence was recorded at Madelia, S. Minnesota (Jelgersma, 1962: Fig. 5 and Fig. 6). The percentages of thermophilous tree pollen during the *Picea* zones in this whole region are consistently low, and characteristically increase in the early Holocene, earlier in the south than in the north. Most of these pollen and macrofossil records in Fig. 5 were analysed in the 1960s and 1970s. There is a need to update the records with new sites analysed with an awareness of vegetative remains of

deciduous trees and with detailed chronological control to enable pollen influx to be calculated and to allow comparison of the timing of vegetational changes over space. Some lake sediments contain abundant macrofossils, although it is not easy to predict this from the topography of the lake basin (Watts, 1978). The Roberts Creek study has strikingly emphasised the importance of macrofossil taphonomy, and it would be rewarding to search for more alluvial sites with Lateglacial sediments if further progress is to be made in solving the question of the Lateglacial occurrence of thermophilous deciduous trees in the Minnesota region.
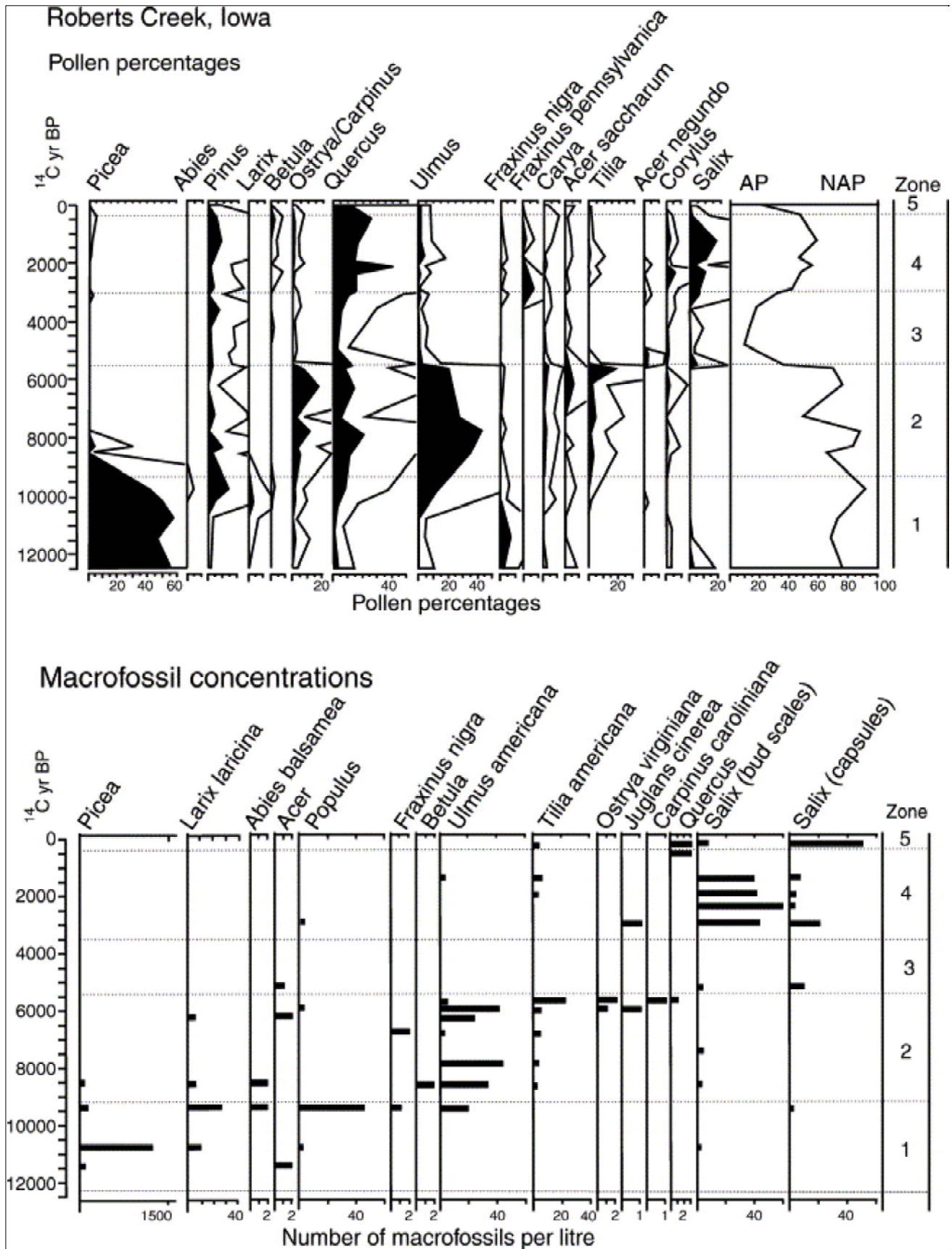
Fig. 9. Comparison of pollen percentages and macrofossil concentrations of tree taxa in Lateglacial and Holocene sediments at Roberts Creek, northeastern Iowa. Redrawn from Baker et al. (1996).

The evidence as available at present can be summarised as showing (a) that northern deciduous trees (*Betula, Populus, Salix, Alnus*) were probably present in small quantities in the *Picea–Larix* forests as proposed by hypothesis 3; and (b) that there is virtually no direct macrofossil evidence for the local occurrence of thermophilous trees following hypothesis 2. Even though

they might produce few, poorly preserved or hard-to-identify remains, it is surprising that there are no records at all, especially as Baker et al. (1996), for example, have shown it is possible to find and identify them. The balance of evidence leads to the conclusion that they were genuinely absent, a conclusion supported by their proven ability to provide long-distance transported pollen, and the occurrence of northern boreal taxa in the macrofossil assemblages indicating a relatively cool climate unsuitable for the growth of the thermophilous tree taxa.

It would be of great interest to know where the thermophilous trees were growing and from where their pollen was being transported during the Lateglacial-Holocene transition. Unfortunately, there is little evidence of their refugia at present. A full-glacial site (16,700–18,000 ^{14}C yr BP) from southeast Iowa (Baker et al., 1986) records a pollen assemblage dominated by *Picea, Pinus*, and Cyperaceae pollen, with very low values of deciduous tree pollen, associated with abundant macrofossils of *Picea* and wetland taxa and small quantities of *Larix*, together with herbs and dwarf-shrubs of treeless upland habitats with both arctic and prairie affinities. In late- and full-glacial sites to the south of Minnesota low percentages of thermophilous tree pollen have been recorded from the *Picea* zone (e.g. Kansas—Grüger, 1973; Van Zant, 1979; Baker et al., 1986; Iowa— Baker et al., 1996). However, the Lateglacial record of *Acer* at Roberts Creek (Baker et al., 1996) may suggest some local presence. To the southeast, Grüger (1972) reported continuous presence of thermophilous deciduous tree pollen (predominantly *Quercus*) during the Wisconsinan full glacial in southern Illinois. However, its amount decreased northwards. A pollen and macrofossil record from northern Indiana (Singer et al., 1996) follows the pattern further east, with no thermophilous deciduous tree macrofossils recorded associated either with the *Picea* zone or the subsequent *Quercus–Ulmus* zone. Obviously more full- and Lateglacial sites with macrofossil records are needed to the south of the Great Lakes region to delimit the extent of the *Picea* zone and locate the refugia and migration routes of the thermophilous trees and to constrain palaeoclimatic inferences (Jackson et al., 2000). The gap needs to be filled between the Mid-West and the lower Mississippi valley at 35°N where full-glacial (ca 18,000 ^{14}C yr BP) occurrences of thermophilous deciduous trees have been established from macrofossil evidence (Jackson et al (1997) and Jackson et al (2000)) leading to the reconstruction of a broadleaved/evergreen mixed warm forest biome at 18,000 yr BP in this area (Jackson et al., 2000; Williams et al., 2000). Recent climate model reconstructions (Jackson et al., 2000) based on pollen analogues yielded cooler temperatures at the LGM than those estimated from earlier climate modelling (e.g. COHMAP members, 1988) for eastern North America. However, when evaluated against data from plant macrofossils, it would seem that the temperatures were not as cool as estimated from pollen, perhaps because of differences in the ecology and phytogeography of especially *Picea* (including the extinct southern *P. critchfeldii*) and *Pinus* spp. that can be resolved by macrofossils but not by pollen, and the local occurrence of thermophilous deciduous trees in the Lower Mississippi valley (Jackson et al., 1997, 2000). An extensive area of no-analogue pollen assemblages to the northwest was inferred to represent a 'cool mixed forest' or a no-analogue 'mixed parkland' (Williams et al., 2001) biome dominated by conifers. Small isolated (cryptic) refugia in places with locally favourable climate may have existed that are virtually undetectable by pollen analysis, but that may be detectable by serendipitous finds of macrofossil remains (e.g. Stewart and Lister, 2001). Thus the improbably rapid rates of migration needed for trees to spread from southern Appalachia, for example, may not be required if small pockets of thermophilous species were surviving in intermediate situations. The early Holocene migration rates and directions of the taxa were all different, emphasising that vegetation is composed of taxa behaving in an individualistic way (e.g. Davis, 1989; Schoonmaker and Foster, 1991).

The presence of the ice-sheet margin over northern Minnesota during the time of the *Picea* zone may have setup a steep climatic gradient (Kutzbach and Webb, 1993), like that reconstructed in southeast Canada by Levesque et al. (1997), which allowed the thermophilous hardwoods to grow relatively close to southern Minnesota and Iowa in areas of sufficient precipitation, especially during the Lateglacial when climate had started to become warmer and moister, although with greater seasonality, after the full-glacial minimum temperatures and

aridity (Kutzbach and Webb, 1993). There is relatively little information available from Lateglacial sites in central USA to track the northward migration of thermophilous trees. However, the proximity of these trees to southern Iowa by that time, perhaps in small populations (Stewart and Lister, 2001) is suggested by their rapid immigration at the start of the Holocene. If this was so, their pollen could perhaps have been transported in sufficiently large quantities to achieve the relatively high percentage representation found in Minnesota pollen diagrams where there was a relatively low local pollen production. In addition, the trees would be poised to migrate rapidly northwards at the temperature rise and final retreat of the ice at the opening of the Holocene.

4. No-analogue pollen assemblages

The proof of local presence is obviously important for the construction of tree migration maps and climate reconstructions made from pollen data. Modern surface samples can be used to match with the fossil assemblages, and thus to infer the past vegetation and climate. Because frequently no good modern matches can be found, Lateglacial pollen assemblages in both North America and Europe have long been characterised as 'no-analogue' and the Lateglacial vegetation is interpreted as 'no-analogue' vegetation. This interpretation is given weight by models of past climate (Kutzbach and Guetter, 1986; Kutzbach and Webb, 1991 (1991) and Kutzbach and Webb, 1993 (1993)) which imply that Lateglacial and early Holocene climate was different from today's in terms of insolation and seasonality. In contrast, everywhere that Lateglacial macrofossil assemblages have been studied, the assemblages make good vegetational sense. The reality would seem to be that Lateglacial pollen assemblages originate from diverse source areas, ranging from the local and regional vegetation to wide heterogeneous (extra-regional) areas, possibly encompassing continents, and even perhaps the whole northern hemisphere. In northern areas whose Lateglacial climate was affected by the proximity of the ice sheets, the vegetation was treeless (northwest Scotland, Norway, northern Minnesota) or composed of trees with low local pollen production (*Picea, Larix* in central and southern Minnesota and Iowa). This allowed long-distance transported pollen, such as thermophilous-tree pollen in Minnesota and *Betula* pollen and pollen of thermophilous steppe taxa in northwest Europe, to reach substantial percentage representation. The assemblages were derived from diverse source areas and have no equivalent in modern pollen samples. It should thus be emphasised that it is unwise to presume the local presence of the parent taxon from the occurrence of a pollen type in any pollen assemblage where local pollen production is low. Additional information from macrofossils is essential in such situations to establish the character of the local vegetation, and to make a climatic interpretation of the assemblage in an informed and realistic way.

5. Key issues

1. The development of greater computer power has enabled large-scale syntheses of fossil pollen data to be used in the reconstruction of past vegetation (biomes) and palaeoclimates through space and time. However, the tacit acceptance of a Lateglacial fossil pollen record as a faithful representation of the local vegetation can result in faulty interpretations and reconstructions of vegetation and climate over small and large scales. This paper discusses anomalies caused by the inherent properties of pollen data from the Lateglacial of Scotland, Norway, and the Mid-West USA that may result in faulty conclusions being drawn. Accurate reconstructions are required for the meaningful validation of model simulations.

2. In Scotland and Norway high percentages of *Betula* pollen in Lateglacial Interstadial sediments have been interpreted as the development of birch woodland. This implies that the mean July temperature exceeded 10–11°C. Plant macrofossil records from the same sites as the pollen records indicate that tree-birches were absent and that the local vegetation was shrub- or herb-dominated with arctic and montane taxa characteristic of vegetation communities beyond

the tree-line today. Low local pollen production by this vegetation has resulted in over-representation of *Betula* pollen derived from long-distance transport. Consequently, the mean July temperature reconstructions from the pollen data are too high, and should be revised to values <10°C, depending on the temperature tolerances of the vegetation types and species occurring locally as proved by the records of their macrofossils. These reconstructions are very important for validating model simulations in this region of strong climate gradients and changes during Lateglacial time.

3. The evidence for the local occurrence of small quantities of thermophilous deciduous trees in the Lateglacial *Picea* and *Larix* forests (*Picea* zone) of the Mid-West USA has been based on the widespread and consistent occurrence of their low pollen percentages. Plant macrofossil data so far have not confirmed their local occurrence. Positive macrofossil evidence shows two types of vegetation in the *Picea* zone in Minnesota. In northern areas close to the Laurentide ice sheet, treeless shrub-tundra prevailed. High percentages of *Picea* pollen and the low percentages of thermophilous deciduous trees must have been derived from remote sources, and were not masked due to the low pollen production of the local vegetation. Thus thermophilous deciduous tree pollen is definitely capable of long-distance transport. Most of the *Picea* zone sequences contain macrofossil records indicative of *Picea* and *Larix*-dominated forest. Associated taxa are characteristic of boreal forest vegetation today, suggesting that the climate was unsuitable for most of the thermophilous deciduous trees. The relatively low pollen representation of *Picea* and minimal representation of *Larix* allowed any long-distance transported pollen to reach detectable low percentages. These two lines of evidence support the hypothesis that thermophilous deciduous trees were not present in the Minnesotan Lateglacial.

4. Local absence of plants cannot be proved by absence of macrofossils for taphonomic reasons. Macrofossils have much more limited dispersal than pollen and often may not reach the centre of a lake where a pollen core is usually taken. Macrofossils, including vegetative parts, of the thermophilous deciduous trees are seldom found in modern samples of lake sediments, partly because they grow on uplands and are prevented from reaching the lake by the surrounding vegetation, partly because they are often poorly preserved (e.g. leaves), and partly because items like budscales and bark are hard to identify. Taphonomy is an important factor in the interpretation of the macrofossil record, in addition to the skill of macrofossil analysts and their awareness of vegetative remains. Skill and awareness are improving, although the number of skilled analysts is exceedingly small. In suitable taphonomic circumstances, mainly stream-laid deposits, vegetative remains of the tree taxa have been recovered and identified in the Holocene, accompanied by high pollen percentages that undoubtedly reflect local presence. Lateglacial deposits of this nature in N.E. Iowa contained one record of *Acer* ([Baker et al., 1996](#)) but the Holocene sediments there contained many records of diverse thermophilous trees, suggesting that their Lateglacial absence is genuine.

5. The taphonomy of pollen assemblages also plays a role in their interpretation. Many Lateglacial pollen assemblages are not matched by modern pollen surface samples from contemporary vegetation and have been termed 'no-analogue' assemblages. They are inferred to have been produced by vegetation different from today ('no-analogue' vegetation). This concept has been generally accepted, especially as Lateglacial boundary conditions at the time of deglaciation (mainly insolation, ice cover, albedo) were unique and result in modelled climates not found on earth today. There is no doubt that 'no-analogue' vegetation types occurred during the Lateglacial as biota responded to the rapidly changing climate and environment. However, all Lateglacial macrofossil analyses to date have yielded assemblages that can be interpreted without difficulty in terms of modern vegetation. Basic pollen analytical theory allows for pollen to be deposited from local, extra-local, regional, and long-distance (extra-regional) sources, the relative proportions of the components depending on their relative production and dispersal. If the local component is large, the long-distance component will be

masked. If it is small, even a small long-distance component will be represented at the sampling point. Its size and composition will depend on the productivity and dispersal ability of the parent taxa, particularly wind dispersal. The strong circulation and wind speeds of the Lateglacial would have caused wind-blown pollen to be widely dispersed. Therefore, 'no-analogue' pollen assemblages may not represent 'no-analogue' vegetation as such, but may result from a mixing of pollen originating from near and distant sources where the long-distance component is not masked by a small local component at the sampling point.

6. Lateglacial chronology is difficult. Sediments are often inorganic, and variations in the amount of ^{14}C in atmospheric CO_2 mean that the measured amount of ^{14}C is not linearly related to age, making age calibration complex. In addition, the dating of bulk lake sediments often results in dates being too old because of old carbon reservoir effects. Only in relatively recent years has AMS dating become important, and now it is realised that terrestrial plant material should, if at all possible, be extracted from lake sediments to avoid reservoir effects. As a consequence, ^{14}C-based chronologies of sites used in Lateglacial data syntheses and reconstructions should be critically assessed, and not taken at face value. The rapid climate changes and vegetation responses during this period make chronology a particularly critical consideration.

7. Because of their various shortcomings in straightforward representation of local vegetation, pollen data should be used with caution in Lateglacial interpretation of vegetation and climate. The reconstructions should be validated by independent evidence of which plant macrofossil evidence is an obvious choice. Of course, the inconsistencies and short-comings of the independent evidence should also be taken into account, and a consensus reconstruction should be built up. Then reconstruction of climatic patterns in space and time can be made with more confidence and the pitfalls inherent in a single line of evidence such as pollen data can be avoided. Validation of model simulations can then be made more critically and meaningfully.

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