

Validation of Pollen Studies

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Plant macrofossils and pollen play complementary roles in paleoecology. Each has its own advantages and shortcomings. Used separately, they provide valuable information about past vegetation. Used together, the two types of data can corroborate or, occasionally, challenge each other, and they can provide more detailed and refined understanding of past vegetation at multiple spatial scales. In this article, we briefly compare and contrast the flora- and vegetation-sensing properties of pollen and macrofossil data and then present a series of case studies in which the two data sets have been used together profitably at spatial scales ranging from local to continental. We focus on macrofossils from 'wet' sediments (lakes, peatlands, buried soils, fluvial deposits, etc.) and do not explicitly treat macrofossils from rodent middens and archeological sites.

Vegetation-Sensing Properties of Pollen and Plant Macrofossil Data

Pollen grains comprise a distinct and uniform stage in the life history of seed plants—the gametophyte generation. Pollen grains are small, with a restricted range of sizes (5–150 µm), and most are packaged in sporopollenin, a refractory organic compound. Plant macrofossils from seed plants represent the sporophyte generation. However, because seed plant sporophytes are multicellular, differentiated entities, plant macrofossils can take any of a variety of forms: seeds, fruits, anthers, microsporangia, megaspores, ovulate cones, leaves, needles, petioles, bud scales, buds, twigs, branches, etc. The size range is potentially vast, from seeds <1 mm³ to buried trees >20 m³. Materials are also variable, although macrofossils preserved in sediments tend to be composed of the more refractory compounds (particularly cellulose and lignins).

Pollen grains are typically morphologically invariant among species within most anemophilous genera and among many genera within certain families. In contrast, interspecific morphological variation of sporophyte plant organs is typically large since plant species are generally described and distinguished based on sporophyte morphology. Accordingly, many plant macrofossils can be identified to species, in contrast to the corresponding

pollen grains. This imparts one of the three unique features of plant macrofossil data compared to pollen: high taxonomic resolution. Macrofossils allow us to surmount the taxonomic smoothing frequently imposed by pollen data.

The second unique feature of plant macrofossils is their local nature. Plant macrofossils generally do not travel far when airborne; the primary mode of transport beyond 10¹–10² m is by surface waters or animals. For depositional basins with no inflowing streams, most plant macrofossils derive from within 10¹–10² m of the shore. For depositional environments with a fluvial component, macrofossils must have been derived from plants growing somewhere within the catchment above the point of deposition. In contrast, pollen grains can be transported by wind for distances up to 10⁴ km, although more typical travel distances are on the order of 10¹–10⁵ m. Pollen assemblages in a lake or wetland basin represent a distance-weighted integration of vegetation surrounding the basin, with significant representation of distant vegetation (i.e., >10³ m). In contrast, plant macrofossils provide a more-local sampling of vegetation, undoubtedly distance-weighted, but with little or no representation beyond ca. 10² m (Table 1).

Many plant taxa are poorly represented in pollen assemblages due to low productivity, poor dispersal, poor preservation, or adaptations for zoophilous transport. Many of these taxa—*Pseudotsuga*, *Larix*, *Abies*, *Dryas*, *Populus*, *Oxyria*, *Polygonum*, and *Nymphaeaceae*—are well represented in plant macrofossil assemblages from lakes and other

Table 1 Systematic studies of modern representation of terrestrial plant macrofossils in lake sediments

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| Birks HH (1973) Modern macrofossil assemblages in lake sediments in Minnesota. In: Birks HJB and West RG (eds.) <i>Quaternary Plant Ecology</i> , pp. 173–189. Oxford, UK: Blackwell. |
| Drake H and Burrows CJ (1980) The influx of potential macrofossils into Lady Lake, north Westland, New Zealand. <i>New Zealand Journal of Botany</i> 18:257–274. |
| Dunwiddie PW (1987) Macrofossil and pollen representation of coniferous trees in modern sediments from Washington. <i>Ecology</i> 67:58–68. |
| Hill RS and Gibson N (1986) Distribution of potential macrofossils I: Lake Dobson, Tasmania. <i>Journal of Ecology</i> 74:373–384. |
| Jackson ST (1989) Postglacial vegetational changes along an elevational gradient in the Adirondack Mountains (New York): A study of plant macrofossils. <i>New York State Museum and Science Service Bulletin</i> 465. |
| Wainman N and Mathewes RW (1990) Distribution of plant macroremains in surface sediments of Marion Lake, southwestern British Columbia. <i>Canadian Journal of Botany</i> 68:364–373. |

depositional environments. Thus, plant macrofossils can provide information about taxa for which the pollen record may be unreliable—the third unique feature of macrofossil data. This complementarity does not hold for all taxa, however; some plants are poorly represented in both pollen and macrofossil assemblages. For example, *Liriodendron*, an important tree species of eastern North America, is entomophilous and hence almost completely absent from pollen records, regardless of local or regional abundance. Fruits, bud scales, and leaves of *Liriodendron* are large and poorly dispersed, and hence show up only rarely in macrofossil assemblages. Some taxa well represented in pollen assemblages (e.g., *Quercus*, *Carya*, and *Corylus*) are poorly represented as macrofossils in many depositional settings.

Macrofossil and Pollen Representation Within and Among Depositional Environments

Representation of plant macrofossils is far more subject to influences of site type and local depositional environment than pollen. Pollen grains may be subjected to some secondary sorting by fluvial transport and sediment focusing. However, pollen assemblages from diverse depositional environments (lakes, wetlands, forest-floor moss polsters, soil samples, alluvium, caves, and rodent middens) are generally similar within a region due to widespread airborne transport and mixing prior to deposition. In contrast, macrofossils are not subject to the same degree of mixing due to large size and poor dispersal. Furthermore, macrofossils are more subject to sorting by airborne and fluvial dispersal processes than pollen (Spicer, 1989; Greenwood, 1991).

Lakes

Lake sediments are generally the most widely used sources of both pollen and plant macrofossil data. Within-lake variation in pollen assemblages is significant, but the variation is generally small relative to variation among lakes. In contrast, plant macrofossil assemblages within a single lake vary substantially, depending on water depth, distance from shore, and vegetation composition on the nearest shore. Most macrofossil deposition to the water surface will occur close to shore, whereas the best environment for macrofossil preservation in sediments will be in deep waters, which tend to be offshore (Watts, 1978). Moderate-sized lakes (5–100 ha) with relatively gentle bottom slopes will have few macrofossils preserved near shore, where influx is highest, because

of high decomposition and low sediment accumulation rates. Deeper waters with good preservation and high sediment accumulation rates will also have few macrofossils because of poor offshore dispersal. Highest macrofossil concentrations will occur in intermediate depths, deep enough to preserve macrofossils and close enough to shore to ensure high macrofossil influx. Since most paleoecologists obtain cores from the deepest portions of lakes, it should come as no surprise that macrofossils are often absent or rare in sediment cores.

Significant sorting of macrofossils occurs with distance from shore due to differential dispersal (and, in some cases, flotation) properties of various plant organs. Large, coarse materials (large, gravity- or animal-dispersed seeds and fruits, ovulate cones, large leaves, branches, etc.) are rarely dispersed more than a few tens of meters from shore, where they are likely to sink and then decompose in shallow benthos. Smaller organs (small seeds and fruits, conifer needles, and bud scales) are dispersed farther from shore and hence are better represented in offshore sediments. In deep waters more than 100 m from shore, only small fragments of small-diameter conifer needles, papery bud scales, and small winged fruits (e.g., *Betula papyrifera* and *B. pubescens*) are typically present. The relative contributions to offshore deposition of airborne dispersal, flotation, and skating across winter ice are inadequately known.

Selection of coring sites for macrofossils thus represents a trade-off between maximizing macrofossil preservation (deep water) and deposition (near shore). For large lakes, it is advisable to run a transect of short cores or dredge samples to determine the ideal site for macrofossil deposition. Alternatively, careful selection of lakes can yield good macrofossil results. In particular, small or moderate-sized lakes with deep waters 10–50 m offshore and steep sides can have very high macrofossil concentrations, yielding excellent records of upland terrestrial vegetation.

Lake sediments are typically sampled using piston-corer with diameters ranging from 5 to 10 cm. Thus, sample volume is limited, and some plant organs of moderate size or intermediate dispersal properties (e.g., *Acer* samaras, most deciduous leaves, and coarse conifer needles) are not reliably sampled: Absence from sediments cannot be attributed to absence from vegetation. However, other plant organs (winged seeds of *Betula*, *Alnus*, and many conifers, conifer needles, and many bud scales) are consistently represented in modern lake sediments (Fig. 1) and between adjacent stratigraphic samples within a core (Fig. 2). In such cases, absence from sediments can be inferred to indicate absence from or rarity in vegetation near the lakeshore. Careful

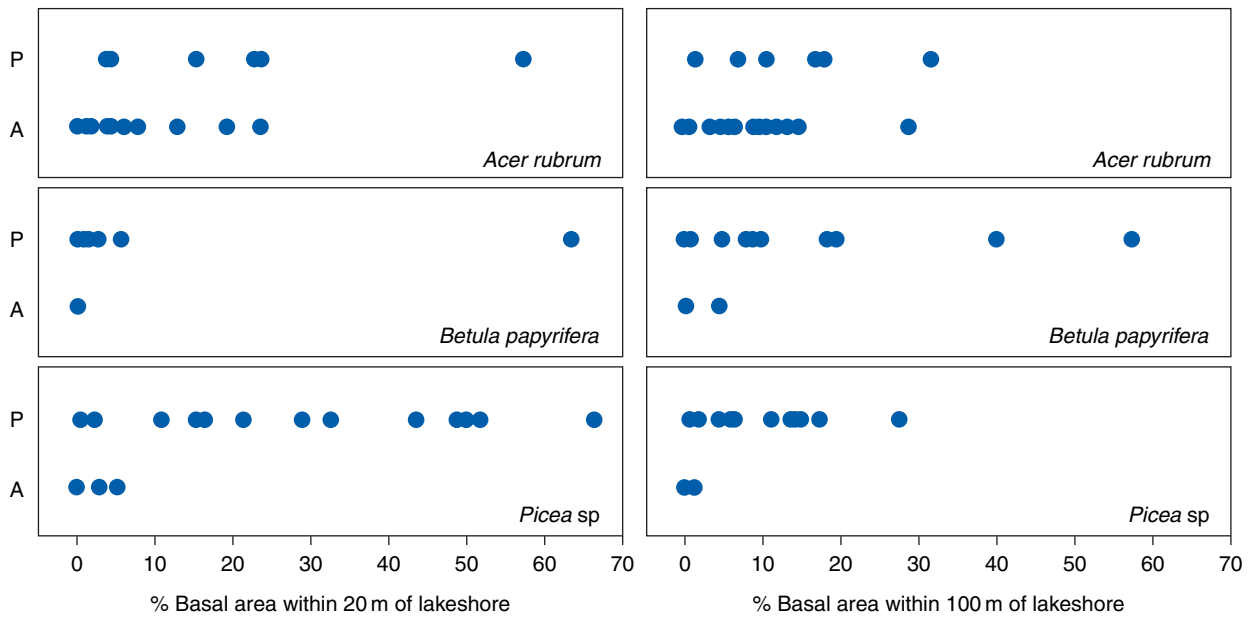


Figure 1 Scatter plots showing the relationship between the presence (P) and absence (A) of macrofossils in modern sediments of 22 lakes and abundance of trees within a 20- and 100-m radius of the lake margin. All sites are small lakes (0.1–2.0 ha) in the northeastern United States (New York, Rhode Island, Massachusetts, and Connecticut). Surface samples comprise 100–200 cm³ obtained using an Ekman dredge from the center of the lake. *Acer rubrum* macrofossils comprise samaras and leaves. *Betula papyrifera* macrofossils comprise samaras and catkin bracts. This taxon includes *B. populifolia* at several sites. Samaras and bracts of the two species are morphologically similar but distinguishable. Because the two species are closely related, have similar growth form, and their macrofossils have similar dispersal properties, we lumped them for purposes of this figure. *Picea* sp. macrofossils include needles, sterigmata, seeds, microsporangia, and twigs. Species at the sites include *P. rubens* and *P. mariana*, which are closely related and morphologically indistinguishable for macrofossil types other than cones. *Acer rubrum* macrofossils are large and poorly dispersed relative to the other two species. The occurrence of *A. rubrum* macrofossils in sediment samples of this size (typical of sediment cores) is inconsistent. The absence of macrofossils cannot be construed as indicating the absence of nearby populations. Larger sediment samples might increase the probability of macrofossil occurrence. *Betula papyrifera* and *B. populifolia* macrofossils are small, abundantly produced, and well dispersed. Macrofossils are consistently represented in sediments even when local populations are very small. Some sites lacking any *B. papyrifera* or *B. populifolia* trees within 20 m of shore have macrofossils in sediments, dispersed from trees between 20 and 100 m from shore. *Picea* sp. macrofossils are also very well represented in sediments. In general, if small populations are present near shore, macrofossils are present in sediments. *Picea* trees produce a variety of small organs that are well dispersed and well preserved in sediments. In the case of both *Picea* and *B. papyrifera*, the absence of macrofossils in sediment samples of this size, in lakes of this size and morphometry, can be interpreted as indicating the absence or scarcity of nearby populations. Consistent absence among adjacent samples in a core can be construed to indicate the absence of nearby populations. Source: S. T. Jackson, unpublished data.

selection of lakes and coring sites within lakes, together with use of large-diameter coring devices (7.5 or 10 cm), can yield records in which the presence/absence of macrofossils in the stratigraphic column can be applied directly to the presence/absence in adjacent vegetation. Also, as discussed later, macrofossil presence/absence and abundance patterns often show close stratigraphic correspondence to pollen abundance of the corresponding taxa.

Wetlands

Macrofossils in wetland sediments can provide excellent records of local wetland vegetation. Shallow water or subsurface water tables limit the extent of waterborne dispersal of macrofossils, and floating-leaved and emergent plants further reduce waterborne dispersal by providing a series of traps and

baffles. This has the advantage of amplifying local representation of macrofossils, which can be used to examine local vegetational and hydrological dynamics within a wetland (Watts and Winter, 1966; Singer *et al.*, 1996; McMullen *et al.*, 2004). In fact, species richness of wetland/aquatic macrofossil assemblages can be very high in wetland sediments. In general, macrofossils from surrounding uplands are restricted to plant organs that are particularly well dispersed by airborne means (small samaras, winged seeds, bud scales, and some conifer needles). Sediments are usually sampled using coring devices, with the sample size limitations described previously for lakes. Wetlands with low sediment accumulation rates, oxygenated waters, and/or sustained drawdown periods can have sediments depauperate in macrofossils, as can humified bog peats.

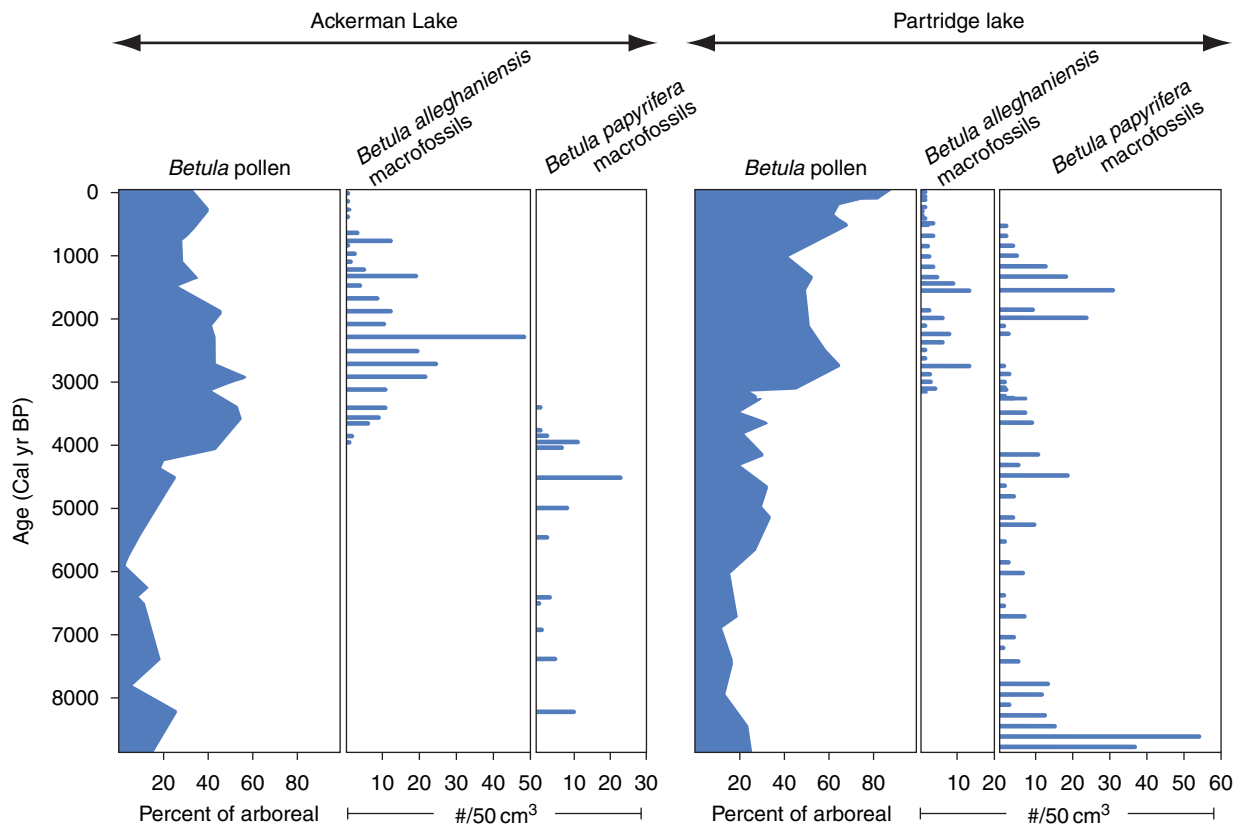


Figure 2 Pollen and macrofossil sequences for *Betula* from two lakes in the Upper Peninsula of Michigan. Ackerman Lake (6 ha) is south of Munising Bay. Steep slopes on the south and east sides, near the coring site, are forested by *Tsuga canadensis*, *Acer saccharum*, *Betula alleghaniensis*, and *Fagus grandifolia*. Partridge Lake (3 ha) is situated near the tip of the Keeweenaw Peninsula, 160 km northwest of Ackerman Lake. The steep slopes surrounding Partridge Lake are forested by *A. saccharum*, *B. alleghaniensis*, *Quercus rubra*, *Picea glauca*, and *Pinus strobus*. *Betula* pollen undergoes a dramatic late Holocene increase at both sites, but the increase at Ackerman Lake occurs approximately 1000 years before the increase at Partridge Lake. This would appear to represent a time-transgressive westward migration or expansion of *Betula*, but the pollen data alone render interpretation difficult. Plant macrofossil data clarify the interpretation: The pollen increase at both sites is coincident with first appearance of macrofossils of *B. alleghaniensis*, which persists in both records until the present. Thus, the pollen pattern represents westward expansion of *B. alleghaniensis* populations. *Betula papyrifera* was the sole or dominant *Betula* species before the *B. alleghaniensis* expansion, and it was associated with lower pollen percentages. *Betula papyrifera* is absent from Ackerman Lake sediments after the *B. alleghaniensis* invasion. This probably represents a climate-driven change in disturbance regime rather than competition; *B. papyrifera* regeneration is dependent on large-scale, stand-replacing disturbances (crownfire and extensive windthrow). *Betula papyrifera* persists at Partridge Lake throughout the late Holocene, co-occurring with *B. alleghaniensis*. Stand-replacing disturbances (particularly crownfires) were probably more prevalent near Partridge in the late Holocene; this is consistent with continued high percentages of *Pinus* pollen. Modified (with updating) from Jackson ST and Booth RK (2002) The role of late Holocene climate variability in the expansion of yellow birch in the western Great Lakes region. *Diversity and Distributions* 8:275–284.

Fluvial Sediments

Fluvial sediments have been underutilized as sources of plant macrofossil data. Concerns with fluvial transport and discontinuous deposition at individual sites have inhibited their use. However, fluvial deposits from low-order (i.e., headwater) streams restrict the potential source area for macrofossils, and individual ‘snapshot’ assemblages can be dated and stacked. Fluvial deposits are usually collected from excavations or from streamcut exposures, and hence

sample size is not limited by a coring device. Furthermore, fluvial transport and deposition can concentrate large plant organs (leaves, large seeds and fruits, branches, etc.) that are rare in sediments of most lakes. Significantly, the only macrofossil records of several North American trees (e.g., *Quercus*, *Juglans*, *Liriodendron*, and *Carya*) are from fluvial deposits. Paleoecologists occasionally turn to fluvial deposits in the absence of better sites. The exemplary studies of Richard Baker and colleagues in the Upper Mississippi River Valley indicate

that macrofossil and pollen studies of fluvial deposits can potentially yield far richer records of upland vegetation change than lakes or wetlands. (see Holocene North America).

Other Depositional Settings

Plant macrofossils are also preserved in a variety of other depositional settings, ranging from glacial and glaciomarine to former land surfaces buried *in situ* with contemporary vegetation. In most of these depositional settings, samples are collected from exposures, and sample size is not as limited as for cores. Buried *in situ* vegetation can provide a unique window on past community composition and population density, and accompanying pollen assemblages are comparable to samples from modern soils.

Data Expression

Quaternary pollen data are most commonly expressed as percentages of a defined pollen sum. Certainly, virtually all applications of Quaternary pollen data are quantitative; presence/absence applications are generally pre-Quaternary. Plant macrofossil data, by contrast, are more heterogeneous in expression. Data range from presence (anecdotal occurrences) to presence/absence to quantitative. Macrofossil data from sediment cores are typically presented as concentrations (number of specimens per unit volume of sediment) or, occasionally, accumulation rates (numbers deposited per unit area per year). These data can, of course, be reduced to presence/absence data. Stratigraphic changes in macrofossil concentrations within a sediment core are generally interpreted as indicating changes in species abundance and vegetation composition. Such interpretations assume that the depositional setting has remained constant. This assumption can be violated in particular if water level changes in the basin have resulted in changes in the preservation environment, distance from the source vegetation along the lake-shore, or density of intervening emergent and aquatic vegetation. However, coring of small deep lakes, or of deep water close to shore, can ensure that this assumption is justified.

Greater difficulties are encountered in comparing assemblages between cores within a lake, or particularly among lakes. Differences in pollen percentages among lakes can be attributed in large part to vegetational differences, whereas differences in pollen concentrations may be attributable to differences in depositional setting or other factors. Macrofossil concentrations can be compared among lakes along environmental transects, and such comparisons often

give sensible results in terms of vegetational patterns. However, such comparisons should be standardized carefully for morphometric and other variables such as distance from shore. Alternatively, a macrofossil sum can be designated and used to calculate macrofossil percentages (Watts and Winter, 1966; Tinner and Kaltenrieder, 2005), facilitating between-site comparison (Jackson and Whitehead, 1991).

For broader comparisons, particularly among different site types, any quantitative expression poses an “apples and oranges” problem, so data are generally reduced to presence/absence. For plant taxa that are particularly well represented in macrofossil assemblages, mapped presence/absence of modern macrofossils closely approximates modern geographic distributions, and hence snapshot maps of past time intervals can be used to map range dynamics of these species (Jackson *et al.*, 1997).

Tandem Applications of Pollen and Plant Macrofossil Data

Macrofossil and Pollen Data from Individual Sites

Innumerable studies comparing pollen and macrofossil stratigraphy from individual sediment cores have been published, and records of the same taxa generally show parallel stratigraphic changes in abundance. In these cases, the pollen and macrofossils provide mutual corroboration. The two data types are subject to completely different taphonomic processes and record surrounding vegetation at vastly different spatial scales. The fact that pollen and macrofossils of the same taxa so often track each other temporally gives us confidence that both data sets are tracking changes in upland vegetation.

Macrofossils provide far more than corroboration of pollen data, and vice versa: The differential taphonomic biases, differential spatial integration, and differential taxonomic resolution can be used in complementary ways to refine our interpretations of past flora, vegetation, and environment. We provide a few representative examples here.

Tandem studies of pollen and plant macrofossil analyses from the same sites are being used to study late Holocene dynamics of birch species in the western Great Lakes region. Pollen records from the region document increasing birch (*Betula*) pollen in the late Holocene. However, two species of birch trees (*B. papyrifera* and *B. alleghaniensis*) with morphologically similar pollen grains occur in the region, hampering detailed ecological and climatic inferences from the birch pollen record. Both species produce morphologically distinct, highly dispersible samaras

and catkin bracts in large numbers. These macrofossils are well represented in sediments of lakes and small peatlands in the region. Detailed studies of pollen and macrofossils from lake sediment cores indicate that *B. papyrifera* has been an important component of regional upland vegetation throughout the Holocene, and that *B. alleghaniensis* has migrated into the region only during the past 4,500 years (Fig. 2). This latter migration resulted in a time-transgressive increase in *Betula* pollen percentages from east to west across the region (Jackson and Booth, 2002). Similar integrated studies of pollen and macrofossils have helped refine interpretation of pollen records from numerous other regions. The increased taxonomic precision imparted by macrofossil records coupled with the regional smoothing of pollen records can lead to detailed reconstructions of vegetation dynamics that could not have been inferred using either method independently.

An extreme example of how the increased taxonomic resolution of macrofossils can alter interpretations of pollen assemblages comes from an extinct species, *Picea critchfieldii* (Jackson and Weng, 1999). Pollen assemblages from much of the unglaciated southeastern United States show high percentages of *Picea* pollen, routinely ascribed to the boreal and montane *Picea* species that grow in eastern North America today. *Picea* macrofossils found at many of these sites corroborated this interpretation, which, together with other evidence, led to the perception of widespread boreal forest or mixed boreal conifers/cool-temperate hardwoods at low latitudes (to 30°N) with accompanying drastically reduced temperatures. More detailed morphological and anatomical studies of the *Picea* cones and needles, respectively, led to the discovery that an extinct species, *P. critchfieldii*, occurred over much of the region and was the only *Picea* species at some sites (Jackson and Weng, 1999). This has led to reevaluation of the Pleistocene biogeography, paleoecology, and paleoclimatology of the entire region (Jackson *et al.*, 2000). Whether the pre-Holocene demise of *P. critchfieldii* is one of many plant extinctions or a singular occurrence remains obscure. However, Pleistocene macrofossils of other taxa should be scrutinized to determine whether they belong to extant species.

Macrofossils are also important in detecting palytologically cryptic populations or taxa. Obvious examples include the taxa that are poorly represented by pollen in modern assemblages due to low productivity, poor dispersal, or rapid decomposition (e.g., *Larix*, *Pseudotsuga*, and *Populus*). However, macrofossil data reveal that pollen assemblages, by virtue of their wide spatial integration, may miss important

aspects of vegetation and flora. This has become particularly obvious in glacial-age and late-glacial settings (Jackson *et al.*, 2000; Willis *et al.*, 2000; Jackson and Williams, 2004; Willis and Van Andel, 2004). Pollen data for the last glacial period in Europe indicate extensive treeless vegetation; low representation of arboreal pollen types suggests the absence of trees anywhere north of the southern Balkans and Iberian and Italian peninsulas (Huntley *et al.*, 2003). However, charcoal of woody plants (*Picea*, *Pinus*, and *Betula*) has been found in glacial-age paleosols and archeological sites in central Europe (Willis *et al.*, 2000; Willis and Van Andel, 2004). Similarly, macrofossils of *Pinus strobus*, *B. papyrifera*, *Fagus grandifolia*, *Quercus* spp., and *Carpinus caroliniana* occur in glacial-age sediments of the unglaciated southeastern United States, even though pollen is absent or occurs in trace amounts at the same sites (Jackson *et al.*, 2000). All of these taxa, both European and North American, are prolific pollen producers that are well represented in modern pollen assemblages. Their poor representation in the Pleistocene assemblages remains enigmatic, potentially attributable to their occurrence in small, scattered populations (e.g., in locally wet sites) or to differential effects of reduced CO₂ on physiognomy and reproductive allocation (Jackson and Williams, 2004). Phylogeographic evidence, particularly from North America, suggests that glacial-age populations of temperate trees may have been substantially farther north than suggested by pollen records (McLachlan *et al.*, 2005).

The apparent discrepancies between glacial-age records of pollen and macrofossils arise in part from the vast differences in spatial integration and source area of the respective data types. These differences have manifestations in the Holocene as well and can be used to tease apart scale-dependent patterns in the paleoecological record. We discuss some examples in the following sections that involve spatial arrays or synoptic networks of sites. Here, we discuss a few site-based case studies from the Holocene. Pollen data are effective in indicating population changes, including invasion/expansion, integrated over a large area. The efficacy of pollen data in detecting small, scattered colonizing populations has been the subject of considerable discussion (McLachlan and Clark, 2004). Comparison of Holocene pollen and macrofossil records indicates that pollen data are in many (and perhaps most) cases ineffective at determining the timing of colonization. Macrofossil occurrences have been observed to precede increases in pollen percentages beyond trace levels by hundreds or thousands of years (Petee, 1991). Petee's study, together with the glacial-age anomalies discussed previously,

indicates that small, scattered populations of tree species can go undetected in pollen records—an observation consistent with what is currently known about pollen dispersal and representation.

Because of long-distance pollen dispersal, plant macrofossil occurrences seldom precede high pollen percentages in migrating populations. For example, in the Adirondack Mountains of New York, *Pinus strobus* pollen percentages increased at least several hundred years before *Pinus strobus* macrofossils first appeared in sediments (Jackson and Whitehead, 1991). However, in northern Michigan, the first occurrence of *P. strobus* macrofossils in lakes is synchronous with the first occurrence of pollen beyond trace amounts (Booth *et al.*, 2004). The difference may stem from the occurrence of extensive lowlands surrounding the Adirondack highlands, which may have fostered extensive *P. strobus* populations before the species migrated upslope.

Macrofossils can also indicate leads and lags in local population response during periods of decline. Macrofossil and pollen data reveal, for example, that as prairie expanded to replace mesic forest in uplands of southeastern Minnesota during the mid-Holocene, local populations of *Ulmus* persisted on floodplains for at least 500 years after the regional shift (Baker *et al.*, 2002). This may represent persistence of one or two tree generations on the more favorable floodplain sites or gradual climate change that passed thresholds for forest growth on uplands first and wetter sites later. If local populations persist, they become ‘relict’ populations, and their development can be observed by comparing pollen and macrofossil data from individual sites (Watts, 1979) and in mapped networks (Fig. 3).

Differences in the source area of pollen and macrofossil records also have enabled comparative investigations of the dynamics of wetland and upland systems. For example, by comparing the timing of changes in pollen derived from upland trees and changes in the concentrations of locally deposited wetland plant macrofossils, several studies have assessed the relative importance of climatic versus autogenic controls on peatland development and dynamics (Singer *et al.*, 1996; Campbell *et al.*, 1997; Booth *et al.*, 2004).

Regional Studies: Site Transects and Networks

Plant macrofossils and pollen have been used together in a number of regional studies, nearly all involving elevational gradients. In typical montane regions, most of the land surface is at low elevations, and frequently the highest pollen productivity is in

low-elevation vegetation (e.g., forests). Widespread pollen dispersal tends to smooth vegetational patterns along elevational gradients, and discrimination of elevation-specific vegetation composition and elevational boundaries of individual species and forest types is difficult. Site transects using both pollen and plant macrofossil data have led to elevationally precise reconstructions of vegetation patterns and species ranges (Table 2). Intersite comparisons impose challenges of macrofossil data expression. Montane studies have variously used presence/absence, concentrations in sediments, and macrofossil percentages based on a defined sum (Table 2). In general, these studies confirm the differential spatial smoothing of pollen and macrofossil data, with the macrofossils providing spatially detailed records of vegetation composition and species ranges.

Macrofossils have not been used as extensively in regional studies focused on landscape patterns (e.g., edaphic mosaics) or geographic gradients (e.g., studies of species invasions). Macrofossils from packrat middens show the potential power of these kinds of studies (Betancourt *et al.*, 1990; Lyford *et al.*, 2003), and similar study designs should be developed using macrofossils from lakes and other sites (Peñalba and Payette, 1997). (see Rodent Middens).

Synoptic-Scale Studies: Mapped Networks

Synoptic-scale studies utilizing pollen data have been a tradition in Quaternary ecology since the pioneering work of Szafer and Sears, and mapping of pollen data at regional to continental scales is now routine (Williams *et al.*, 2004). Plant macrofossils, in contrast, have not been widely applied in synoptic-scale studies. One of the challenges in doing so, of course, is determining data expression. Presence/absence has worked well in recent applications, and the most comprehensive applications to date have been in eastern North America (Jackson *et al.*, 1997, 2000). These studies show generally corresponding patterns between pollen and macrofossil data (Fig. 3). For several taxa (e.g., *Pinus*, *Picea*, and *Betula*), the higher taxonomic resolution of the macrofossil data clarifies interpretational uncertainties in the pollen mapping. Also, the maps reveal patterns of occurrence of taxa that are cryptic in the pollen record, particularly for the Last Glacial Maximum. These studies of a select number of taxa provide an indication of the potential power of systematic comparison of mapped patterns of pollen and macrofossil data.

Other mapping efforts involving pollen and macrofossil data include those by Tarasov *et al.* (1998), Gunin *et al.* (1999), McLachlan and Clark (2004), and Edwards *et al.* (2005). The latter study shows

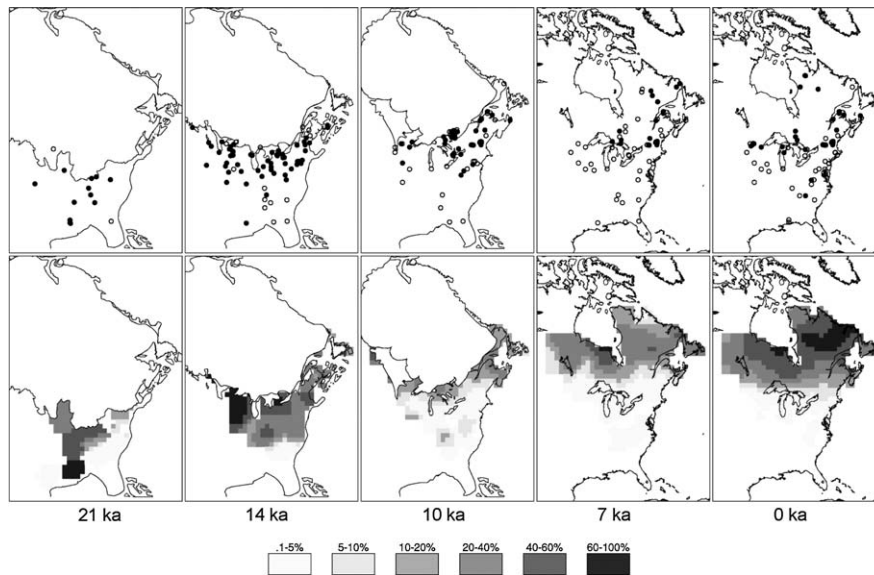


Figure 3 Mapped patterns of macrofossil presence/absence (top) and pollen percentages (bottom) of *Picea* in eastern North America since the Last Glacial Maximum. Open and closed circles in the top map respectively represent the absence and presence of *Picea* macrofossils at sites corresponding to the respective time periods. Time windows for the mapping are broad, encompassing approximately 1,000 years for the Holocene (10 ka, 6 ka, and the present), 2,000 years for the Late Glacial (14 ka), and 3,000 years for the Last Glacial Maximum (21 ka). Comparison of the maps shows general correspondence between pollen and macrofossils. Disappearance of macrofossils from some individual sites lags behind pollen declines during the northward retreat of the southern range limit of *Picea* in the Late Glacial and early Holocene. Local *Picea* populations occurred across a wide swath south of the ice margin during the early Holocene (10 ka), despite the poor representation of pollen in sediments of this period. These patterns probably arise from the persistence of local *Picea* populations in favorable sites (e.g., in wetlands and along lake margins) after regional, upland populations had declined. Modified from Jackson ST, Overpeck JT, Webb T III, Keatch SE, and Anderson KH (1997) Mapped plant macrofossil and pollen records of Late Quaternary vegetation change in eastern North America. *Quaternary Science Reviews* 16:1–70; and Jackson ST, Webb RS, Anderson KH, *et al.* (2000) Vegetation and environment in unglaciated eastern North America during the last glacial maximum. *Quaternary Science Reviews* 19:489–508.

how pollen and macrofossils can give contrasting and complementary views of regional vegetation composition and physiognomy.

Future Prospects

Plant macrofossils can serve as equal or even superior partners with pollen data in many contexts and for many questions. However, despite widespread application in Quaternary paleoecology and paleoclimatology, plant macrofossils continue to play a subservient role to pollen in most studies. The primary exceptions are fossil rodent middens and some studies of fluvial deposits, ombrotrophic bogs, and buried soils. Plant macrofossils have been largely underutilized in other contexts, particularly lakes. Carefully and creatively designed studies using macrofossils and pollen together can greatly advance our understanding of vegetational and biogeographic history. Macrofossil analysis should be incorporated at early stages of paleoecological study design, site selection, and core location rather than as an ad hoc addition to studies centering on pollen and/or

paleolimnology. This may require more sites (the best macrofossil sites may not be the most suitable for pollen records and vice versa) and multiple cores (to maximize macrofossil representation and temporal resolution simultaneously). Utilization of macrofossil-rich deposits, such as fluvial sediments, can lead to great advances. Such deposits record species poorly represented in lacustrine sediments and can yield large quantities of megascopic macrofossils capable of species identification. Pre-Quaternary paleobotanists focus on these kinds of sediments, with excellent results, and Quaternary paleoecologists would benefit from adopting similar approaches when possible. Plant macrofossil study in subtropical and tropical regions is vastly underdeveloped; few studies have assessed the potential for tropical macrofossil analysis. Continued development of public-access macrofossil databases (e.g., www.ncdc.noaa.gov/paleo/plantmacros.html) is needed to support synoptic-scale studies, and macrofossil analysts must continue to be active contributors and users of these databases. Finally, systematic studies of macrofossil taphonomy are needed to support inferences and test assumptions.

Table 2 Systematic studies using pollen and plant macrofossil data along elevational gradients in mountainous regions

- Anderson RS (1990) Holocene forest development and paleoclimates within the central Sierra Nevada, California. *Journal of Ecology* 78:470–489.
- Anderson RS (1996) Postglacial biogeography of Sierra lodgepole pine (*Pinus contorta* var. *murrayana*) in California. *Ecoscience* 3:343–351.
- Barnekow L and Sandgren P (2001) Palaeoclimate and tree-line changes during the Holocene based on pollen and plant macrofossil records from six lakes at different altitudes in northern Sweden. *Review of Palaeobotany and Palynology* 117:109–118.
- Davis MB, Spear RW, and Shane LCK (1980) Holocene climate of New England. *Quaternary Research* 14:240–250.
- Dunwiddie PW (1986) A 6000-year record of forest history on Mount Rainier, Washington. *Ecology* 67:58–68.
- Jackson ST (1989) Postglacial vegetational changes along an elevational gradient in the Adirondack Mountains (New York): A study of plant macrofossils. *New York State Museum and Science Service Bulletin* 465.
- Jackson ST and Whitehead DR (1991) Holocene vegetation patterns in the Adirondack Mountains. *Ecology* 72:641–653.
- Spear RW (1989) Late-Quaternary history of high-elevation vegetation in the White Mountains of New Hampshire. *Ecological Monographs* 59:125–151.
- Spear RW, Davis MB, and Shane LCK (1994) Late Quaternary history of low- and mid-elevation vegetation in the White Mountains of New Hampshire. *Ecological Monographs* 64:85–109.
- Tinner W and Kaltenrieder P (2005) Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. *Journal of Ecology* 93:936–947.
- Weng C and Jackson ST (1999) Late-glacial and Holocene vegetation and climate history of the Kaibab Plateau, northern Arizona. *Palaeogeography, Palaeoclimatology, Palaeoecology* 153:179–201.

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See also: **Plant Macrofossil Introduction. Plant Macrofossil Methods and Studies:** Mire and Peat Macros; Surface Samples, Taphonomy, Representation. **Plant Macrofossil Records:** Greenland; Holocene North America.

References

- Baker, R. G., Bettis, E. A., III, Denniston, R. F., *et al.* (2002). Holocene paleoenvironments in southeastern Minnesota—Chasing the prairie–forest ecotone. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177, 103–122.
- Betancourt, J. L., Van Devender, T. R. and Martin, P. S. (Eds.) (1990). *Packrat Middens: The Last 40,000 Years of Biotic Change*. University of Arizona Press, Tucson.

- Booth, R. K., Jackson, S. T., and Gray, C. E. D. (2004). Paleocology and high-resolution paleohydrology of a kettle peatland in Upper Michigan. *Quaternary Research* 61, 1–13.
- Campbell, D. R., Duthie, H. C., and Warner, B. G. (1997). Post-glacial development of a kettle-hole peatland in southern Ontario. *Ecoscience* 4, 404–418.
- Edwards, M. E., Brubaker, L. B., Lozhkin, A. V., and Anderson, P. M. (2005). Structurally novel biomes: A response to past warming in Beringia. *Ecology* 86, 1696–1703.
- Greenwood, D. R. (1991). The taphonomy of plant macrofossils. In *The Processes of Fossilization* (S. K. Donovan, Ed.), pp. 141–169. Columbia University Press, New York.
- Gunin, P. D., Vostokova, E. A., Dorofeyuk, N. I., Tarasov, P. E., and Black, C. C. (1999). *Vegetation Dynamics of Mongolia*. Kluwer, Dordrecht, The Netherlands.
- Huntley, B., Alfano, M. J., Allen, J. R. M., *et al.* (2003). European vegetation during Marine Oxygen Isotope Stage 3. *Quaternary Research* 59, 195–212.
- Jackson, S. T., and Booth, R. K. (2002). The role of late Holocene climate variability in the expansion of yellow birch in the western Great Lakes region. *Diversity and Distributions* 8, 275–284.
- Jackson, S. T., and Weng, C. (1999). Late Quaternary extinction of a tree species in eastern North America. *Proceedings of the National Academy of Sciences, U.S.A.* 96, 13847–13852.
- Jackson, S. T., and Whitehead, D. R. (1991). Holocene vegetation patterns in the Adirondack Mountains. *Ecology* 72, 641–653.
- Jackson, S. T., and Williams, J. W. (2004). Modern analogs in Quaternary paleoecology: Here today, gone yesterday, gone tomorrow?. *Annual Review of Earth and Planetary Sciences* 32, 495–537.
- Jackson, S. T., Overpeck, J. T., Webb, T., III, Keatts, S. E., and Anderson, K. H. (1997). Mapped plant macrofossil and pollen records of Late Quaternary vegetation change in eastern North America. *Quaternary Science Reviews* 16, 1–70.
- Jackson, S. T., Webb, R. S., Anderson, K. H., *et al.* (2000). Vegetation and environment in unglaciated eastern North America during the Last Glacial Maximum. *Quaternary Science Reviews* 19, 489–508.
- Lyford, M. E., Jackson, S. T., Betancourt, J. L., and Gray, S. T. (2003). Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecological Monographs* 73, 567–583.
- McLachlan, J. S., and Clark, J. S. (2004). Reconstructing historical ranges with fossil data at continental scales. *Forest Ecology and Management* 197, 139–147.
- McLachlan, J. S., Clark, J. S., and Manos, P. S. (2005). Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86, 2088–2098.
- McMullen, J. A., Barber, K. E., and Johnson, B. (2004). A paleoecological perspective of vegetation succession on raised bog microforms. *Ecological Monographs* 74, 45–77.
- Peñalba, M. C., and Payette, S. (1997). Late-Holocene expansion of eastern larch (*Larix laricina* [Du Roi] K. Koch.) in north-western Québec. *Quaternary Research* 48, 114–121.
- Peteet, D. M. (1991). Postglacial migration history of lodgepole pine near Yakutat, Alaska. *Canadian Journal of Botany* 69, 786–796.
- Singer, D. K., Jackson, S. T., Madsen, B. J., and Wilcox, D. A. (1996). Differentiating climatic and successional influences on long-term development of a marsh. *Ecology* 77, 1765–1778.
- Spicer, R. A. (1989). The formation and interpretation of plant fossil assemblages. *Advances in Ecological Research* 16, 95–191.
- Tarasov, P. E., Webb, T., III, and Andreev, A. A. (1998). Present-day and mid-Holocene biomes reconstructed from

- pollen and plant macrofossil data from the former Soviet Union and Mongolia. *Journal of Biogeography* 25, 1029–1053.
- Tinner, W., and Kaltenrieder, P. (2005). Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. *Journal of Ecology* 93, 936–947.
- Watts, W. A. (1978). Plant macrofossils and Quaternary paleoecology. In *Biology and Quaternary Environments* (D. Walker and J. C. Guppy, Eds.), pp. 53–67. Australian Academy of Science, Canberra.
- Watts, W. A. (1979). Late Quaternary vegetation of central Appalachia and the New Jersey coastal plain. *Ecological Monographs* 49, 427–469.
- Watts, W. A., and Winter, T. C. (1966). Plant macrofossils from Kirchner Marsh, Minnesota—A paleoecological study. *Geological Society of America Bulletin* 77, 1339–1360.
- Williams, J. W., Shuman, B. N., Webb, T., III, Bartlein, P. J., and Leduc, P. (2004). Late Quaternary vegetation dynamics in North America: Scaling from taxa to biomes. *Ecological Monographs* 74, 309–334.
- Willis, K. J., Rudner, E., and Sümegei, P. (2000). The full-glacial forests of central and southeastern Europe. *Quaternary Research* 53, 203–213.
- Willis, K. J., and Van Andel, T. H. (2004). Trees or no trees? The environments of central and eastern Asia during the Last Glaciation. *Quaternary Science Reviews* 23, 2369–2387.

PLANT MACROFOSSIL RECORDS

Contents

Arctic Eurasia

Arctic North America

Greenland

Holocene North America

Late Glacial Multidisciplinary Studies

Arctic Eurasia

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Arctic Vegetation History – Eurasia

Even though the number of Quaternary plant macrofossil records in the Arctic has increased considerably in recent years, the lack of fossil sites is still problematic. We are consequently still far from gaining a complete understanding of the complex interactions between Quaternary climate fluctuations and vegetation responses. The Arctic, in all likelihood, is the region that will be affected first and most by the predicted anthropogenic global warming (ACIA, 2004). Expected future vegetation changes, conversely, may affect global climates by their impact on albedo and permafrost. Arctic permafrost is climatically important because it forms a large and very susceptible sink for terrestrial carbon. The few macrofossil records already studied enable us, in conjunction with other disciplines such as palynology, chorology, and molecular genetic analysis, to delineate the consequences of past climate changes on high-latitude vegetation. Given the results already in hand, the response of arctic vegetation to global temperature fluctuations

depends highly on the direction and extent of changes in humidity. In the following discussion, the climatic causes of vegetation development during the Quaternary are highlighted.

The Arctic Today

Recent Vegetation

The Arctic is regarded as the region north of the polar circle, which, in consequence of the Earth's axial precession, is characterized by extreme seasonal fluctuations of incoming solar radiation, culminating in the semiannual alternation of polar day and polar night. Due to the low altitude of the Sun in the sky, the radiant flux density is very low. Nevertheless, the radiation balance is positive in summer and, owing to the polar day, the radiation supply during the growing season is among the highest in Eurasia. In a geobotanical sense, the Arctic is the region of tundra beyond northern treeline, which correlates approximately with the 10 °C mean July isotherm in West Eurasia or with the 12 °C July isotherm in the more continental East. As apparent by ancient *in situ* wood remains beyond the treeline, the northernmost tree limit shifted, during the Quaternary, numerous times far to the south and to the north of its modern location in response to climate fluctuations and coast-line shifts (MacDonald *et al.*, 2000; Fig. 1).