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Microscopic fungi as subfossil woodland indicators

Jonathan GA Lageard¹ and Peter A Ryan²

Abstract

An in situ subfossil oak trunk located on the Lancashire coastal plain in northwest England provided a unique opportunity for a detailed multiproxy investigation attempting to link precisely macrofossil evidence for a palaeowoodland to its microfossil depositional record. Dendrochronological analyses revealed that the tree died shortly after 4189 BC and that it was part of a mire-rooting woodland between 4433 and 4165 BC. Rising water levels are implicated in prolonged growth restrictions evident in this woodland and inferred subsequent widespread tree mortality. The novelty of the research reported here is in the use of microscopic fungal indicators to identify precisely a stratigraphic horizon that can be correlated with this specific palaeoecological event, providing a routine method for future correlations of macro- and microfossil records.

Keywords

dendrochronology, microscopic fungi, northwest England, pollen analysis, *Quercus* spp.

In loving memory of Valerie Beatrice Lageard, 1936–2013.

Introduction

Macrofossil evidence for mire-rooting and mire-proximal woodland in the British Isles growing during the mid and late Holocene is plentiful (Atkinson et al., 1999; Bennett, 1984, 1995; Birks, 1975; Boswijk and Whitehouse, 2002; Lageard, 1998; Lageard and Chambers, 1994; Lageard et al., 1999; Pilcher et al., 1995; Tallis, 1975). From these woodlands Scots pine (*Pinus sylvestris*) and oak (*Quercus* spp.) have most frequently been the focus of palaeoecological research owing to their widespread occurrence, preservation and suitability for dendrochronological study. Their investigation and interpretation are, however, frequently hampered by uncertainties, including the correlation of palaeowoodland layers to their pollen depositional record. The latter is particularly problematic because of insufficient resolution in pollen stratigraphies and imprecision associated with radiocarbon dating of both peat and wood samples (Baillie, 1991; Bell et al., 2001; Bridge et al., 1990; Eckstein et al., 2010; Gear and Huntley, 1991; Lageard et al., 1999). Despite the increasingly routine and widespread absolute dating of macrofossils (Boswijk and Whitehouse, 2002; Eckstein et al., 2009, 2010), uncertainties in precisely pinpointing the pollen record of palaeowoodlands persist.

Pollen analysis is a key and widely used technique for environmental reconstruction in Quaternary research (Fægri and Iversen, 1989; Lowe and Walker, 1997; Moore et al., 1991) and has seen considerable technical advancements in recent decades. Amongst these are the identification, quantification and comparison of non-pollen microfossils and other material that survive palynological laboratory procedures. Of particular importance has been the analysis of microscopic charcoal (Rhodes, 1998), testate amoebae (Charman et al., 2000) and also microscopic fungi (van Geel et al., 1989). Multiproxy investigations are now the norm and are capable of providing a sharper focus on the palaeoecological record.

The research presented here represents a detailed investigation of an in situ subfossil oak trunk (*Quercus* sp.) preserved in a peaty soil at Balls Farm, Lancashire, UK, one of 22 sites that form the nucleus of the prehistoric English dendrochronological record (Baillie, 1995; Brown and Baillie, 1992; catalogued in Atkinson et al., 1999). This field locality provided a unique opportunity to study an in situ palaeowoodland component and its closely associated palaeoecological record.

Method

Site location

Ball's Farm lies to the south of the Ribble Estuary approximately 1.5 km to the northeast of the small settlement of Banks (Figure 1) on former marshland that has been reclaimed over the centuries for agriculture. The west Lancashire coastal plain has witnessed considerable geomorphological change during the Holocene as a result of rising sea level and associated sedimentary accumulation, particularly in estuarine environments such as the Ribble (Plater et al., 1999; Tooley, 1978). Interbedded marine clays, peats and peaty soils are common and their disturbance during drainage or ploughing activities have revealed stumps and fallen trunks, the preserved remnants of former oak woodlands. Trunks and stumps are often removed, left in piles, sometimes burnt as domestic fuel, but in the Lancashire coastal plain they have also provided

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Figure 1. Location of the Ball's Farm sampling site northeast of the small settlement of Banks on the Lancashire coastal plain to the south of the Ribble Estuary.

invaluable material for building long dendrochronological records (Baillie, 1995; Brown and Baillie, 1992). Associated with these macrofossil remains are their preservational environments, anaerobic clays and peats which contain microfossil pollen and other palaeoecological material that have given insights into palaeo-woodland composition and dynamics (Tooley, 1978, 1985a, 1985b). An undergraduate dissertation at Manchester Metropolitan University (Durber, 2009) provided an initial opportunity to collect wood and sediment samples that have subsequently been the focus of more detailed analyses reported here.

Field sampling

An in situ oak trunk was found exposed in the side of a v-shaped drainage ditch approximately 0.5 km to the south of Ball's Farm. The exposed end of the trunk had been considerably weathered, but careful excavation of the trunk from the ditch side into the field and away from the ditch revealed generally sound preservation. Initial fieldwork involved recording the stratigraphy of the deposits in which the trunk was preserved and sampling a 1 m column of

sediment, a peaty soil, from a prepared vertical profile using two consecutive 0.5 m long monolith tins (Figure 2a). The monolith tins were located horizontally within 10 cm of the fallen trunk, and as such both can be regarded as part of the same stratigraphic profile. A disc sample was removed from the trunk using a chainsaw (Figure 2b), together with a sample of *Phragmites* peat that had taken the shape of the curved underside of the trunk (Figure 2c). The relative stratigraphic positions of the oak trunk, peaty soil monolith and *Phragmites* peat sample are shown in Figure 3.

Dendrochronology

Dendrochronology followed standard procedures (Hillam, 1998; Lageard et al., 1999). A radial section of the oak trunk disc was air-dried and then polished using sandpapers of increasing grit size in order to clearly see tree-ring boundaries under a binocular microscope. A series of ring-width measurements were then made from the oldest to the youngest preserved treering using a computer-based measuring system. Measurement series from two separate radii were combined to produce a mean ring-width

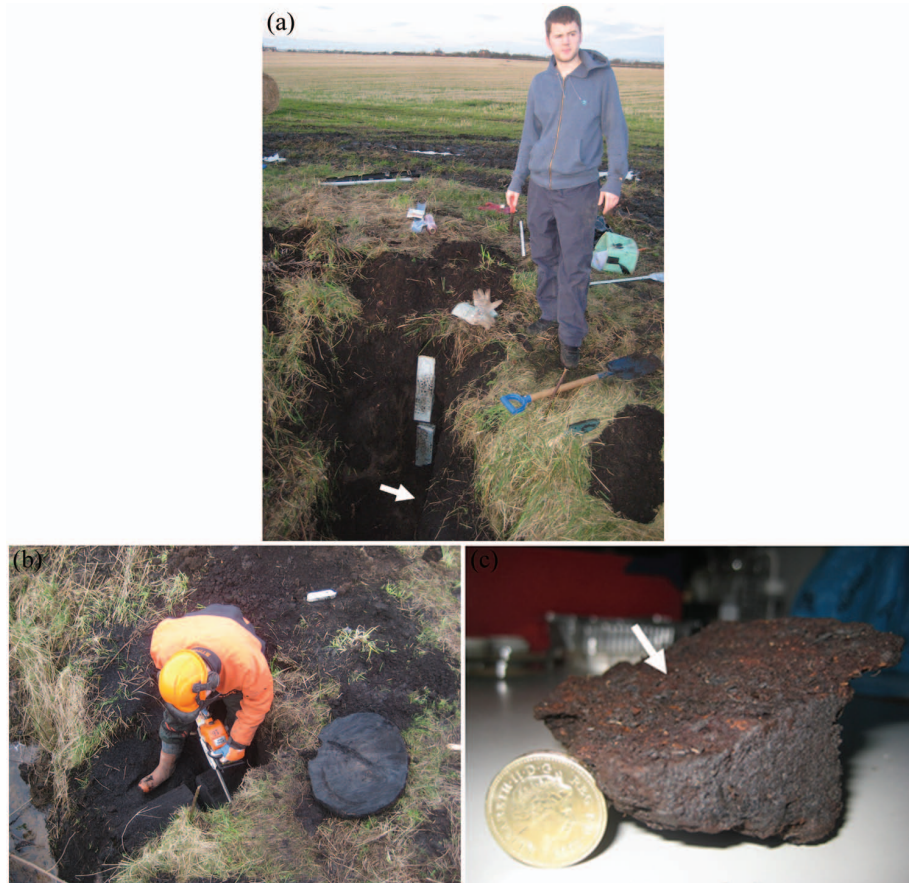


Figure 2. (a) Two 0.5 m long monolith tins containing clay and peaty soil from the stratigraphic section prior to their removal. (b) Sampling a disc from the fallen oak trunk using a chainsaw. (c) *Phragmites* peat sampled from underneath the bog oak disc removed in Figure 2b. Arrow indicates the upper peat surface moulded by the shape of the underside of the trunk.

record for the sample (BF01M), which was then crossmatched using Dendro software (Tyers, 1999) against the pre-existing site master chronology held by the Dendrochronology Laboratory, Queens University, Belfast.

Pollen analysis

0.5 cm³ samples for pollen analysis were taken from the peaty soil monolith at 40 mm depth intervals between 500 and 1020 mm below the modern field surface and at 20 mm intervals between 1020 and 1160 mm in order to detail the lowest peaty soils and clays underlying the oak trunk. Five contiguous 0.5 cm³ samples were taken from the *Phragmites* peat found directly underneath the trunk. The positions of samples taken for pollen are shown in Figure 3.

Preparation of samples followed standard procedures outlined in Moore et al. (1991). All samples were digested in potassium hydroxide before being passed through a 125 µm fine mesh sieve. For samples containing a higher proportion of clay, a heavy liquid flotation procedure using sodium polytungstate (specific gravity altered to 1.95 cm³; Zabenskie and Gajewski, 2007) was employed to separate pollen from minerogenic material. Samples then underwent standard acetolysis (acetic acid; then acetic anhydride-sulphuric acid) followed by dehydration (ethanol; then tert-butyl alcohol) prior to storage and mounting in silicon oil. Pollen grains were identified using the keys of Fægri and Iversen (1989) and Moore et al. (1991) and by comparison with reference material held in the Geography Laboratories, University of Manchester. A sum of at least 300 terrestrial pollen taxa was counted for each sample, with microscopic fungi recorded concurrently. Pollen and fungi are expressed as a percentage of total land pollen (TLP). Diagrams plotting the pollen, fungi and microscopic charcoal were produced using the TGView 2.0.2 software (Grimm, 2004).

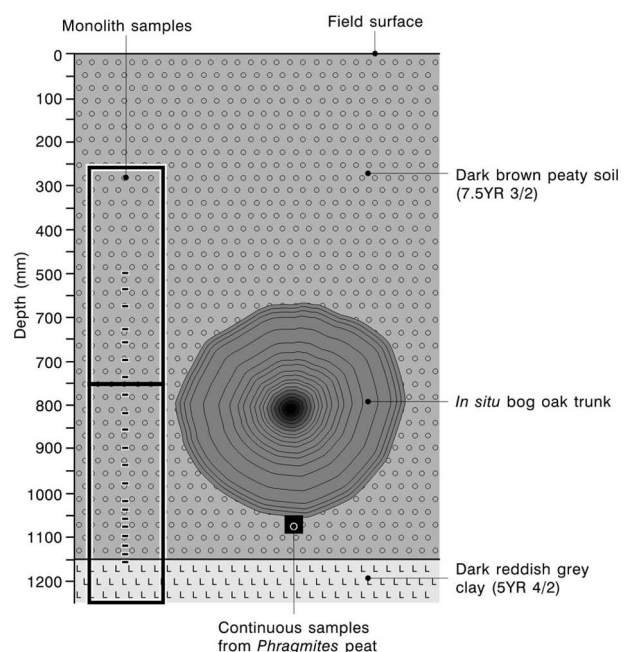


Figure 3. Characterization of the peaty soil monolith and relative stratigraphic positions of the oak trunk, *Phragmites* peat sample and depths sampled for subsequent laboratory analyses.

Microscopic fungi and charcoal

Fungi were identified by comparison with the descriptions and photomicrographs published in Bakker and van Smeerdijk (1982), Kuhry (1985), Pals et al. (1980), van der Wiel (1982), van Geel

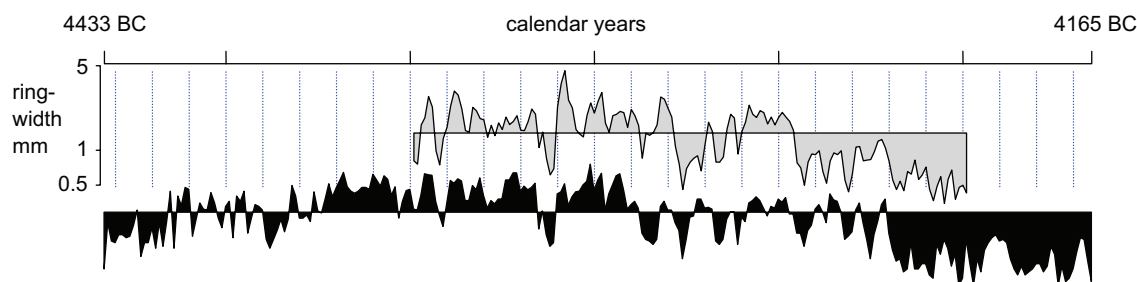


Figure 4. Mean ring-width record for sample BF01M, grey shading, dated to 4349–4199 BC against the pre-existing site chronology Balls Farm Mean, black shading (data courtesy of David Brown, Dendrochronology Laboratory, Queen's University Belfast).

(1972, 1978) and van Geel et al. (1981, 1983, 1989). Fungi are prefixed HdV- and are given the type numbers assigned by the Hugo de Vries Laboratory, Amsterdam (Feaser and O'Connell, 2010).

Charcoal was identified as fragments that were black, opaque and angular in form $>3 \mu\text{m}$ (Blackford, 2000; Rhodes, 1998). An areal estimate of charcoal was made by using a gridded eyepiece graticule. Charcoal area is expressed as relative to the numbers of terrestrial pollen grains (μm^2 pollen/grain).

Results

Dendrochronology

A 151-year mean record was created for the Balls Farm bog oak disc sample, laboratory code BF01M. BF01M was then compared using computer-assisted cross-matching against the pre-existing data, Balls Farm Mean (Atkinson et al., 1999; Brown and Baillie, 1992), a six-sample site chronology covering the period 4433 BC to 4165 BC (data courtesy of the Dendrochronology Laboratory, Queens University Belfast). Crossmatching of the two data series revealed a highly significant correlation (t 10.62) and subsequent visual verification confirmed their contemporaneity. The ring-width record for BF01M can therefore be assigned the calendar dates 4349 BC to 4199 BC, and the synchronization of the ring-width curves for BF01M and the Balls Farm Mean chronology is shown in Figure 4. Ring-width measurements commenced within five years of the pith and the absence of sapwood on BF01 and use of modern sapwood estimates (Tyers, 1999, cited in Hillam, 1998) means that this tree died after 4189 BC.

Pollen, fungi and charcoal

Phragmites peat (local pollen assemblage zone [LPAZ]-Bfb). The results of the pollen, fungi and charcoal analyses from *Phragmites* peat preserved beneath the oak trunk are shown in Figure 5.

The pollen assemblage of all samples is dominated by arboreal and shrub pollen (c. 85%). Dominant types are *Alnus* (25–37%), *Quercus* (16–24%), *Betula* (10–20%) and *Corylus avellana* (7–12%). Herbaceous types are less prominent, with only Cyperaceae (3–8%) and Poaceae (3–6%) recorded in significant amounts. Ferns are represented by *Polypodium* (2–5%) and Pteropsida indet. (1–5%). *Sphagnum* frequencies are very low until the final sample from immediately underneath the oak trunk (7%). There are rises first in *Fraxinus* (to 4%) peaking at 12.5 mm and then *Salix* (to 19%) peaking at 7.5 mm, corresponding to declines first in *Quercus* and then concurrently in *Alnus* and *Corylus*.

Interpretation. The pollen assemblage is indicative of a mixed *Quercus* woodland, with *Alnus* growing in wetter locations perhaps close to the sampling site with *Betula* an important secondary element. Scalariform plates from either *Alnus* or *Betula* wood remains are recorded in the lowest sample showing the local growth of at least one of these trees. *Corylus* may have grown as

an understorey shrub along with ferns. Openings or gaps appear to have occurred in this woodland allowing *Fraxinus*, *Salix* and then *Betula* to flourish. Scalariform plates from *Salix/Populus* wood remains are recorded as *Salix* pollen frequencies peaked and so probably confirm the local growth of *Salix* species. Records of Chenopodiaceae and Caryophyllaceae indicate the presence of disturbed ground as gaps in the canopy were formed that provided suitable habitats for *Plantago lanceolata* and Rubiaceae. Charcoal frequencies are low throughout suggesting that fire was not a significant element.

Microscopic fungi *Sordaria* (HdV-55A), *Cercophora* (HdV-112) and Sordariaceae (HdV-168) could indicate the presence of animal dung suggesting that browsing animals, wild or domesticated, could have had some impact on the bog oak woodland. Most of these sordariaceous taxa are coprophilous, but decaying wood and other plant material could provide suitable substrates for these fungal types (Lundqvist, 1972). *Kretzschmaria deusta* (HdV-117 or HdV-44) causes soft rot in trees (van Geel, 2001) and is recorded in three of the five samples. Disease may have played a part in creating some of the gaps in this woodland. *Pleospora* (HdV-3B), which occur on dead and decaying plant remains (Ellis, 1971, 1976; van Geel, 1978), *Coniochaeta xylariispora* (HdV-6), which occurs on decaying wood (van Geel, 1978), and *Chaetomium* (HdV-7A), which are common saprophytic cellulose decomposers (Dennis, 1977; Ellis and Ellis, 1988; van Geel et al., 2003) are recorded in significant numbers in the uppermost sample together with *Byssothecium circinans* (HdV-16), a parasite on woody substrates (van Geel and Aptroot, 2006). These would have grown on the dead and decaying wood provided by the oak trunk.

Peaty soil monolith. The results from the peaty soil monolith are shown in Figures 6 and 7. These diagrams have been divided into five local pollen assemblage zones (described individually below) based on changes in the pollen types.

LPAZ-BFa: 1160–1110 mm. Arboreal and shrub types form 95–98% of the pollen assemblage, with fern spores also well represented (13–34% – mainly Pteropsida indet. and *Polypodium*). In the lowest sample from the reddish grey clay, *Alnus* (44%), is the dominant arboreal type with *Corylus* (35%), *Quercus* (10%) and *Betula* (4%) also significant. With the change in stratigraphy from reddish grey clay to the peat soil at 1150 mm, *Alnus* declines to 20%, whilst *Quercus* increases to 25% and *Polypodium* peaks at 18%. Charcoal abundance also increases to $35 \mu\text{m}^2$ pollen $^{-1}$. *Corylus* increases, reaching 54% at 1120 mm.

LPAZ-BFb: 1110–1030 mm. *Alnus* expands (35–43%) whilst *Corylus* declines (24–11%). *Quercus* initially rises to 29%, but then falls back to 7% by the end of the zone. *Betula* increases to 13% before peaking at 43% in the uppermost level. *Ulmus* expands to 3% and is present throughout, whilst *Salix* peaks

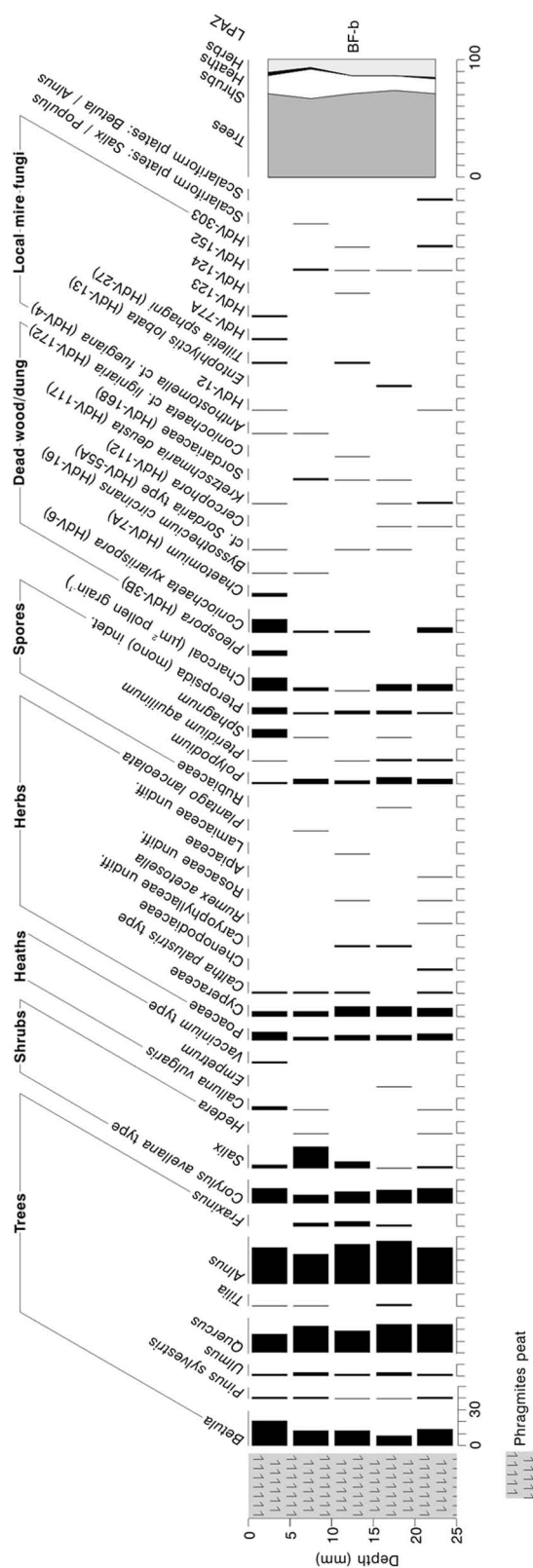


Figure 5. Pollen, spore, fungi and charcoal data from the *Phragmites* peat preserved beneath the oak trunk BF01M. Pollen and spore data are expressed as percentages of total land pollen.

(11%) at 1080 mm, a level at which *Fraxinus* is first recorded. Pteropsida indet. fall steadily and *Polypodium* is also less frequent. At 1080 mm there is synchronous occurrence of *Pleospora* (HdV-3B), *Kretzschmaria deusta* (HdV-117), *Microthyrium* (HdV-8B), *Coniochaeta xylariispora* (HdV-6), *Sordaria* (HdV-55A) and *Cercophora* (HdV-112), with *Byssosporium circinans* (HdV-16) recorded in the next sample level. Charcoal abundance remains low, but rises through the zone.

LPAZ-BFc: 1030–880 mm. *Betula* falls steeply to 21%, gradually rises but then falls away to 10%. *Alnus* increases to 33%. *Quercus* is initially less frequent, but then rises to 10–19%. *Salix* is reduced to scarce occurrences. *Corylus* increases (18–33%) and Poaceae (5–15%) are more frequent. *Calluna vulgaris* (9%) and *Sphagnum* (14%) both peak at 980 mm, but are less frequent by the end of the zone. *Urtica*, Chenopodiaceae, *Rumex acetosa* and Lamiaceae are also present. *Polypodium* reaches 7%, but Pteropsida indet. are less frequent. Charcoal abundance fluctuates, but there is a sharp peak to 26 $\mu\text{m}^2/\text{pollen}$ at 980 mm. *Coniochaeta xylariispora* (HdV-6), *Cercophora* (HdV-112) and cf. *Sordaria* (HdV-55A) peak at 1020 mm. Cf. *Sordaria* (HdV-55A) then increases to 5%, and *Coniochaeta cf. ligniaria* (HdV-172) are recorded towards the end of the zone. Scalariform plates from *Betula/Alnus* wood appear at the start and end of the zone.

LPAZ-BFd: 880–760 mm. *Betula* increases and is well-represented throughout (17–31%); *Quercus* is present at lower levels (4–6%), whilst *Alnus* and *Corylus* expand to 25% and 36%, respectively. *Calluna vulgaris*, briefly absent in the lowest level, shows increased representation from mid-way through the zone, with a continuous sustained presence also throughout LPAZ-BFe above. *Urtica*, *Rumex acetosa*, *Trifolium*-type and Lamiaceae are recorded. Poaceae pollen appears in much higher numbers (14–35%) and in the uppermost sample there is a sharp peak in *Polypodium* to 34%. *Sphagnum* spores increase from 1% to 14%, an expansion that is mirrored by declining charcoal representation from high levels of 73 $\mu\text{m}^2/\text{pollen}$. *Gelasinospora* (HdV-1) occurs for the first time in the diagram. *Sordaria* (HdV-55A) spores are present only in the lowest sample, but *Coniochaeta xylariispora* (HdV-6) rises to sustained high levels of 3–9% and *Cercophora* (HdV-112) is also present throughout (up to 2%) and *Sporormiella*-type (HdV-113) is recorded at 820 mm.

LPAZ-BFe: 760–500 mm. Shrub and arboreal pollen generally form a lower proportion of the assemblage in this zone (c.50–65%). *Betula* has generally lower representation (8–24%), whilst *Alnus* (12–15%) and *Corylus* (16–29%) have a sustained presence. *Quercus* increases (to 8–10%), *Fraxinus* is a more common occurrence, *Fagus* is recorded in levels at 700 and 740 mm, with *Sorbus*-type at 700 mm. *Calluna vulgaris* is more frequent (11–18%), as are Poaceae (11–28%) and Cyperaceae (2–6%). *Ranunculus acris*-type, *Urtica*, *Plantago lanceolata*, *Rumex acetosa* and *Melampyrum* are recorded more regularly, as are Chenopodiaceae, Caryophyllaceae, Brassicaceae and a range of Asteraceae. A single cereal-type grain (*Triticum* type) was recorded at 700 mm, with six cereal-type grains (*Triticum* type) recorded in the final sample level at 500 mm. *Sphagnum* continues to rise, peaking at 60% at 630 mm.

With the exception of the sample at 540 mm, charcoal is encountered at consistently high levels (above 35 $\mu\text{m}^2/\text{pollen}$) reaching over 70 $\mu\text{m}^2/\text{pollen}$ at 660 and 630 mm. *Gelasinospora* (HdV-1) at 660 mm and *Neurospora* at 630 mm are recorded. *Sordaria*-type (HdV-55A) is more frequent, but *Coniochaeta xylariispora* (HdV-6) is less so and *Cercophora* (HdV-112) and *Coniochaeta cf. ligniaria* (HdV-172) are absent from the zone. Local mire and aquatic types become more important in the non-pollen microfossil (NPM)

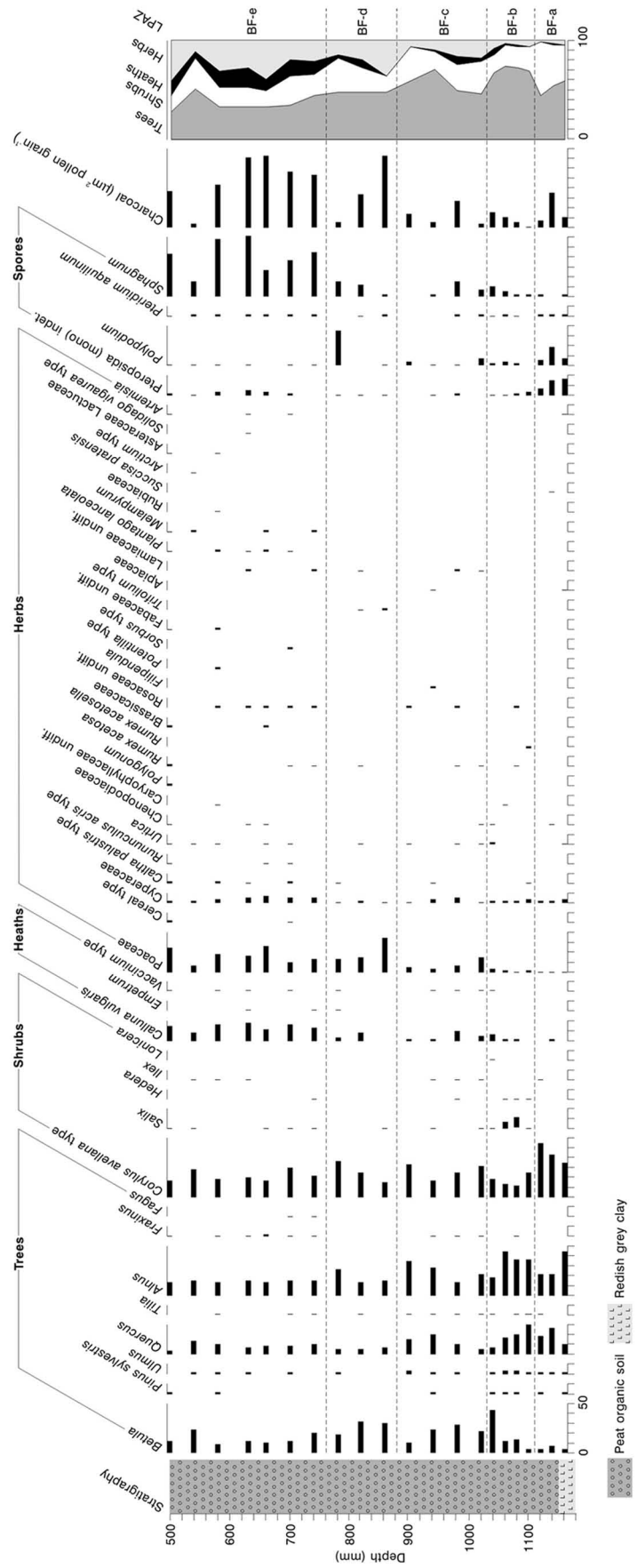


Figure 6. Pollen, spore and charcoal data for the peaty soil monolith retrieved from Balls Farm.

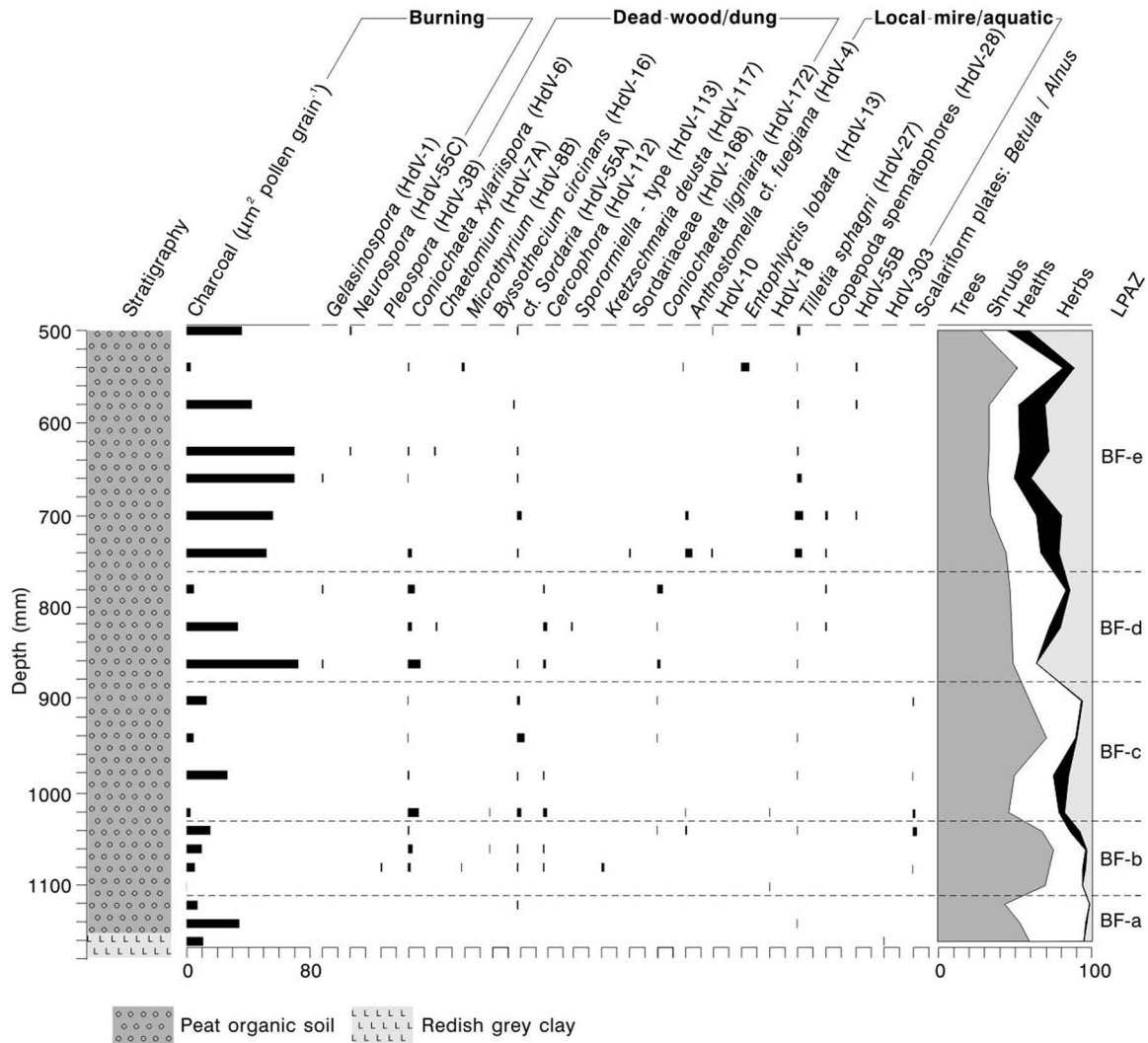


Figure 7. Charcoal and fungi data related to a summary of fluctuating percentages of tree, shrub, heath and herb pollen from the peaty soil monolith.

assemblage with *Anthostomella cf. fuegiana* (HdV-4; 5%), *Tilletia sphagni* (HdV-27; up to 6%) and *Entophlyctis lobata* (HdV-13; 6%) recorded in significant numbers.

Interpretation

LPAZ-BFa: 1160–1110 mm. The pollen assemblage represents dense woodland cover with *Quercus*, *Alnus* and *Corylus*, with dark, shaded habitats that encouraged ferns. *Ulmus* apparently never formed a significant component in this woodland. It is possible that some burning encouraged *Corylus* shrubs, but there were insufficient breaks in the canopy cover to allow heaths and herbaceous species to expand.

LPAZ-BFb: 1110–1030 mm. There is evidence for gaps appearing in the woodland canopy, but heathland and herbaceous species were apparently unable to take advantage. Fire was not prevalent at this time and it is possible that the area around the site became wetter, allowing *Alnus* and *Salix* to expand at the expense of *Corylus*. The lack of *Ulmus* pollen at the start of LPAZ-BFb may mean that 1030 mm marks the mid-Holocene *Ulmus* decline at Balls Farm.

The fungal assemblage indicates the presence of dead and decaying wood, occurring suddenly in the stratigraphy at 1080

mm. *Coniochaeta xylariispora* (HdV-6) and *Byssothecium circinans* (HdV-16) occur on woody substrates (van Geel and Aptroot, 2006), whilst *Pleospora* (HdV-3B) and *Microthyrium* (HdV-8B) which are saprophytic on plant remains (van Geel, 1978; van Geel and Aptroot, 2006) would also have been encouraged by an increase in dead and decaying wood. *Kretzschmaria deusta* (HdV-117) causes soft rot in trees (van Geel, 2001), perhaps suggesting that disease played some role in opening the woodland canopy in this zone. Innes et al. (2006) found an increase in *K. deusta* as *Ulmus* and other deciduous trees declined in the mid Holocene at Moel y Gerddi, north Wales, a pattern repeated at Bluewath Beck, North York Moors, north east England (Innes et al., 2010).

LPAZ-BFc: 1030–880 mm. There is a significant opening of the *Quercus-Alnus* woodland that allowed species of Poaceae to expand. *Calluna vulgaris* and other heathland species, as well as *Betula* and *Corylus* were also able to take advantage. Increased presence of animal dung, and through implication animal grazing, may be recorded in this zone. Most species of *Cercophora* (HdV-112) are coprophilous (Lundqvist, 1972) as are most species of *Sordaria* (HdV-55A; Ellis and Ellis, 1988). *Cercophora* (HdV-112) have been widely used as an indicator of increased animal dung in many palaeoecological studies (Innes and Blackford, 2003; Innes et al., 2010; Ralska-Jasiewiczowa and

van Geel, 1992; Ryan and Blackford, 2009, 2010; Schofield and Edwards, 2011; van Geel, 1986, 2001; van Geel et al., 1981), as have cf. *Sordaria* (HdV-55A; Bakker and van Smeerdijk, 1982; Feeser and O'Connell, 2010; Gauthier et al., 2010; van Geel et al., 1981; Willemsen et al., 1996). Occurrences of *Urtica*, *Rumex acetosa* and Lamiaceae could be a floristic response to increased grazing, with Chenopodiaceae able to grow in ground disturbed by animal trampling and rooting. Fire may have been significant in the wider landscape, but the absence of *Gelasinospora* (HdV-1) and *Neurospora* (HdV-55C) suggests that local fires were largely absent at the study site. Towards the end of the zone *Quercus-Alnus-Corylus* woodland appears to recover, reducing the habitats available for *Betula*, Poaceae and heathland species. The presence of *Sordaria* (HdV-55A) may indicate continued animal grazing even as the woodland regenerated, although *Sordaria* species can occur on a range of substrates including dead and decaying plant matter (Lundqvist, 1972). *Coniochaeta* cf. *lignaria* (HdV-172) is common on dung (Dennis, 1977; Munk, 1957) and was frequently recorded at a Roman period settlement site known to have had a large number of domesticated animals (van Geel et al., 2003), but is also common on dead wood (Dennis, 1977).

LPAZ-BFd: 880–760 mm. There is another opening in the *Quercus-Alnus-Corylus* woodland that allowed the significant expansion of species of Poaceae. *Betula* was also encouraged, perhaps along the woodland edge. Fire may well have caused this opening with the presence of *Gelasinospora* (HdV-1) indicating local burning at the site. Studies of Holocene peats have shown *Gelasinospora* (HdV-1) spores to have their highest frequencies in layers containing charcoal and charred plant remains (Innes et al., 2004; Kuhry, 1985; van Geel, 1978) and they have been used as an indicator of local burning in palaeoecological studies (Boyd, 1986; Innes and Blackford, 2003; Ryan and Blackford, 2009, 2010). Animal grazing apparently increased with *Coniochaeta* cf. *lignaria* (HdV-172) and *Cercophora* (HdV-112), this time accompanied by *Sporormiella* (HdV-113), an obligate dung genus (van Geel and Aptroot, 2006). *Sporormiella* (HdV-113) has been extensively used as a dung indicator in palaeoecological studies (e.g. Davis, 1987; Feeser and O'Connell, 2010; Gauthier et al., 2010; Hausmann et al., 2002; Hoan and Coles, 2000; Innes and Blackford, 2003; Schofield and Edwards, 2011; Speranza et al., 2000) and are probably the most reliable of all fungal spores in this respect (Blackford et al., 2006; Hoan and Coles, 2000). *Trifolium*, *Rumex acetosa*, Lamiaceae and *Urtica* must have grown in the grazed grasslands. *Sphagnum* was able to expand in wetter locations as the peat around the site developed, with species susceptible to infection by *Tilletia sphagni* (HdV-27) growing at the site. As burning receded, the woodland was able to regenerate, with *Polypodium* able to flourish, although *Quercus* did not recover.

LPAZ-BFe: 760–500 mm. A further reduction in woodland species, this time including *Betula*, is recorded in this zone. *Calluna vulgaris* and other heathland species expanded possibly onto the more acidic soils formerly occupied by *Betula*. The more open woodland may also have allowed space for *Fraxinus* as well as *Fagus* to grow. *Plantago lanceolata*, *Urtica*, *Rumex acetosa*, *Ranunculus acris* and *Melampyrum* may all suggest grazing of the grasslands and heathlands that developed in this zone (Behre, 1981), with Chenopodiaceae, Caryophyllaceae, Brassicaceae and the Asteraceae indicative of disturbed ground, some of which may have been caused by animal trampling. Increased Chenopodiaceae and Asteraceae may also be associated with marine transgression at this time, as salt marsh vegetation colonized closer to the study site.

The NPM assemblage does not, however, appear to corroborate the presence of animal dung. This apparent contradiction might be due to the different spatial scales covered by the pollen and fungal spore records, the latter shown at times to be sensitive

to very local-scale grazing (Blackford and Innes, 2006; Graf and Chmura, 2006). The pollen record may therefore reflect wider development of grazing resources, without concurrent local animal dung being reflected in the NPM assemblage at the site (Blackford et al., 2006; Ryan and Blackford, 2010).

The occurrence of *Triticum* type grains at 700 mm and 500 mm, as well as the disturbed ground indicators mentioned earlier, seem to indicate the cultivation of cereals in the time period represented by this zone. Although the separation of the pollen of wild from cultivated grasses is problematic (Tweddle et al., 2005), particularly in coastal areas (Joly et al., 2007), *Triticum* type is recognized with most certainty and conformed to the specific identification criteria of both Tweddle et al. and Joly et al.

A mixed arable and pastoral farming economy around Balls Farm is indicated by the pollen record in LPAZ-BFe. Fire again seems to have been an important factor in opening the woodland, but possibly more in the wider area than locally at the site, with only limited evidence of local burning. As burning receded at 540 mm, woodland was able to regenerate. *Sphagnum* expanded further, with mire types in the NPM assemblage suggesting that the sampling site became wetter.

Discussion

Defining subfossil woodland

Localized occurrences and also large tracts of subfossil woodland have routinely been exposed on and adjacent to mires throughout northwestern Europe, most commonly resulting from human impacts such as drainage, farming and peat harvesting (Boswijk and Whitehouse, 2002; Eckstein et al., 2009, 2010; Lageard and Chambers, 1994; Lageard et al., 1999; Pilcher et al., 1995). However, uncertainties persist as to whether individual subfossil trunks and stumps preserved in peats and other sedimentary units can be considered part of single layers, series of layers, or a continuum of natural woodland regeneration.

Munaut, writing about a subfossil *Pinus sylvestris* woodland uncovered near the Dutch coast, captures the sentiments of many researchers both before and also often after palaeowoodland investigations:

Quelle était la durée d'occupation du site par les pins? Devait-on admettre la croissance simultanée de tous les arbres, ou au contraire, l'existence de plusieurs générations successives? Comment s'étaient effectuées la naissance et la mort des arbres ...? [How long did the pines occupy the site? Did the trees grow at the same time or alternatively were there several successive generations? What was responsible for tree germination and mortality ...?]. (Munaut, 1966: 361)

Increasingly sophisticated palaeoenvironmental investigations in recent decades have revealed that past mire hydrologic and vegetational dynamics have been far from straightforward, with apparently synchronous event stratigraphies such as the *Grentzhorizont* c. 2.5 ka BP (Bell and Walker, 1992; Godwin, 1975) now considered misnomers. The advent of routine radiocarbon determinations, and more recently dating by dendrochronology, has revealed a more complex picture of mire colonization by woodland during the Holocene. Research in Ireland, England, Germany, the Netherlands and southern Sweden has shown tree colonization of raised mire systems in series of waves, dated absolutely by dendrochronology (Boswijk and Whitehouse, 2002; Eckstein et al., 2009; Edvardsson et al., 2012; Leuschner et al., 2002), permitting in-depth consideration of palaeowoodland form and dynamics and their relation to past climate change, evidence of increasing mire surface wetness and hydroseral pathways (Eckstein et al., 2010; Leuschner et al., 2002).

However, doubts persist when making direct comparisons between macrofossil and microfossil evidence for the same subfossil

woodland. Pollen data can reveal broad vegetational change relating to mire developmental stages (Eckstein et al., 2010), but in previous studies, the exact horizon/s that can be equated to a specific palaeowoodland macrofossil component remain unclear, despite attempts to isolate and date the pollen fraction in palaeo-ecological samples (Brown et al., 1989). Bridge et al. (1990) found a series of peaks in pine pollen in Scottish peat profiles, but relating these to adjacent pine stumps was 'far from straight forward' (Bridge et al., 1990: 91), largely because of uncertainties resulting from radiocarbon age estimates for both micro- and macrofossils. Similar difficulties were experienced by Lageard et al. (1999), despite achieving an absolutely dated site ring-width chronology containing 26 subfossil pine trees. Further evidence supporting the vagaries of the pollen production of local mire-rooting woodland has been provided by Hall et al. (1994), who clearly showed that a phase of dendrochronologically dated pine trees in Ireland could only have been represented in the pollen record by pine pollen <5% (total land pollen), owing to protracted low pollen representation of the taxon. This finding, although highly significant in its own right (and also in relation to the impact of Hekla 4 tephra), is a precise pollen record by default, rather than one achieved through stratigraphic pin-pointing.

In other investigations attempts have been made to relate individual tree stumps to their adjacent stratigraphic context. Careful excavation and recording of a subfossil oak stump on the Gwent Levels, south Wales revealed 'a very thin organic clay band ... interpreted as the top of the old land surface on which the oaks grew' (Bell et al., 2001: 44). This tree was a component of a 420-year floating ring-width chronology (dated by radiocarbon to 6270–6090 cal. BC), but although the thin organic clay is highly likely to represent a contemporaneous woodland floor, 'interpretation' is no substitute for conclusive proof of correlation with a contemporaneous pollen record.

Uncertainties also linger concerning the stratigraphic homogeneity of palaeowoodland 'layers' or continua. In Ireland dendro-chronologically dated subfossil pine stumps can be viewed in situ in peat faces produced by hand peat cutting, but their calendar ages appear to defy the law of superposition (D Brown, personal communication). This may allude to a phenomenon whereby macrofossils of differing densities, depending on size and age, can move selectively within the wet/unconsolidated peat matrix.

Regional palynological context

Despite a paucity of radiocarbon-dated vegetation reconstructions in the Lancashire coastal plain, it is possible to gain a generalized picture of regional woodland development during the Holocene. Early-Holocene woodlands appear to have been dominated by *Betula* spp. and *Pinus sylvestris* (Hibbert et al., 1971), which were replaced in the mid Holocene by a *Quercus* spp.–*Alnus glutinosa*–*Corylus avellana* climax, including *Ulmus glabra* and *Tilia cordata* components (Cundill, 1984; Hibbert et al., 1971; Innes and Tomlinson, 1983; Tooley, 1978, 1980, 1985a, 1985b).

Although macrofossil remains of the mid-Holocene woodland have been extensively preserved (Atkinson et al., 1999), it has been impossible to identify and to study in detail the dynamics of local woodland in the Lancashire coastal plain from pollen records alone (Innes et al., 1999). It is, however, possible to make an interesting observation from the pollen data presented in this paper. Woodland recorded in zones BF-a and BF-b contained significant *Quercus* and *Corylus* components with only limited evidence of animal grazing. Conversely, the strongest floral and mycological grazing signals are found in BF-d and BF-e when *Quercus* pollen representation is reduced. This suggests animal grazing is not necessarily a prerequisite for the creation of open wood parkland (Vera, 2000) in which *Quercus* and *Corylus* were able to regenerate concurrently.

Ball's Farm bog oak woodland demise: Fungal indicators

Oak BF01M was one component of a mire-rooting woodland that grew during the period 4433–4165 BC at Ball's Farm, although this woodland undoubtedly grew during a longer period than indicated by tree ring-width records alone. The final 21 years (average ring-width 0.55 mm) of the BF01M 151 year growth record (average ring-width 1.38 mm) coincides with a period of depressed growth also reflected in the last 56 years of the Belfast Balls Farm Mean chronology (Figure 4).

This picture of declining mire oak woodland is enhanced by stratigraphic comparison of BF01M and its closely associated microfossil fungal record. BF01M lay on *Phragmites* peat at a depth of 1050 mm below the current land surface (Figure 3), and it is immediately pre-dated by the sudden appearance of dead wood and dung microfossil fungal indicator species at 1080 mm in adjacent peat stratigraphy. This fungal assemblage contained *Pleospora* (HdV-3B), *Kretzschmaria deusta* (HdV-117), *Microthyrium* (HdV-8B), *Coniochaeta xylariispora* (HdV-6), *Sordaria* (HdV-55A) and *Cercophora* (HdV-112), and appears to be closely associated with the mortality of bog oak BF01M and its wider mire woodland.

There is therefore not only clear evidence for protracted woodland decline from reductions in tree growth, but also the sudden appearance of a diverse microscopic fungal spore assemblage isolates for the first time, a specific stratigraphic level associated with widespread tree mortality. The 30 mm gap between the appearance of fungal dead wood/dung indicators and the base of BF01M in the stratigraphy may reflect a period of standing dead-wood prior to the tree trunk falling and being incorporated within the peat deposit.

Bog oak mortality: Subfossil trees and pollen record

Northwest European bog oak chronologies can be utilized to define periods of reduced growth and also phases of tree mortality. The latter are interpreted as tree responses to deteriorating environmental conditions. Narrow ring-width series have in many studies been related to increasing mire surface wetness and climatic deterioration (Baillie, 2000; Edvardsson et al., 2012; Kelly et al., 2002; Leuschner et al., 2002; Pilcher, 1990; Pilcher et al., 1996), although other mechanisms for instance human intervention cannot be ruled out in some circumstances.

In a stratigraphic context, bog oak woodland is invariably associated with the fen carr stages in wetland landscape development, with trees either rooting directly in mineral soils or on shallow peats (Bell et al., 2001; Eckstein et al., 2010; Lageard and Chambers, 1994). Macrofossil remains of these woodlands are often overlain by poorly hummified *Sphagnum* peat, implicating elevated water-tables and concurrent rapid peat growth in tree mortality, precipitating a switch from fen to ombrotrophic raised mire (Eckstein et al., 2010).

In England, prehistoric bog oak woodland has been uncovered in many low-lying areas, including East Anglia and on the Lancashire coastal plain. Dendrochronological records obtained from these woodlands have permitted the construction of an English bog oak chronology (Brown and Baillie, 1992). Trees comprising Balls Farm Mean (4433–4165 BC) are an early constituent of this chronology, and Figure 4 shows that tree BF01M, sampled in the current research, grew generally well for over 100 years before being subjected to sustained growth reduction. This phase of poor growth is also evident in the responses of trees comprising the Balls Farm Mean chronology and is consistent with the fungal evidence for widespread tree mortality probably caused by rising water levels.

Pollen stratigraphy at Balls Farm records a distinct rise in *Salix* (up to 11% TLP) together with the sudden appearance of fungal

indicators of woodland mortality at 1080 mm depth. The *Salix* rise is immediately followed by increased *Alnus* and subsequently a sharp rise in *Betula*. This pollen signature can be specifically associated at this site with local woodland dynamics at a time of widespread mortality in fen oak woodland, dated by dendrochronology to shortly before 4100 BC. As noted previously, the quality of dating control in vegetation records from the Lancashire coastal plain is largely poor, but similar *Salix–Alnus–Betula* sequences are found at Hoscarr Moss, northeast of Liverpool, leading to the possible conclusion of local fen woodland demise either side of the elm decline at that site (Cundill, 1984). In contrast, no pollen woodland mortality signatures are discernible in the radiocarbon-dated record from Red Moss near Bolton (Hibbert et al., 1971), possibly relating to its location further inland and differing local hydrogeology and vegetation dynamics.

The woodland mortality signature in the pollen record at Balls Farm is accompanied by a modest rise in charcoal in zone BF-d, which in turn is post-dated by an expansion in *Calluna*. The pollen and fungal spore evidence suggest the establishment of local pastoral farming, with fire used initially in creating woodland openings, with later deliberate burning to maintain and manage *Calluna* heath as grazing for animals.

Conclusion

Subfossil trees provide intriguing and tangible evidence of pre-historic woodland and their precise dating using dendrochronology in recent years has revealed wave-like colonization of mire surfaces throughout northwestern Europe during the Holocene.

Correlating these woodlands accurately with their pollen depositional records has until now proved illusory because of dating uncertainties inherent in obtaining radiocarbon dates from peat samples. The research reported here incorporates microscopic fungi in a multiproxy palaeoecological investigation and in doing so provides for the first time a routine method for isolating horizons associated with widespread tree mortality, precisely linking micro- and macrofossil records.

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