



# The Ecology of Late Mesolithic Woodland Disturbances: Model Testing with Fungal Spore Assemblage Data

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Pollen, charcoal and fungal spore analysis of the base of a radiocarbon-dated peat profile at North Gill, North York Moors, N.E. England, provides detailed evidence for an episode of fire-disturbance of woodland at c. 6300 BP (uncalibrated), within the Late Mesolithic cultural period. As with other similar episodes in the uplands of Britain, the pollen data documents post-disturbance regeneration to woodland through ruderal and grassland herb, heath and successional shrub plant communities. Such seral ecological changes have previously been interpreted as the desired result of deliberate disturbance by Mesolithic foragers, as part of a conscious land-use strategy designed to attract ungulate populations to the disturbed areas and increase hunting efficiency and yield. Fungal spore analyses through the North Gill disturbance phase support the indirect ecological inferences from the pollen and charcoal data, provide the first circumstantial evidence of animal concentration in post-fire disturbed areas during the Late Mesolithic and so test and support the basic ecological premise of the Late Mesolithic fire ecology/land-use model.

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## Introduction

In recent decades received wisdom regarding the ecological context of Mesolithic hunter-gatherers in Britain has changed from a minimalist view in which human influence on Holocene forests was of only the most ephemeral kind to one in which Mesolithic land-use may well have had significant and lasting impacts upon the development of vegetation communities. The great increase in the volume and detail of palynological analyses, supplemented by other environmental proxies such as charcoal data, has shown that throughout the Mesolithic period woodlands were subject to periodic disturbance (Zvelebil, 1994; Simmons, 1996). The pollen evidence suggests that these events represent the creation of localized breaks in the tree cover or at least the thinning of the forest matrix (Edwards, 1982), followed by the regeneration of some form of woodland after succession through seral communities. Most disturbances are small-scale, sporadic and temporary in nature, although several are repetitive and/or severe. Many are associated with visible or microscopic charcoal, so that fire seems to have been a regular mechanism of vegetation change (Edwards, 1990; Innes & Simmons, 1988, 2000; Simmons & Innes, 1996b) and while the majority of these disturbances have been recorded from upland contexts, an increasing proportion has been reported

from lowland locations (Simmons & Innes, 1995, 1987; Zvelebil, 1994; Simmons, 1996).

### *Disturbance ecology and the Late Mesolithic*

The ecological effects of woodland fire have been described by many authors (Ahlgren, 1974; Ahlgren & Ahlgren, 1960; Clark & Robinson, 1993; Whelan, 1995). Opening of the forest canopy, removal of undergrowth and dead wood and perhaps even the killing of trees dramatically increases the input of light to the forest floor, stimulates profuse sprouting of surviving forest-edge shrub taxa and sets in train rapid growth of grasses, herbs and successional shrub communities until the tree canopy is restored. These modern field observations concur with pollen stratigraphies from disturbance phases of Mesolithic age, where initial post-burn taxa like *Melampyrum* and a suite of ruderal weeds are replaced by *Calluna*, *Corylus*, *Salix* and other regeneration shrubs until frequencies of forest trees return to their pre-disturbance values and the heliophyte taxa fade from the pollen record (Behre, 1981; Edwards, 1998). Compared with undisturbed forest, the range and quantity of edible plant foods for humans is much greater in this post-fire vegetation (Ahlgren & Ahlgren, 1960; Zvelebil, 1994). This is even more so for wild ungulates, however, with

grazing and browsing resources dramatically increased (Heinselman, 1973; Bendell, 1974; Mellars, 1976). This has been best documented for deer (Leopold, 1950; Dills, 1970; Chaplin, 1975), probably the most favoured Mesolithic game animal (Jarman, 1972; Evans, 1975; Bay-Petersen, 1978), but would also have been true for elk, aurochs and pig (Grigson, 1982; Legge & Rowley-Conwy, 1988). All of these game animals may have concentrated within highly productive, post-disturbance feeding areas and were in turn exploited by humans, greatly improving hunting efficiency and yield.

The apparent ubiquity of forest disturbance by fire during the Mesolithic and the potential material benefits of the ecological changes which it will have caused have encouraged the view that Mesolithic people were probably responsible for starting many or even most of the fires. The degree to which this human application of fire to the woodland landscape was accidental, casual, deliberate/sporadic or deliberate/systematic remains the subject of much debate (Bennett *et al.*, 1990; Caseldine & Hatton, 1993; Moore, 1997, 2000; Welinder, 1978, 1989). The possibility of systematic human fire-setting, however, has allowed the formulation of models in which Late Mesolithic groups were operating a sophisticated land-use system which involved manipulation of the vegetation and so some control of food production and distribution, managing the forest ecosystem to maximize the yield of a range of resources (Jacobi *et al.*, 1976; Jacobi, 1978; Mellars, 1975; Mellars & Reinhardt, 1978; Simmons, 1975*a, b*, 1979, 1993, 1996; Mason, 2000). These models are supported by data showing that fire was habitually applied to the landscape by recent hunter-gatherers and horticulturalists (Lewis, 1982), most relevantly in the temperate deciduous forests of North America (Russell, 1983; Myers & Peroni, 1983; Patterson & Sassaman, 1988; Clark & Royall, 1995; Delcourt *et al.*, 1998), discussed by Moore (2000).

#### *Testing the model*

The general acceptance that Mesolithic people had both the potential means and motive to cause significant opening of closed-canopy forest has encouraged an almost routine acknowledgement in papers on early and mid-Holocene vegetation history that even small scale pollen fluctuations or minor increases in microscopic charcoal may well reflect the impact of Mesolithic land-use upon the environment. Although the recorded number and distribution of pre-Neolithic disturbances steadily increases and the weight of palaeoecological data seems compelling (Zvelebil, 1994), the evidence that Mesolithic foragers were actually responsible for these events is unavoidably circumstantial, as is equally the case for many "clearance" events in later prehistory. Even when Mesolithic artifacts are directly stratified with charcoal and pollen disturbance phases (Dimbleby, 1962; Jacobi *et al.*,

1976; Cloutman, 1988; Simmons & Innes, 1988) the association may be coincidental, or at least Mesolithic people may have been attracted to the disturbed area without having created it. Proponents of the Mesolithic fire-ecology land-use hypothesis have accepted that a proportion of disturbances will have been caused by natural processes such as lightning strike or storm (Simmons & Innes, 1987; Simmons, 1996) and authors have recently urged caution regarding evidence for any systematic Mesolithic strategy of disturbance and vegetation manipulation (Tipping, 1996; Brown, 1997). Broad inferences regarding human impact and fire ecology need to be refined by the focused recovery of less ambiguous palaeoecological data (Edwards & Whittington, 2000; Innes & Simmons, 2000) so that multi-causal hypotheses, including the Mesolithic land-use model, may be tested. In this paper we test the proposition, at present inferred theoretically and from modern analogues, that the post-fire regeneration vegetation within early to mid-Holocene British woodlands attracted increased concentrations of large herbivores, a key element in the Mesolithic fire ecology/land-use model.

We have used fungal spore analysis as a new proxy to complement pollen and charcoal data, as fungal growth is stimulated after woodland fires (Ahlgren & Ahlgren, 1960; Whitehouse, 2000) and many taxa are specific ecological indicators of relevant factors such as burning, dead wood or animal dung (van Geel, 1978, 1986; Blackford, 1998; Hoaen & Coles, 2000). Spore frequencies of dung fungi in particular should demonstrate any increases in herbivore populations in these supposed preferred feeding areas and show at what stages of vegetation succession these occurred.

#### **The Site**

The site chosen for investigation was North Gill (NZ726007) on Glaisdale Moor, where a stream has cut sections through the peat cover of the Central Watershed of the North York Moors (Figure 1). This upland plateau in north-east England contains many Late Mesolithic flint sites and several peat sites which preserve charcoal and "disturbance" pollen evidence of Late Mesolithic age (Spratt, 1993). It is an area which figured largely in the formulation of the fire ecology/land-use model (Simmons, 1975*a, b*). North Gill is by far the most intensively studied site, publication of its Late Mesolithic palaeoecological record having started thirty years ago (Simmons, 1969*a, b*) after which the results of increasingly detailed and focused research have been reported in a series of papers (see Innes & Simmons (1999, 2000) for a site bibliography). Many pollen profiles within a small area at the site, including several in which millimetre interval sampling has revealed pattern and structure in "disturbance" phases at almost annual time-scales, has meant that the detailed palaeoecological history at North Gill in the

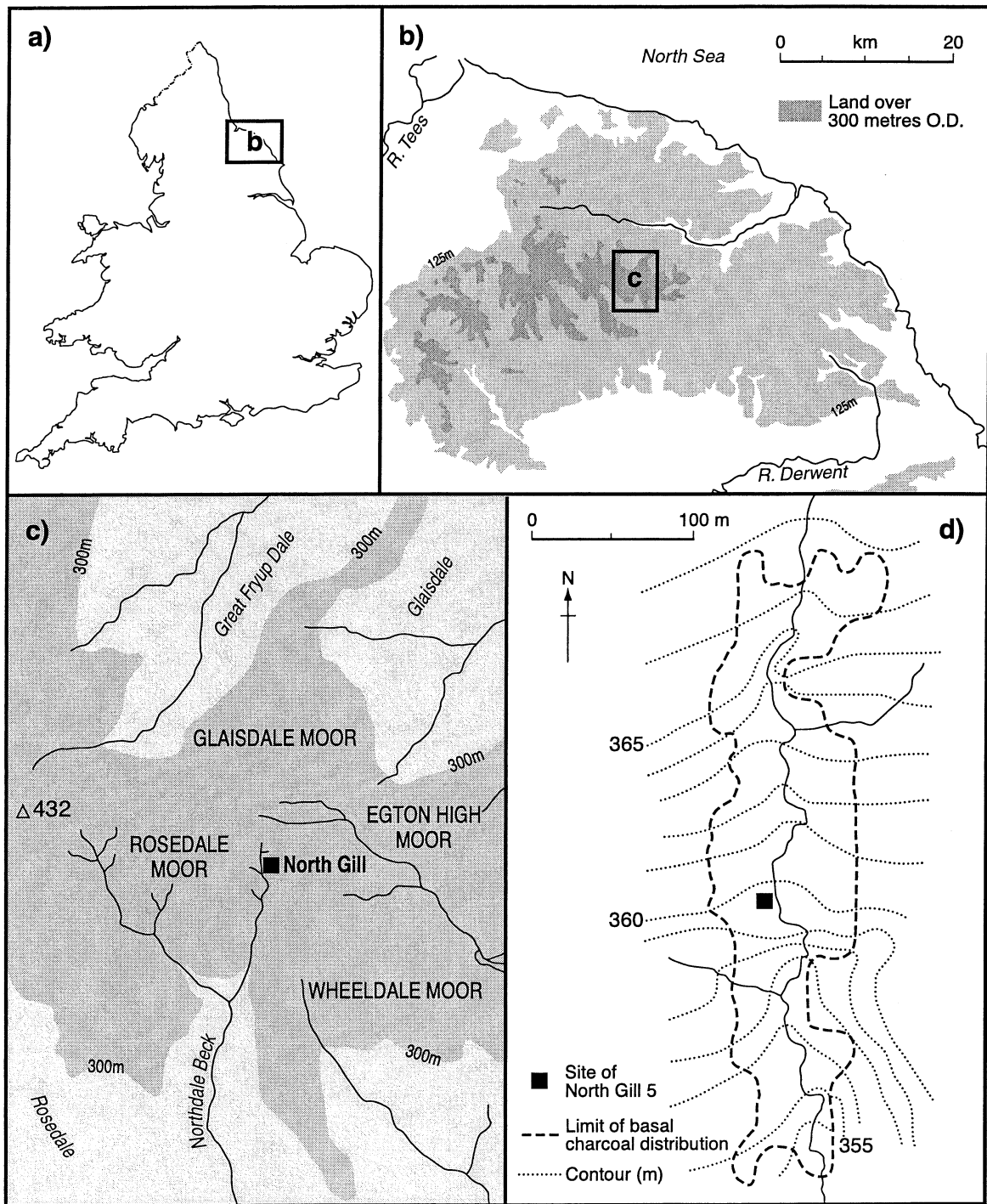


Figure 1. Location of the study site of North Gill 5 and of the North York Moors within England and Wales. The limit of the basal charcoal layer is also shown.

Late Mesolithic is probably better known than for any comparable location. The site therefore acts as a field station where research hypotheses can be tested within a well established palaeoecological databank. Several exposed peat sections at the site include charcoal-rich peat at the base which contains a classic “fire disturbance” pollen signature of ruderal and pyrophyte

herbs followed by seral regeneration through grass, heath and shrub communities to the eventual re-establishment of woodland. One of these basal disturbance phases, at North Gill 5 (Figure 1), was selected to study the fungal spore data, using the original pollen slides and the original pollen and charcoal counts which had previously been published



(Turner *et al.*, 1989, 1993; Innes & Simmons, 2000). At 99.5 cm a charcoal-rich peat about 4 cm thick, with most charcoal near its base, overlies a sandy, minerogenic unit which is the pre-peat soil and which contains charcoal in its upper part. This basal charcoal-rich peat unit, which contains a high silt fraction, is traceable laterally. Its extent, and so the initial area of peat accumulation at the site, is shown on Figure 1. In a section only a few tens of metres away from North Gill 5 (Simmons, 1969*a, b*) it has been dated to  $6316 \pm 55$  BP (BM-425) and this is almost certainly also the age of the base of the organic profile at North Gill 5. No direct dating is available for the lower section of North Gill 5 discussed in this paper, although a date of  $5760 \pm 90$  BP at 73 cm (Turner *et al.*, 1993) supports the inferred age of the basal peat. It therefore lies securely within the Late Mesolithic period, a millennium before the dates of both the final Late Mesolithic and the earliest Neolithic archaeological sites in this area (Spratt, 1993). The *Ulmus* decline in the North York Moors upland is even later, at around 4700 BP (Innes, 1999).

## Methods

Samples were taken at 1-cm intervals and prepared using standard pollen preparation techniques, including alkali digestion, sieving at 180  $\mu\text{m}$ , hydrofluoric acid digestion and acetolysis (Moore *et al.*, 1991). Fungal spores have been found to be common in pollen slides prepared in this way and their concentrations are not adversely affected by pollen preparation techniques. Fungi were identified using the published illustrations and descriptions of van Geel (1978), van Geel *et al.* (1981, 1983) and checked by van Geel and others at a workshop in January 2001 (cf. Mighall, 2001).

## Results

### *Pollen, micro-charcoal and fungal analyses*

The pollen and micro-charcoal evidence through the basal disturbance phase at core North Gill 5B is shown in Figure 2, calculated as percentages of a dryland tree pollen sum from which *Alnus* is excluded because of its potential pollen superabundance in streamside locations. One hundred and fifty dryland tree pollen were counted in the sum at each level, providing a total land pollen count of at least 500 in each case. Figure 2 continues into the higher part of the pollen diagram, in which *Alnus* and *Quercus* rise to high percentages and dominate the assemblage after regeneration is complete. Previously counted pollen levels above 84 cm are not shown. The diagram is divided into seven phases on the basis of disturbance, transition or regeneration characteristics. The fungal spore evidence from the same levels as the pollen data is shown in Figure 3, calculated as percentages of total fungal spores. Fungal

spores were much less abundant than pollen in every level, but at least 100 fungal spores and non-pollen microfossils were identified in each case. Fungi and other non-pollen microfossils are identified taxonomically where possible and fungal catalogue Type-numbers are shown in all cases (van Geel, 1978). Their ecological affinities are also shown where these are known or may be surmised from previous research. Micro-charcoal data are included, calculated as percentages of the total fungal spore count. Diagram description phases are common to both diagrams.

(a) (99 and 98 cm) This early post-disturbance sediment is rich in macro- and micro-charcoal, *Quercus* and *Alnus* pollen frequencies are very low and peak *Melampyrum* percentages occur, almost reaching 30% of tree pollen. *Rumex* also peaks in this basal phase and high *Sphagnum* spore frequencies reflect processes of paludification and local peat formation. *Betula* and *Corylus* frequencies are very high and probably represent increased flowering and sprouting of populations at the edge of the opened area and those which survived within it. *Ulmus* percentages are steady at a little over 20% here and in almost all succeeding phases, as though local elm populations were not greatly involved in this burn and its consequences.

The pollen and charcoal evidence of burning is supported by high frequencies of the Sordariaceous fungus *Neurospora* (55C) and *Gelasinospora*. Percentages of Type 55A and also 55B are high, both reflecting meso- to eutrophic conditions and the latter also perhaps the minerotrophic nature of the lowest peat and buried soil (van Geel, 1978). Type 16C is important at the start of the phase and may be associated with local grasses (van Geel, 1978) as peat began to form. Spores of the dung fungus *Sporormiella* and of Type 18A occur at around 20% in the phase.

(b) (97 cm) This transitional phase shows a reduction in the inferred post-burn herb taxa *Melampyrum* and *Rumex*, although still high charcoal frequencies indicate continued charcoal transport into the peat-forming area. *Corylus* values remain very high but *Betula* declines as *Quercus* and *Alnus* begin to recover. *Pinus* is still high.

Little change occurs in the fungal assemblage except that Type 55A is reduced and dung or dead wood fungi *Chaetomium* (7A), *Coniochaeta* cf. *lignaria* (172) and *Coniochaeta xylariispora* (6) increase. 16C no longer occurs.

(c) (96, 95 and 94 cm) Steadily increasing *Quercus* and *Alnus* frequencies and a consistent *Tilia* record reflect continuing regeneration of these trees, as do consistent values for *Lonicera* and *Polypodium*. As a consequence *Betula*, *Pinus* and particularly *Corylus* decline. Higher *Salix* and also some members of the increased undifferentiated Rosaceae curve indicate the shrub stages of the regeneration complex. High Gramineae, Cyperaceae and *Pteridium* frequencies indicate development of ground cover in the more open areas of the site. The start of a consistent *Succisa*

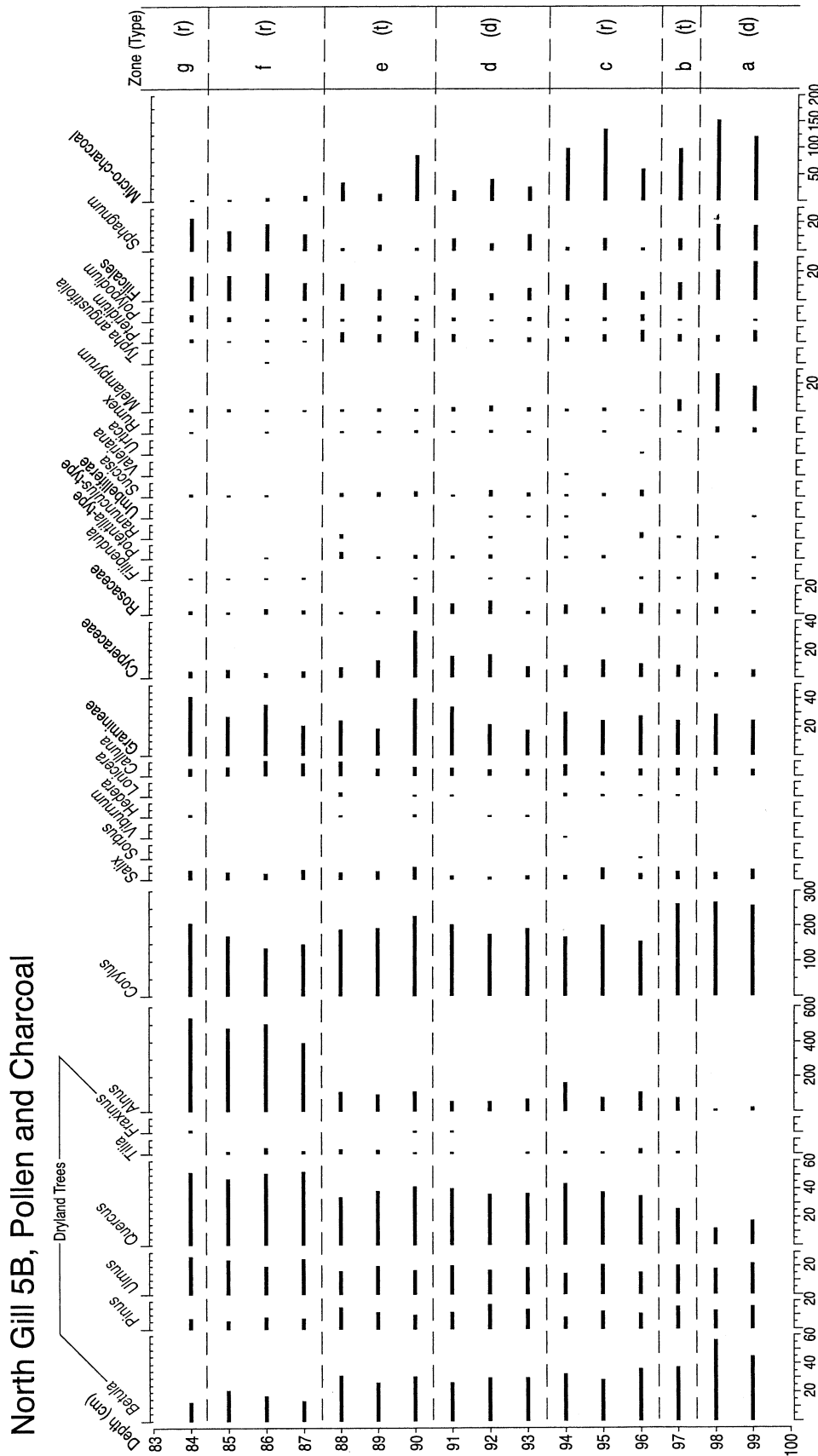


Figure 2. Pollen diagram through the basal "disturbance, transition and regeneration" phases at North Gill 5B, continuing into the succeeding "post-regeneration" pollen assemblage. Pollen frequencies are calculated as percentages of the sum of dryland trees shown on the diagram. Note the changes in horizontal scale for abundant taxa. Micro-charcoal frequencies are also shown, calculated in the same way. The profile comprises amorphous peat resting on sand at 100 cm. Macroscopic charcoal occurs in the top of the sand and the lower 5 cm of the peat, concentrated at the base of the peat.

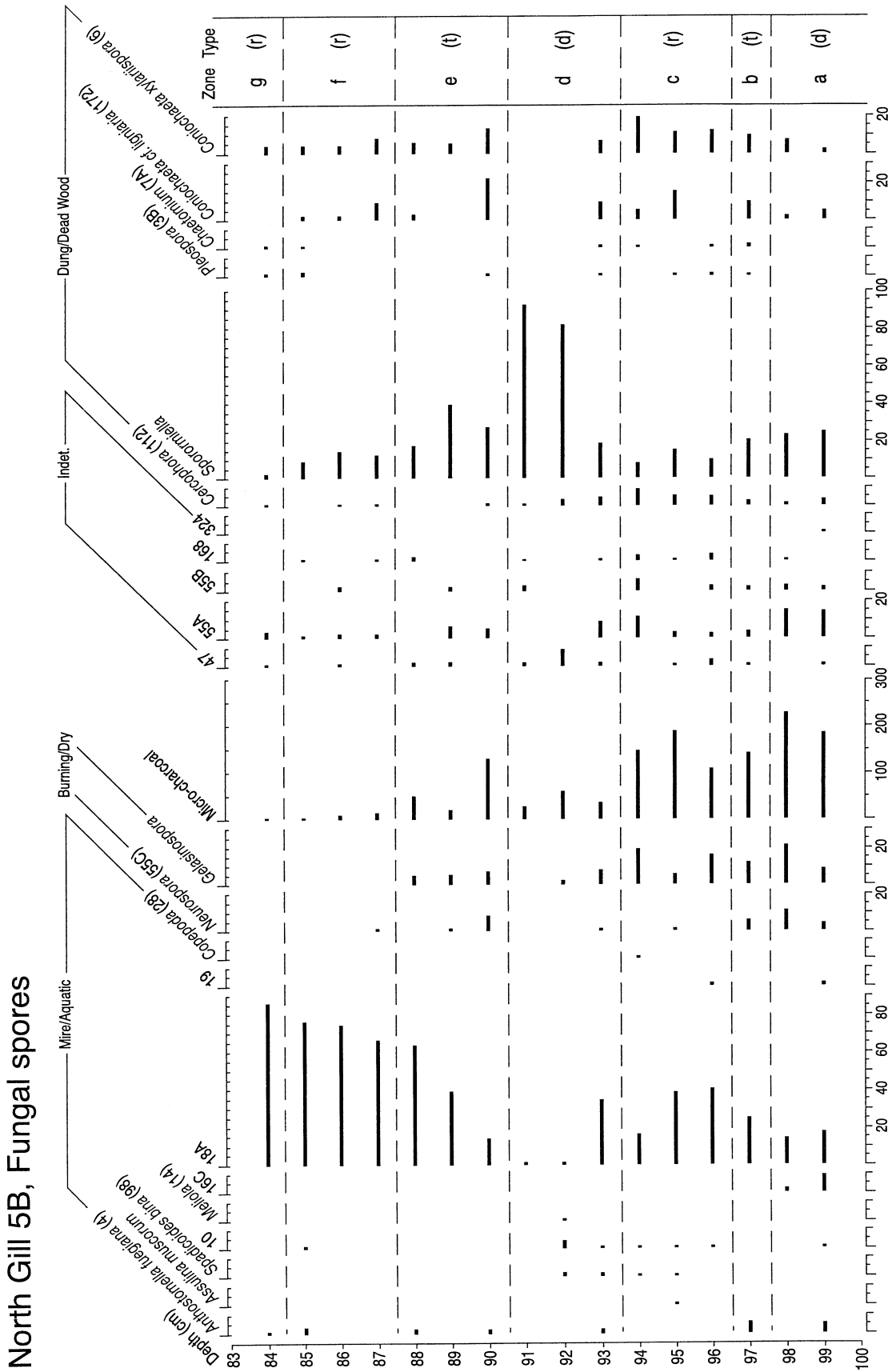


Figure 3. Fungal spore counted from the same pollen slides as were the data shown in Figure 2, calculated as percentages of total fungal spores. Identifications and taxa catalogue Type numbers follow van Geel (e.g. 1978). Taxa are grouped by ecological affinities where known or surmized from previous research, or placed within an indeterminate category. The micro-charcoal curve from Figure 2 is shown recalculated as percentages of total fungal spores.

curve supports the presence of damp wood pasture. Micro-charcoal remains high but *Melampyrum* falls to background levels, suggesting continued charcoal transport rather than new burning, or burning at a distance from the site.

In these three levels Type 18A spores increase in importance and the Sordariaceae Types 55A, 55B and *Neurospora* (55C) are much reduced, as is *Sporormiella*. *Gelasinospora* maintains its relatively high frequencies. *Coniochaeta xylariispora* (6), dung fungus *Cercophora* (112) and probable Sordariaceae fungus Type 168 all increase.

(d) (93, 92 and 92 cm) In this phase the recoveries of *Alnus* and *Quercus* are retarded and both taxa suffer a fall in pollen frequency, oak only slightly. *Salix* and *Tilia* also fall markedly, while Gramineae and *Pteridium* decline also. Increases in *Rumex*, *Succisa* and *Potentilla*-type suggest some disturbance pressure, although a major fall in micro-charcoal to background levels and the absence of macroscopic charcoal indicate renewed burning was not the cause. *Betula* and *Corylus* are unaffected. Gramineae, Cyperaceae and Rosaceae values rise late in the phase.

In this phase of arrested regeneration the fungal assemblage is dominated by very high frequencies of *Sporormiella* in two levels, reaching over 80%. All other taxa percentages are severely reduced except for a peak of the otherwise minor contributor Type 47, the ecological meaning of which has yet to be established.

(e) (90, 89 and 88 cm) *Alnus*, *Tilia* and *Salix* values rise again as regeneration recommences. *Quercus* and *Corylus* values also rise slightly before subsiding. *Pteridium* frequencies increase while Gramineae, Cyperaceae and Rosaceae percentages fall through the phase. Substantial *Succisa* and *Potentilla*-type values remain.

In this phase of renewed regeneration *Sporormiella* frequencies are greatly reduced although still high. Most previously important fungal taxa return to the assemblage. Spore percentages of Type 18A rise steadily through the phase.

(f) (87, 86 and 85 cm) In this phase big rises in *Alnus* and *Quercus* frequencies and falls in *Betula*, *Pinus* and *Corylus* suggest the successful regeneration of a closed deciduous tree cover, with oak woods and alder carr becoming established. *Pteridium* and open habitat weed taxa fall very sharply in frequency. Post-disturbance succession appears completed.

Type 18A spores dominate the fungal assemblage with lower counts of *Sporormiella* and *Coniochaeta* species. Very low Sordariaceae values correspond to the low micro-charcoal frequencies and perhaps a change to a more acidic peat.

(g) (84 cm) Pollen frequencies are very similar to the previous zone, with high *Alnus* and *Quercus* and lower percentages of all the indicators of disturbance.

Type 18A spores achieve complete domination of the fungal assemblage with indicators of dung or burning falling to very low, background values. This zone is

separated from zone f by the fall to very low values of *Sporormiella*.

## Discussion

The pollen data indicate fire disturbance of oak–alder woodland followed by successional regeneration until the re-establishment of alder carr and oakwoods. Regeneration was interrupted by a minor phase of disturbance pressure not caused by fire. The ecology of regeneration conforms with expected post-fire plant community succession. The abundance of *Melampyrum* among the initial post-fire herb flora is a commonly observed feature of such events (Simmons & Innes, 1988) followed by the expansion of bracken and several grassland herbs. *Succisa* and then *Potentilla*-type are the most important successors to *Melampyrum* at North Gill 5, a pattern observed at several disturbance sites of Late Mesolithic age in the North York Moors (Simmons & Innes, 1998, 1996a; Simmons, 1996). In the Pennine upland Soyland Moor (Williams, 1985) is a very clear example but this disturbance association also occurs at Robinson's Moss (Tallis & Switsur, 1990; Tallis, 1991), Pawlaw Mire (Sturludottir & Turner, 1985) and several other sites (Turner & Hodgson, 1983). In mid-Holocene Orkney Blackford *et al.* (1996) recorded abundant *Potentilla*-type pollen after a phase of high charcoal values in which *Melampyrum* occurred. While *Melampyrum* may well have been encouraged by the hydrological change of peat inception as well as by ground burning (Moore *et al.*, 1986), *Succisa* and *Potentilla*-type may indicate relatively intensive grazing of wet grassland pasture. Grass pollen values are high throughout the aftermath of this disturbance event and an open, grassy, meadow-like glade within the woodland seems likely. Less abundant wet pasture taxa like *Ranunculus*, Umbelliferae, *Urtica* and *Filipendula* support this interpretation. This grassland oasis within the woodland must have attracted grazing animals including aurochs (Evans, 1975; Rowley-Conwy, 1982), which would also have exploited the increased *Pteridium*, a favoured food of wild pig (Grigson, 1982). Browsers like roe deer would have exploited the profuse glade-edge *Corylus*, *Salix*, Rosaceous and other shrubs, while the intermediate feeders red deer would have exploited the whole range of the mosaic of plant resources provided. The pollen evidence for a reversal in regeneration in phase d could be interpreted as a temporary increase in the intensity of the grazing and browsing pressure which would have been acting to prolong the existence of the open area (Buckland & Edwards, 1984; Rowley-Conwy, 1982). Modern grazing experiments within woodland (Groenman-van Waateringe, 1993) have shown that low intensity grazing stimulates grass pollen production, whereas high intensity grazing suppresses it. A fall in grass pollen values in phase d supports the hypothesis of increased



grazing pressure at that time, with huge increases in the dung fungus *Sporormiella*, with lower grazing intensity leading to higher grass pollen frequencies before and after that phase.

This indirect evidence of forest grazing is confirmed and amplified by the independent proxy of fungal spore analysis which provides direct evidence of the presence of grazing animals. The Sordariaceous fungus *Neurospora* (55C) and *Gelasinospora* match initially high but declining charcoal levels and reflect burning and dry conditions, while fungi *Sporormiella*, *Cercophora*, *Coniochaeta* spp. and *Chaetomium* appear to support the presence of herbivores throughout the post-disturbance transitional phases. Comparable fungal data, with particularly high *Coniochaeta*, have been reported from Shetland by Hooen & Coles (2000) and from mid-Holocene charcoal rich peat in Orkney (Blackford *et al.*, 1996). Ralska-Jasiewiczowa & van Geel (1992) have interpreted *Cercophora* records in sediments as evidence for increased herbivore numbers during disturbance phases of Mesolithic and early Neolithic age in central Poland. The palynology of herbivore faeces can yield information regarding local environmental conditions (Moe, 1983; Rasmussen, 1993). High percentages of Sordariaceae ascospores in modern and Iron Age cow dung from southern Africa (Carrion *et al.*, 2000) suggest that members of this family of fungi are also indicators of stock grazing, as well as burning. At North Gill 5B dung fungi diversity is highest in phase c, but *Sporormiella* becomes abundant in phase d. Shown by modern analogues to be an obligate dung fungus, high frequencies of *Sporormiella* have been used as a signal of high herbivore numbers in Late Quaternary contexts in North America and Europe (Davis, 1987, 1992; Speranza *et al.*, 2000). The domination of the phase d assemblage by the *Sporormiella* dung fungus supports the pollen inference that grazing intensity and so herbivore concentrations were highest during this period. The restoration of closed canopy woodland in phase f is associated with a much reduced presence of dung fungi and in phase g the very low percentages of dung fungi spores suggest the return of dung and possibly dead wood fungal populations to a low, background level. The ecological affinities of Type 47 fungus are not known. Its peak frequencies coincide with those of *Sporormiella* but comparable ecology cannot be assumed. Sordariaceae Type 55A is most abundant in zone a and may be associated with the disturbance and burning event of that time. However, as it is regarded as an indicator of meso- to eutrophic sediments (van Geel, 1978) it may merely have been favoured by eutrophic conditions during paludification in the shallow stream valley around North Gill 5.

This first fungal spore analysis through a Late Mesolithic age disturbance event from an area with a high density of Late Mesolithic flint sites has shown that the method is a valuable independent proxy in addition to pollen and charcoal data. The results from

North Gill 5 support the ecological interpretations of the pollen and charcoal data, providing more direct evidence of animal concentrations in Mesolithic-age post-fire areas and so offer support for the basic ecological premise upon which models of Late Mesolithic environmental manipulation stand.

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