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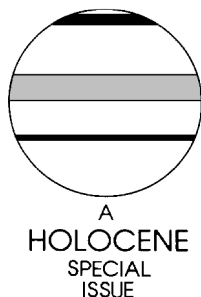
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Mineral deficiency and the presence of *Pinus sylvestris* on mires during the mid- to late Holocene: palaeoecological data from Cadogan's Bog, Mizen Peninsula, Co. Cork, southwest Ireland

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Abstract: Pollen records across parts of Ireland, England and northern Scotland show a dramatic collapse in *Pinus* pollen percentages at approximately 4000 radiocarbon years BP. This phenomenon has attracted much palaeoecological interest and several hypotheses have been put forward to account for this often synchronous and rapid reduction in pine from mid-Holocene woodland. Explanations for the 'pine decline' include pre-historic human activity, climatic change, in particular a substantial increase in precipitation resulting in increased mire wetness, and airborne pollution associated with the deposition of tephra. Hitherto, one largely untested hypothesis is that mineral deficiency could adversely affect pine growth and regeneration on mire surfaces. The discovery of pine-tree remains (wood pieces, stumps and trunks) within a peat located at Cadogan's Bog on the Mizen Peninsula, southwest Ireland, provided an opportunity to investigate the history of *Pinus sylvestris* and also to assess the importance of mineral nutrition in maintaining pine growth on mires. Pollen, plant macrofossils, microscopic charcoal and geochemical data are presented from a radiocarbon dated monolith extracted from this peat together with tree ring-width data and radiocarbon dated age estimates from subfossil wood. Analyses of these data suggest that peat accumulation commenced at the site around 6000 years BP when pine was the dominant local tree. Thereafter *Pinus* pollen percentages diminish in two stages, with the second decline taking place around 4160 ± 50 years BP. Concomitant with this decline in *Pinus* pollen, there is a noticeable, short-lived increase in wet-loving mire taxa and a decrease in the concentration of phosphorus, potassium, magnesium, calcium, sodium, iron and zinc. These results suggest that increased mire surface wetness, possibly the result of a change in climate, created conditions unsuitable for pine growth c. 4000 years BP. Mire surface wetness, coupled with a period of associated nutrient deficiency, appears to be a possible explanation for a lack of subsequent pine-seedling establishment for most of the later Holocene.

Key words: *Pinus sylvestris*, pine decline, pine pollen, dendrochronology, subfossil wood, peat chemistry, mineral deficiency, Mizen Peninsula, southwest Ireland, Holocene.

Introduction

Pinus sylvestris colonized and spread throughout the British Isles between 9500 and 8000 radiocarbon years BP (Birks, 1989) and

established itself as a dominant component of early- to mid-Holocene woodland (Bennett, 1984), extending beyond its present limits (Birks, 1975). Despite its abundance in early- and mid-Holocene woodland, and the presence of pine stumps preserved in peat bogs scattered across the British Isles, Birks (1975),

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McNally and Doyle (1984) and Anderson (1995) have argued that much is still unknown concerning the palaeoecological history of Scots pine. In particular, many researchers have used the presence of pine macrofossils preserved in peat to infer past changes in climate (cf. Ellis and Tallis, 2000) although some doubts as to a casual connection have been expressed by Birks (1975), Dubois and Ferguson (1985) and Bridge *et al.* (1990). Such an approach is also problematic because of the circularity of the argument and the acceptance of a climatic cause when other hypotheses have not been considered fully.

The mid-Holocene decline of *Pinus sylvestris* c. 4000 years BP in northern Scotland, England and western Ireland is well documented (Bridge *et al.*, 1990; Gear and Huntley, 1991; Pilcher *et al.*, 1995; Lageard *et al.*, 1999). Several competing hypotheses have been proposed to account for the 'pine decline', including prehistoric human activity, climatic change, fire, pollution from volcanic activity, a change in mire hydrology resulting in an increase in mire surface wetness, and the expansion of blanket peat. Of these, a combination of climatic change resulting in an increase in mire surface wetness is most favoured (Birks, 1975; Bennett, 1984; Dubois and Ferguson, 1985; McNally and Doyle, 1984; Bradshaw and Browne, 1987; Bridge *et al.*, 1990; Anderson, 1995; Lageard *et al.*, 1999).

Human activities may have contributed to the decline of pine during the mid-Holocene in some local areas of Ireland (e.g., Dodson, 1990) but palynological evidence is lacking on a regional scale (e.g., Dwyer and Mitchell, 1997). The volcanic-activity hypothesis is also problematic. Blackford *et al.* (1992) suggested a possible link between the deposition of Icelandic Hekla-4 tephra and an abrupt decline in pine pollen values at Altnabrec in northern Scotland. They suggest that the direct effects of acid pollution, or a volcanically induced climatic perturbation, possibly caused the southward migration of pine from northern Scotland. However, Hall *et al.* (1994; 1996) and Dwyer and Mitchell (1997) have shown that the deposition of tephra and the reduction in pine pollen percentages are asynchronous. Charman *et al.* (1995) argue that the direct or indirect effects of a volcanic eruption on vegetation and soils are diverse and are still poorly understood.

Other possible causes of the pine decline include environmental disturbances, such as windthrow, fire, strangulation by ice, and biological agencies, such as animal damage, disease or fungal pathogens. Many of these are untested, as is mineral deficiency, which is surprising given that McVean (1963a; 1963b) and Carlisle and Brown (1968) suggest that a common cause of mortality in natural pine saplings is the gradual weakening by faulty mineral nutrition and competition from other plants. Suboptimal N and P frequently retard seedling growth where the colonization of heath, moorland and bog is taking place.

The limitation of nutrients in fen and bog ecosystems necessitates the widespread application of fertilizer and the drainage of peatlands to establish tree growth for afforestation projects (Malcolm and Cuttle, 1983a; 1983b). Satisfactory growth rates of coniferous trees, including Scots pine, can only be achieved on oligo-mesotrophic peatlands by fertilization of the peat with P, N and K, which maintain a balanced nutrient status (Wells and Miller, 1994; Silfverberg and Hartman, 1999). Brække (1977), Paavilainen (1984) and Wells and Miller (1994) suggest that refertilization of P and K is needed even on nitrogen-rich, minerotrophic peat to stimulate height and diameter growth of coniferous trees.

Mineral deficiency has been cited, in combination with changing mire hydrology, to account for contractions in prehistoric pine populations reconstructed using pollen and/or macrofossil data (e.g., Birks, 1975; McNally and Doyle, 1984). None of these studies has supported these assertions with geochemical data while others simply overlook the possible role of changing/marginal nutrient status (e.g., Anderson, 1995). As a result, the role of

mineral nutrition and/or deficiency remains an assumed rather than a certain influence on the population of prehistoric pine woodland, especially those established on mires.

The discovery of pine-tree remains in a peat at Cadogan's Bog in Ratooragh Townland on the Mizen Peninsula, southwest Ireland, provided an opportunity to investigate the Holocene history of *Pinus sylvestris* and, in particular, to examine the contention that nutrient availability influenced the establishment and development of mire pine populations. Thus, the aims of the research were fourfold: (1) to reconstruct the vegetational and geochemical history of the mire; (2) to develop a tree-ring record for the site; (3) to examine the role of nutrient availability on pine populations based on pollen and macrofossil data; and (4) to ascertain the cause of the mid-Holocene pine decline.

The problems of relying solely on macrofossils or pollen to reconstruct Holocene vegetation changes, including the latitudinal and altitudinal range of trees, has been widely discussed (e.g., Bridge *et al.*, 1990; Fossitt, 1994; Birks *et al.* 1996; Barnekow, 1999; Lageard *et al.*, 1999). Dubois and Ferguson (1985) and Birks *et al.* (1996) argue that there could be differential preservation of macrofossil wood remains owing to variations in climate that may result in inconsistent and fragmentary records. Given these problems, Birks *et al.* (1996) suggest that a more reliable approach to reconstruct local forest development combines both pollen and macrofossil data. Trautmann (1953), Ammann and Wick (1993), Fossitt (1994) and Cooney (1996) have further illustrated the utility of this approach, showing that pine stomata guard cells are useful indicators of locally rooting pine trees and can be preserved in samples prepared for pollen analysis. However, Birks *et al.* (1996) suggest that an absence of pine stomata in sediments does not preclude a local pine presence.

Several authors have noted that reconstructing the postglacial history of *Pinus sylvestris* by pollen analysis is problematic. Pine is a prolific pollen producer and its pollen grains are well adapted to disperse over long distances making it difficult to distinguish between local and regional pollen sources (Pilcher *et al.*, 1995; Lageard *et al.*, 1999). Modern pollen studies have shown that pine pollen percentages can reach 10% in forests where pine is absent. In order to overcome this problem, Huntley and Birks (1983), Bennett (1984) and Gear and Huntley (1991) employed pollen percentage criteria of between 20 and 30% in order to infer the local presence of pine. In contrast, Turner (1970) demonstrated that most pine pollen is deposited within 600 m from its source, while Fossitt (1994) and Hall *et al.* (1996) have argued that locally present pine can be represented by pollen percentages as low as 5% total land pollen (TLP), based on palaeoecological data. Lageard *et al.* (1999) found that pine pollen percentages between 3 and 9% TLP in palaeoecological studies on bogs can reflect local pine trees, and so this range is used to infer local pine presence in this study.

The study area

Cadogan's Bog (grid reference 898416 34269) is situated in the Ratooragh Townland, approximately 5 km northwest of the village of Schull located on the southernmost peninsula of County Cork (the Mizen), southwest Ireland (Figure 1). Here Holocene blanket peat has accumulated on sedimentary rocks of Devonian (Old Red sandstone) and Carboniferous age (O'Brien, 1999). Most of the Mizen Peninsula receives between 1500 and 1750 mm of rainfall annually. High rainfall, combined with low evaporation rates, accounts for the dominant soil types across the peninsula: peat, peaty podzols and gleys. Peat of a high-montane type (above an elevation of 150 m) and a low-lying Atlantic type (less than 150 m elevation) is present on the Mizen Peninsula and is characterized by *Eriophorum angustifolium*, *Scirpus cespitosus*,

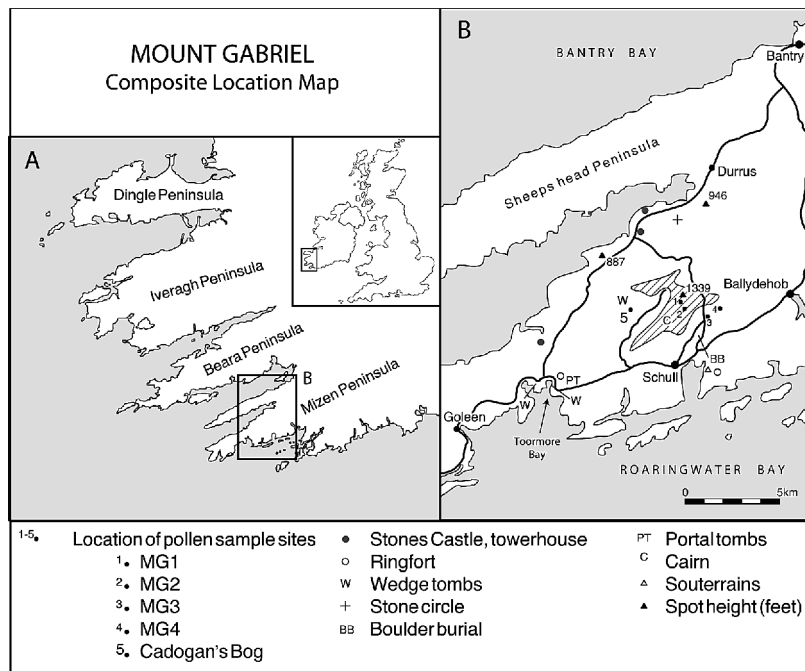


Figure 1 Location of Cadogan's Bog.

Myrica gale, *Narthecium ossifragum*, *Schoenus nigricans* and *Molinia caerulea* (Carey and Hendrick, 1986; O'Brien, 1999).

Cadogan's Bog forms part of an expanse of peat that has accumulated in a shallow depression on the valley floor. The study area is c. 150 m by 200 m in size and is at an elevation of 69 m OD (Figure 2a). Pine stumps and trunks can be found scattered across the area. Peat-cutting has exposed three peat sections. Most of the root crowns occur in the area cut for peat, although several stumps and trunks are exposed within the peat sections. All of the trunks and stumps appear to be undisturbed by the peat-cutting. Oak and birch have also been recovered from the bog by the landowner but no oak was found *in situ* during this study.

Methods

A peat monolith of 137 cm depth was extracted into 15 × 15 × 100 cm aluminium monolith tins from a freshly exposed section of peat adjacent to a *Pinus sylvestris* tree trunk preserved *in situ* (Figure 2a). Peat stratigraphy was described in the field using the sediment description system developed by Troels-Smith (1955). The peat monoliths were wrapped in polythene tubing, sealed and stored in a cold store room before laboratory analysis.

Radiocarbon dating

Seven tree-ring samples, one wood piece extracted from the peat and six peat samples were radiocarbon dated using standard procedures. Sampling of peat for radiocarbon dating followed the rationale outlined in Laguard *et al.* (1999), so that peat samples were taken from horizons with peaks in the pine pollen curve and also from a horizon associated with the subsequent decline in pine pollen to low/background levels (<3–5% TLP). Tree-ring sequences of 10–40 rings were subsampled from discs taken from *in situ* trees in order to estimate the age of key ring-width series. These samples were chosen to represent the full range of stratigraphic depths encountered for *in situ* pine stumps. Ring-width series were also subsampled to test contemporaneity (established by cross-matching ring-width records) between two trees (CR016 and CR017). A ring-width sequence was also originally taken from pine disc CR018 for radiocarbon dating in order to relate an *in situ* subfossil pine to the adjacent pollen stratigraphic record.

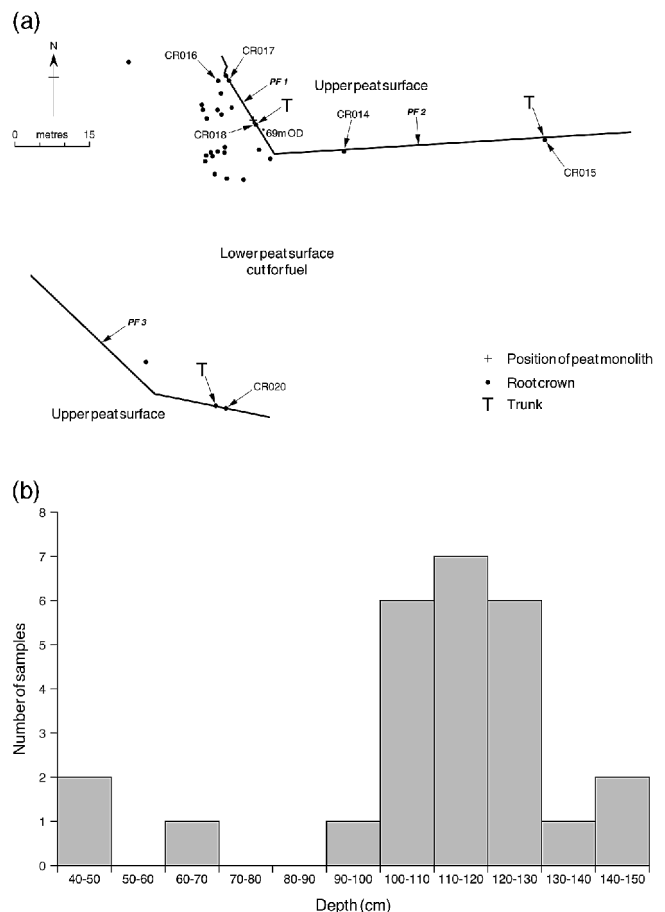


Figure 2 (a) The distribution of tree remains in the study area. (b) Stratigraphic position of tree remains within the exposed peat section. T shows the position of fallen trunks. CR0 codes relate to sampled and dated root crowns or trunks (Table 2).

Dendrochronology

Subfossil *Pinus sylvestris* L. was sampled *in situ* from exposed peat sections and from locations where the relative stratigraphic position of trees could not be established. A chainsaw was used

to take disc samples from trunk sections of stumps. Disc samples were allowed to air-dry and were then sanded in order to differentiate clearly between tree-ring boundaries. Ring-width measurements and cross-matching procedures followed the methodology described in Lageard *et al.* (1999) and ring-width series are illustrated using Dendro software (Tyers, 1999).

Pollen and charcoal

Subsamples of 0.5 cm thickness and 2 g wet weight were prepared for pollen and charcoal analyses after Barber (1976). One tablet of *Lycopodium* was added to each sample (Stockmarr, 1971) to calculate pollen and charcoal concentrations. At least 500 land pollen grains were counted for each subsample except where pollen preservation was extremely poor. Pollen was identified with the aid of keys (Faegri *et al.*, 1989; Moore *et al.*, 1991; Andrew, 1984) and supported with the use of photographs (Reille, 1992) and a modern type slide collection. Microscopic charcoal was counted using the method devised by Clark (1982).

The pollen diagrams for Cadogan's Bog were drawn using Tilia version 2.0.b.4 and Tilia.graph (Grimm, 1991–93). Pollen data are presented as percentages of total land pollen (TLP), excluding spores and aquatics. Spore and aquatics are also expressed as a percentage of total land pollen (Figure 3). Pollen concentrations were also calculated to help infer a local presence (Hirons, 1983) and are expressed in Figure 4 as the number of pollen grains per cm³ (Benninghoff, 1962). Plant nomenclature follows Stace (1991) and recommendations made by Bennett *et al.* (1994). *Corylus avellana* and *Myrica* pollen were not separated (following Edwards, 1981) and they are collectively termed *Corylus avellana*-type. Summary curves for trees, shrubs (constituting arboreal pollen, AP), dwarf shrubs and herbs (non-arboreal pollen NAP) are shown in Figure 3. Pollen-assemblage zones were constructed using CONISS (Grimm, 1991–93).

Plant macrofossils

Following pollen and geochemical analyses, three 5 cm thick slices of peat were cut from the monolith between 67 and 62 cm, 55 and 50 cm and 50 and 45 cm respectively across the pine pollen decline to identify plant macrofossil remains (unfortunately, there was insufficient sample material between 62 and 55 cm). The procedure followed conventional plant macrofossil analytical procedures (Field *et al.*, 2000). Subsamples of 200 g were disaggregated in water, sieved through a nest of sieves to 150 µm. Macrofossils were then picked from the residues using a low-power binocular microscope and identified by comparison to a modern reference collection.

Peat chemistry

Atomic absorption spectrophotometry (AAS), using a Kjeldahl acid digestion method to produce the aliquot, was used to extract and determine total element concentrations. Contiguous samples of 1 cm thickness were prepared for chemical analysis by acid digestion (HNO₃, HClO₄ and H₂SO₄) and AAS following the procedure outlined in detail by Foster *et al.* (1987). Elements were measured using a Varian model 1472 atomic absorption spectrophotometer. Phosphorus was determined colorimetrically by the ammonium molybdate/stannous chloride method (Hesse, 1971) using a Corning Eel Model 197 at 640 nm.

Results

Radiocarbon dates

The results of the radiocarbon assays are shown in Tables 1 and 2 in which the calibration age ranges (in calibrated years BC) to two sigma, produced using CALIB 4.1.2 radiocarbon calibration program and IntCal98 (Stuiver and Reimer, 1993; Stuiver *et al.*,

1998), are shown. The radiocarbon dates referred to in the text are in uncalibrated years BP unless stated otherwise. A time/depth graph for the Cadogan's Bog peat profile is shown in Figure 5 with the changes in peat-accumulation rate. The peat-accumulation rate varies from 10.8 cm yr⁻¹ between 125 and 87 cm and 85.13 cm yr⁻¹ in the top 38 cm.

Peat stratigraphy

The stratigraphy of the monolith is provided in Table 3. Birks (1975) and Ross (1988) suggest that *Phragmites* and some members of the Cyperaceae family (e.g., *Carex*) can generate nutrient-rich, mesotrophic peat that can support pine. It is therefore significant that abundant macrofossil remains of *Phragmites* occur throughout the Cadogan's Bog peat profile and *Carex* nutlets and *Potentilla palustris* (L.) Scop. were identified in samples analysed for plant macrofossils. The peat is similar to a transitional mire-fen peat.

The positions of *in situ* pine stumps and some fallen tree trunks were surveyed in three exposed peat sections and across the area cut for fuel. Stumps were firmly held within the substrate suggesting that they were still in their position of growth and unaffected by the disturbance. The irregular tops of each stump were presumably the remains left after the rest of the trunk had either rotted or snapped off. There is evidence of snapped trunks still preserved within the peat sections. CR015, CR018 and CR020 are all trunks rather than upright stumps. The relative depth in the peat stratigraphy and location of the tree remains in the study area are shown in Figure 2.

Pollen and plant macrofossils

Because concentrations of identifiable macroscopic plant remains were low and the assemblage is not very diverse, they are simply referred to in the discussion when appropriate.

Percentage pollen and concentration diagrams for Cadogan's Bog are shown in Figures 3 and 4. A brief description of each zone is provided in Table 4. High *Pinus* pollen concentrations and percentages exceeding 50% TLP characterise zone CB1. Both decrease, with percentages falling below 20% TLP by the start of zone CB2. Conversely, Cyperaceae and Poaceae pollen percentages and concentrations increase during zone CB1. Apiaceae and *Osmunda* concentrations also peak during zone CB1. From zone CB2 to the end of CB4 *Pinus* percentages fluctuate between 20 and 25% TLP, while Cyperaceae and Poaceae pollen generally exceed 40% and 10% TLP in zones CB2 and 3, respectively. These increases are also recorded in the pollen concentration diagram. *Sphagnum* spores are well represented at the end of zone CB2 and increase in representation along with *Potentilla*-type percentages and concentrations during the second part of zone CB3. Single or double peaks in the pollen concentration of several taxa including *Pinus*, *Quercus*, *Betula*, *Potentilla*-type, Poaceae and *Pteropsida* (monolete) indet. occur during zone CB4. There is a noticeable drop in Cyperaceae pollen during zone CB4 as Poaceae percentages and concentrations increase. *Pteropsida* (monolete) indet. percentages and concentrations peak at the start of zone CB4 zone, while *Sphagnum* spores are prominent in the middle of this zone. *Filipendula* is also well represented. A permanent decline in *Pinus* pollen percentages commences at the very end of zone CB4 and continues until it becomes a rare taxon halfway through zone CB6. Arboreal and Cyperaceae pollen concentrations are at their highest at the start of zone CB5. They decrease as *Calluna*, *Potentilla*-type, Poaceae and *Osmunda* concentrations increase. *Sphagnum* spores reach their highest representation during zone CB5, which is also characterized by the maximum representation of *Calluna* and *Osmunda*. A resurgence in *Pinus* and *Corylus avellana*-type pollen percentages occurs at the top of zone CB7 and a dramatic increase in the pollen concen-

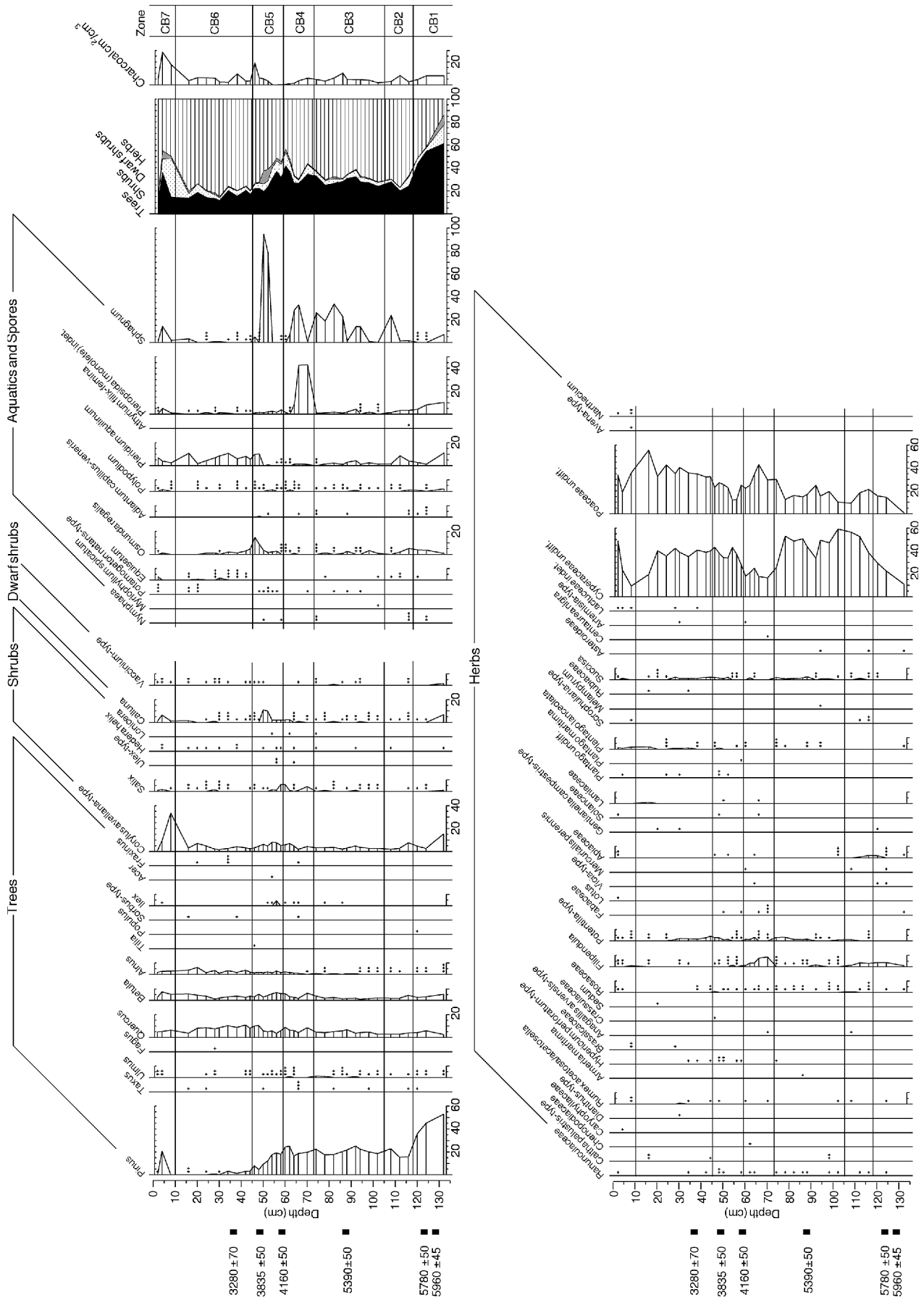


Figure 3 Percentage pollen diagram for Cadogan's Bog. Percentages are expressed as percentages of total land pollen (TLP) excluding spores and aquatics. Spores and aquatics are also expressed as percentages of TLP. A cross denotes one grain. Charcoal concentrations are expressed as cm³/cm³.

Table 1 Radiocarbon dates from peat samples and wood pieces extracted from the peat at Cadogan's Bog

Lab. code	Sample description	Depth (cm)	Uncalibrated age	Calibrated age range (2 σ)
B-122058	Peat	35–38	3280 \pm 70	cal. BC 1737–1411
SRR-6550	Peat	48–50	3835 \pm 50	cal. BC 2464–2139
SRR-6551	Peat	58–60	4160 \pm 50	cal. BC 2885–2577
SRR-6552	Peat	87–89	5390 \pm 50	cal. BC 4341–4046
SRR-6553	Peat	123–125	5780 \pm 50	cal. BC 4773–4465
GrN-18901	Peat	128–130	5960 \pm 45	cal. BC 4941–4720
AA36254	Wood pieces	58–60	4485 \pm 70	cal. BC 3369–2918

tration of all of the arboreal and several non-arboreal pollen and spores also takes place.

Peat chemistry

Down-profile concentrations for selected elements are presented in Figure 6. A cursory examination of these shows five main trends. First, relatively high concentrations occur between the base

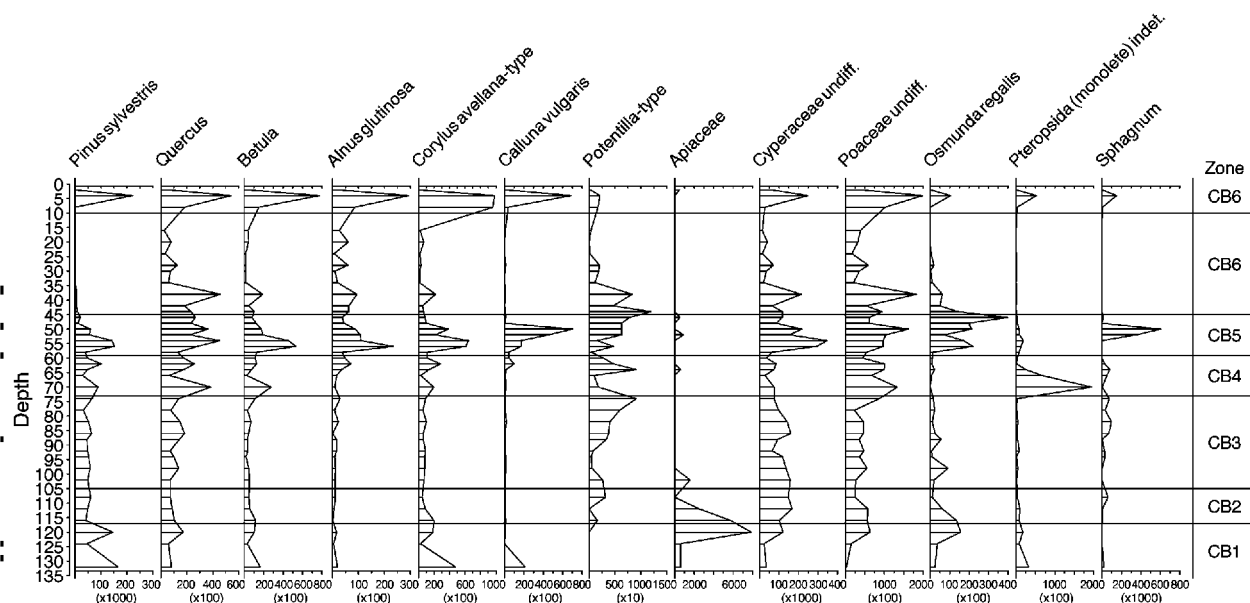
of the peat and 48 cm. Second, there is a noticeable decrease in several chemical elements during pollen zone CB4 and the first part of CB5. Magnesium (Mg) decreases from 75 to 58 cm, iron (Fe) decreases from 70 to 54 cm, calcium (Ca) concentrations decrease from 65 to 54 cm, and sodium (Na) concentrations between 74 and 50 cm. Only Na fails to recover. Third, potassium (K) gradually increases throughout zones CB4 and CB5. Fourth, all elemental concentrations are relatively low from 45 to 18 cm except for the occasional reversal: phosphorus (P) at 23 cm, Mg between 40 and 34 cm and Na from 32 to 28 cm. Fifth, concentrations increase in the top 18 cm for most elements. Manganese (Mn), which has a fairly constant concentration, except a large peak at 88 cm, can be excluded from these general observations.

Dendrochronology

Of the 11 pine trees sampled, 10 proved suitable for ring-width analysis, fulfilling the criteria of a minimum 50 consecutive rings to facilitate the use of computer cross-matching programs (Baillie and Pilcher, 1973; Munro, 1984). Ring-width records were made for each pine sample producing ring-width sequences ranging from 66 to 344 years (Table 2; Figure 7). Records were cross-matched, revealing a low t-value ($t = 5.36$) between samples

Table 2 Summary statistics of the tree-ring analysis including uncalibrated and calibrated radiocarbon dates

Sample ID	Type of tree remain	Depth of root crown (cm) Unstratified (U)	Preservation Pith (P) Bark (B)	No. of tree rings	Tree rings sampled for ^{14}C	^{14}C age estimate years BP (lab. code)	2 sigma calibrated age range
CR014	Root crown	134	P-?	149	129–149	4815 \pm 40 (SRR-6544)	cal. BC 3659–3521
CR015	Fallen trunk	137	P-B?	139	109–139	4170 \pm 50 (SRR-6545)	cal. BC 2890–2580
CR016	Root crown	146	P-?	113	38–58	6610 \pm 45 (SRR-6546)	cal. BC 5624–5477
CR017	Root crown	143	P-B?	171	39–48	6410 \pm 70 (B-114958)	cal. BC 5477–5302
CR018	Fallen trunk with root crown	110	P-B	66	56–66	4805 \pm 45 (SRR-6547)	cal. BC 3659–3385
CR019		45	Below root crown –	–	–	–	–
CR020	Fallen trunk	66	P-B?	132	–	–	–
CR021	Root crown	U	P-B?	344	1–20 314–344	4580 \pm 40 (SRR-6548) 4355 \pm 55 (SRR-6549)	cal. BC 3498–3104 cal. BC 3257–2882
CR022	Root crown	U	P-B?	165	–	–	–
CR023	Root crown	U	P-?	89	–	–	–
CR024	Root crown	U	P-?	135	–	–	–

**Figure 4** Pollen concentrations of selected taxa for Cadogan's Bog. Pollen concentrations are calculated using the indirect method described by Benninghoff (1962) and are expressed as number of pollen grains per cm^3 .

CR016 and CR017 (Figure 7a). This low value is probably attributable to missing or false rings in one or both of these sequences (a narrow ring series is evident within CR016). The contemporaneity of these samples is further supported by the results of radiocarbon assay on subsamples from the two trees (Table 2).

Discussion

Age and chronology of macrofossil and pollen records

Several studies have compared pine microfossil and macrofossil analyses to reconstruct the history of woodland cover during the Holocene (Tallis and Switsur, 1983; Wilkins, 1984; Bridge *et al.*, 1990; Gear and Huntley, 1991; Lageard *et al.*, 1999). Most of these studies are concerned with woodland history on regional scales and there are very few studies that examine the relationship between tree macrofossils and pollen records on a local scale. While both Mitchell (1956) and Tallis and Switsur (1983) suggest that there is a good correlation between the stratigraphic position of tree remains and high pine pollen percentages in the peat, the results from this study suggest that there can be a discrepancy. First, there is a significant difference between the age of the pine stumps but only a small change in stratigraphic depth. For example, stump CR014 occurs at a depth of 134 cm and is older than stump CR015 which occurs at 137 cm (Table 2). Second, there is also a difference in the age of the peat and the stratigraphic position of the pine stumps. For example, stumps (CR014 and CR015) occur at 134 and 137 cm beneath the present surface respectively, while peat of a similar radiocarbon age range is stratigraphically higher up the profile between *c.* 75 cm and 60 cm. While the sites of these macrofossils are 19 m and 59.5 m, respectively, away from the position of the monolith (Figure 2b) and so might account for the discrepancy, wood pieces extracted from the monolith between 60 and 58 cm produced a radiocarbon date of 4485 ± 70 years BP, which is older than the age of the peat (4160 ± 50 years BP) (Table 1).

These discrepancies are best explained by either downward movement of the pine macrofossils or a variation in peat-accumulation rates over distances of centimetres to tens of metres. Ohlson and Dahlberg (1991) imply that larger pine trees could be prone to downward movement from their growing position on mires. Wilkins' (1984) study of the distribution of tree remains across the Isle of Lewis also noted that tree stumps of different ages appear to be at approximately the same level in the basal 20 cm of peat. The age range of the tree remains was from 1160

to 310 years. Wilkins (1984) suggests that a slow rate of peat-accumulation growth could allow several generations of tree to appear to be at approximately the same level. The slow peat-accumulation rate of 42.41 years per cm between 89 and 58 cm (Figure 5) at Cadogan's Bog clearly exacerbates the problem of sinkage of stumps or trunks, as a relatively small downward movement would represent a substantial period of time.

At present, it is not possible to explain fully the reasons for the stratigraphic differences that occur between the age of the peat and the macrofossils at Cadogan's Bog. Nor is it possible, therefore, to compare directly the microfossil and macrofossil data using their stratigraphic position and so the impression of phases of pine growth during the accumulation of peat indicated by Figure 2b must be treated with caution.

A viable alternative to reconcile the macrofossil and microfossil data is to use their radiocarbon age and this method is used in this paper. The oldest pine stumps appear to be rooted within the basal clay beneath the peat sections between 150 and 145 cm. Two tree stumps (CR016 and CR017), thought to be representative of this population, produced radiocarbon ages of 6610 ± 45 and 6410 ± 70 years BP, respectively. While their ages pre-date peat initiation, it is noteworthy that pine pollen percentages are at their highest, over 50% TLP, at the base of the Cadogan's Bog profile.

Three stratified stumps produced radiocarbon dates. CR014, CR018 and CR015 produced dates of 4815 ± 40 , 4805 ± 45 and 4170 ± 50 , respectively. Two samples from CR021, an unstratified root crown, produced two radiocarbon dates within this age range: 4580 ± 40 and 4355 ± 55 years BP (Table 2). If compared chronologically, the pine stumps represent trees that grew when the peat accumulated from 74 to 60 cm. Thus, the age range of the macrofossils coincides with pine pollen percentages of between 25.8 and 16% TLP. The presence of sclerotia (resting body) of the soil fungus *Cenococcum geophilum* Fr. between 67 and 62 cm also suggests that trees were growing on the mire surface. This fungus is an ectomycorrhizal species, which has mutualistic associations with some tree roots, particularly members of the Betulaceae and Pinaceae (Hudson, 1986).

No pine stomata were recorded during routine pollen counting. This is surprising given that Fossitt (1994) and Cooney (1996) recorded pine stomata frequently in lake sediments in western Donegal and Killarney respectively, although pine pollen percentages rarely exceeded 20% TLP. However, pine stomata were found in only one sample analysed from a forest hollow site in Upper Michigan where pine pollen percentages generally exceed 40% TLP (Mighall, unpublished data). The results here suggest that their preservation is less likely in peat.

The radiocarbon dates suggest that there are two distinct chronological periods of pine colonization: the first in the basal clay between 6610 ± 45 and 6410 ± 70 years BP and the second on the mire surface between 4900 and 4000 years BP. Despite the small sample size, the bimodality in dates at Cadogan's Bog appears to be genuine and concurs with the radiocarbon dating of tree remains in other parts of the British Isles (Tallis and Switsur 1983; Wilkins, 1984; Bridge *et al.*, 1990). Many researchers have cited selective tree-stump preservation as a reason to account for the absence of tree macrofossil remains in peat bogs during the mid-Holocene. The general consensus is that some wide-ranging climate influence was able to bring about the preservation of tree remains at particular times rather than others (Wilkins, 1984; Bridge *et al.*, 1990; Gear and Huntley, 1991). However, the peat-accumulation rate at Cadogan's Bog is relatively fast, 36 cm yr^{-1} from 5960 ± 45 (130 cm) to 5780 ± 50 years BP (123 cm) and 10.8 cm yr^{-1} from 5780 ± 50 to 5390 ± 50 years BP (from 123 cm to 87 cm) and therefore it is unlikely to prevent macrofossil preservation.

Notwithstanding the limited exposure of the peat sections in

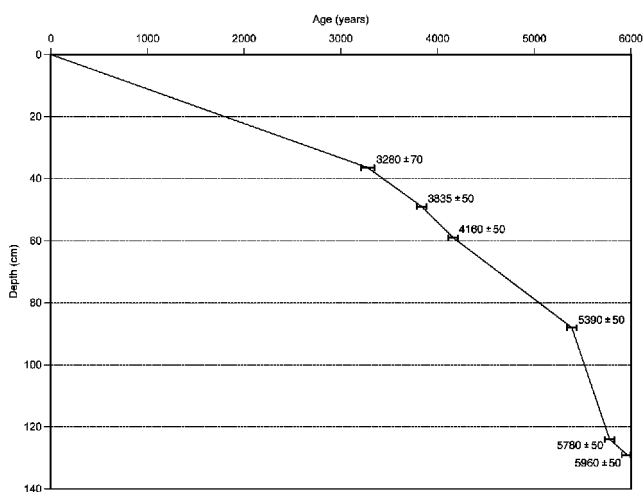


Figure 5 An age/depth graph for Cadogan's Bog.

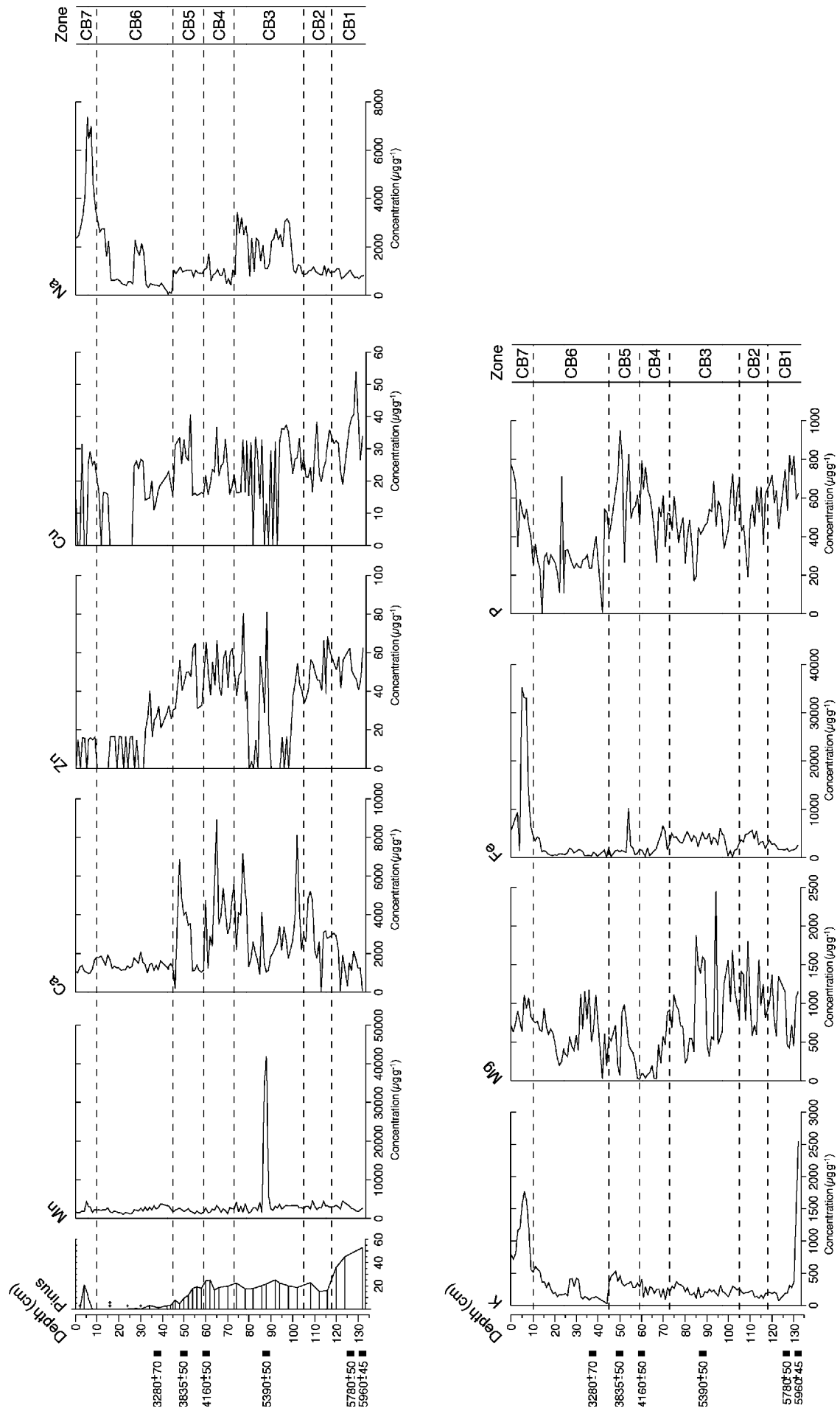


Figure 6 Profiles for selected chemical elements at Cadogan's Bog.

Table 3 Stratigraphy of Cadogan's Bog peat monolith with Troels-Smith sediment descriptions

Depth (cm)	Sediment characteristics
0–13	Dark brown, well-humified fibrous peat. Th ²⁴ , sicc 3.5, nig 2.5, strf 0.
13–56	Dark brown fibrous peat with occasional <i>Phragmites</i> ; wood at 56 cm. Th ²⁵⁴ sicc 2.5; nig 3, strf 0.
56–105	Brown reed peat with <i>Phragmites</i> and wood. Wood layer recorded between 58 and 68 cm. Th ²⁵⁴ , sicc 2.5, nig 2.5, strf 0.
105–111	Dark brown reed peat with <i>Phragmites</i> . Th ³⁴ sicc 2.5, nig 3, strf 0.
111–132	Fibrous reed peat with birch twigs, charcoal flecks and <i>Phragmites</i> ; small pieces of charcoal occur. Pine branch occurs between 126 and 128 cm. Th ³⁴ sicc 2.5, nig 3, strf 0.
132–137	Light grey clayey peat with distinct charcoal at base of peat.

Table 4 Pollen percentage assemblage zone descriptions for the Cadogan's Bog

Zone	Depth (cm)	Characteristics
CB7	0–10	<i>Pinus</i> , <i>Corylus avellana</i> -type increase; rising Cyperaceae, high Poaceae.
CB6	10–45	Low total AP; increasing Poaceae and high Cyperaceae percentages; <i>Pteridium</i> is well represented.
CB5	45–59	Falling <i>Pinus</i> , higher <i>Corylus avellana</i> -type; rising Cyperaceae and Poaceae; lower <i>Filipendula</i> ; higher <i>Osmunda</i> ; <i>Sphagnum</i> spores peak mid-zone.
CB4	59–70	<i>Pinus</i> >20% TLP, lower Cyperaceae, higher Poaceae; increasing <i>Filipendula</i> ; high Pteropsida (monolete) indet. <i>Salix</i> increases in representation at the beginning and end of the zone.
CB3	70–105	<i>Pinus</i> c. 20% TLP, high Cyperaceae, Poaceae 10–20% TLP; <i>Sphagnum</i> increases in the second half of the zone.
CB2	105–120	Lower <i>Pinus</i> , high Cyperaceae, Poaceae decreasing; <i>Sphagnum</i> increases at the end of the zone.
CB1	120–base	High but falling <i>Pinus</i> ; <i>Corylus avellana</i> -type decreases while Cyperaceae and Poaceae percentages increase. <i>Filipendula</i> , Pteropsida (monolete) indet. and <i>Osmunda</i> are regularly recorded.

the study area and the possibility of poor preservation, no macrofossils were recorded above 45 cm, suggesting that either pine did not grow on the mire surface or no macrofossils have been preserved or discovered. This is also supported by the decline in pine pollen percentages below 5% TLP and much lower pollen concentrations by 40 cm. Thus, there appears to be a good degree of comparability between the relatively high pine pollen percentages and concentrations and the sustained presence of tree remains when based on radiocarbon ages.

The history of *Pinus sylvestris* at Cadogan's Bog

The presence of macroscopic charcoal at the clay/peat transition strongly implicates fire in the initial stage of peat development (Table 3). Burning is known to reduce soil porosity by blocking pore space and increase waterlogging (Mallik *et al.*, 1984), a process that could decrease decay and lead to peat formation

(Charman, 1992). The presence of a significant fire scar encapsulated within the ring series of CR017 confirms the occasional burning of local woodland and fire possibly assisted in regenerating these pine woodlands (cf. Lageard *et al.*, 2000).

At Cadogan's Bog, a major fall in *Pinus* pollen percentages (Figure 3) occurs after peat initiation across the CB1/CB2 zone boundary, which is not seen elsewhere on the Mizen Peninsula (Mighall and Lageard, 1999; Timpany, 2001), and therefore suggests a contraction of the mainly local pine. Moreover, pollen percentages and concentrations for mire taxa such as Poaceae, Cyperaceae, Apiaceae, *Potentilla*-type and *Osmunda* increase as *Pinus* declines, which supports the idea that local pine was most affected, possibly as a result of changing substrate hydrology as the peat formed.

Woodland composition does not appear to undergo any significant changes during zones CB2 to CB4. It is difficult to establish whether pine continued to grow on the mire surface at Cadogan's Bog between 6410 ± 70 years BP and 4815 ± 40 years BP owing to the absence of radiocarbon dated pine tree remains and pine stomata in the peat. While the pine percentages exceed 9% TLP, to imply local pine presence (cf. Lageard *et al.*, 1999), both the pollen percentages and concentrations possibly represent a stronger regional component from pine growing on mineral soils. Pine concentrations are not adversely affected by increases in mire taxa, such as Poaceae, Cyperaceae and *Potentilla*-type, *Sphagnum* and *Osmunda*, which might be expected if pine was growing on the mire surface.

Irrespective of whether pine grew on Cadogan's Bog during zones CB2 and CB3, *Pinus* pollen regularly exceeds 20% TLP and has higher pollen concentrations compared with other arboreal taxa, suggesting that pine was the dominant constituent of local mixed woodland that also comprised *Quercus*, *Corylus*, *Betula* and *Alnus* (Figure 3). Such woodland appears to be typical of the Mizen Peninsula between 7600 and 3800 years BP (Mighall and Lageard, 1999; Timpany, 2001).

By 4815 ± 40 years BP, the macrofossils radiocarbon dated suggest that pine recolonized Cadogan's Bog or that conditions for the preservation of tree remains returned. The radiocarbon dates of macrofossils and wood pieces suggest that pine was present on Cadogan's Bog throughout the fifth millennium BP. It appears that a similar situation occurred across other parts of Britain and Ireland as tree remains have been discovered in mineral soil and peat bogs between 5200 and 4000 years BP (e.g., Dwyer and Mitchell, 1997). The increased number of tree remains during this part of the mid-Holocene possibly represents a regional expansion of *Pinus* as pollen percentages also increase during this period in northwest Ireland and parts of Scotland (e.g., Bridge *et al.*, 1990; Gear and Huntley, 1991; Fossitt, 1994).

Despite the presence of tree remains, pine percentages and concentrations at Cadogan's Bog do not show a major increase between 4800 and 4170 years BP. The pollen concentration at 70 cm is the highest during zones CB2 and CB3 but this is not matched in pollen percentages. An increase at 74 cm does not even exceed the maximum percentage for *Pinus* pollen during CB2 and CB3 when pine macrofossils are absent. Moreover, *Pinus* pollen percentages then decrease until a sudden rise from 62 to 60 cm. Although *Pinus* pollen concentrations fluctuate, they are slightly higher during CB4 compared to CB3 and CB2. The peaks in *Pinus* (from 74 cm to 70 cm and 62 cm) might represent the increase in pine on the mire surface as the concentration of other trees and mire taxa also increase at one or both of the peaks, including *Quercus*, *Betula* (known to have grown on the bog), *Corylus avellana*-type (possibly *Myrica*), Poaceae, *Potentilla*-type and *Pteropsida* (monolete) indet. That there is not a simultaneous increase in the concentrations of all taxa suggests that a change in the peat-accumulation rate cannot fully explain the trends in the data. One possibility is that most of the tree remains recorded

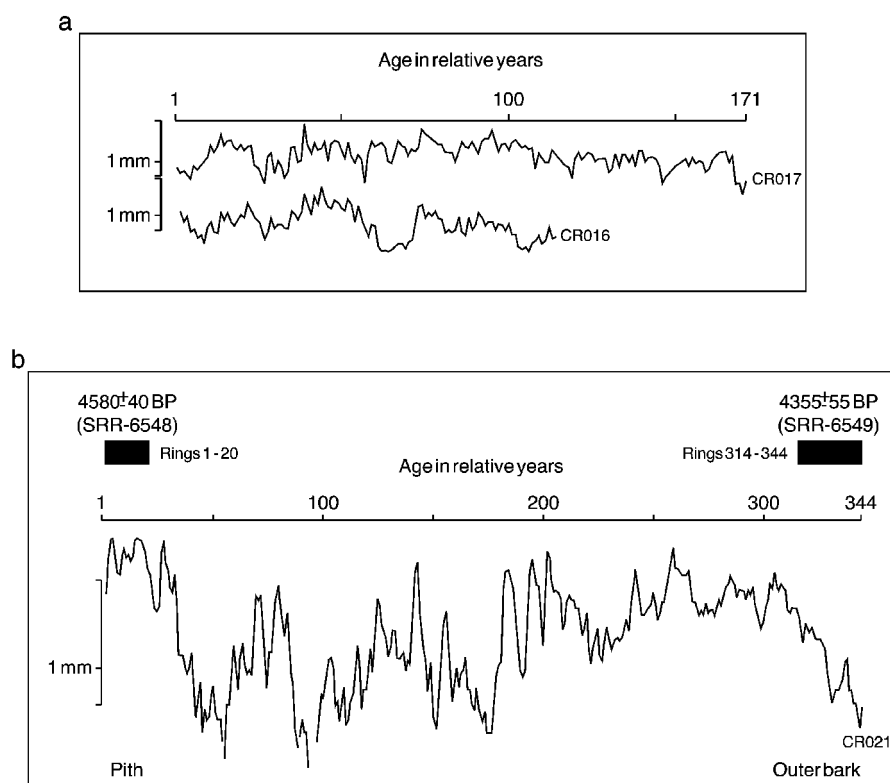


Figure 7 Tree-ring data from Cadogan's Bog. (a) Probable contemporaneity of *in situ* subfossil pine trees CR016 and CR017 supported by cross-matching of ring-width series and radiocarbon age estimates. (b) A 344-year sensitive ring-width record and associated radiocarbon age estimates from subfossil pine sample CR021, measured from pith to very close to outer bark surface.

in the study area represent remnants of pine woodland established during the seventh millennium BP, which is represented in this study by CR016 and CR017 (Table 2), and therefore only a few trees recolonized the mire between 4900 and 4000 years BP. A second possibility is that pine continued to grow on the mire surface from peat initiation up until 4000 years BP and poor tree preservation occurred between 6410 ± 70 and 4815 ± 40 years BP, resulting in the absence of tree remains, while favourable preservation conditions occurred between 4900 and 4000 years BP. Third, the small sample size of trees selected for radiocarbon dating and dendrochronology has not provided evidence for the existence of trees on the mire at certain periods of time.

The mid-Holocene *Pinus* decline at Cadogan's Bog

There is now a plethora of pollen diagrams from peat bogs and lakes in Ireland that record a sizeable decrease in *Pinus* pollen percentages during the mid-Holocene around 4000 years BP (e.g., Lynch, 1981; Watts, 1984; Bradshaw and Browne, 1987; Barnosky, 1988; Mighall and Lageard, 1999; Timpany, 2001). At Cadogan's Bog, *Pinus* pollen percentages fall rapidly from 62 to 58 cm and then between 56 and 48 cm. They continue to decline more gradually and fall below 3% TLP by 34 cm (Figure 3). This decline commenced around 4160 ± 50 years BP based on pollen representation in the peat stratigraphy and continued until approximately 3280 ± 70 years BP. Pollen percentages for other arboreal taxa either do not change significantly, for example *Quercus* and *Betula*, or they increase, for example *Corylus avellana*-type and *Alnus*. *Salix* pollen percentages decrease only after the initial drop in *Pinus* pollen.

In contrast to the pollen percentage data, *Pinus* concentrations increase between 56 and 54 cm along with *Quercus*, *Betula*, *Alnus* and *Corylus avellana*-type. This change can be explained as a response to a variation in peat-accumulation rates as all the main taxa increase. The tree concentrations then decrease throughout the rest of zone CB5 before their recovery during the first part of

zone CB6, except *Pinus*, which never recovers. As the arboreal concentrations begin to decrease, first Poaceae, then *Calluna*, *Sphagnum*, *Osmunda* and finally *Potentilla*-type concentrations all increase. That *Pinus* is the only arboreal taxon to remain at lower concentrations as mire taxa increase suggests the decrease includes the loss of local pine on the mire surface.

The radiocarbon date for the decline in *Pinus* pollen percentages and concentrations coincide with the last radiocarbon age estimate for a *Pinus* tree remains of 4170 ± 50 years BP. No pine-tree remains are recorded in the peat above 45 cm when pine pollen percentages fall below 8% TLP, suggesting that pine has been inhibited from growing on the mire surface, although differential preservation cannot be ruled out. A study of tree remains elsewhere in Ireland and Scotland has also suggested that pine rooted on many bogs died out around 4000 years BP (Bridge *et al.*, 1990; Gear and Huntley, 1991; McNally and Doyle, 1984; Pilcher *et al.*, 1995).

The role of nutrient deficiency

Ross (1988) and Shotyk (1996) have commented upon the difficulties involved in interpreting the chemistry of a peat profile and in particular the postdepositional mobility of elements. While peat materials have a high affinity for cations, a change in environmental conditions, such as redox conditions and pH, can alter the distribution of an element in the peat (Shotyk, 1988; 1996; Livett, 1988; Stewart and Fergusson, 1994). While evidence for the post-depositional transformation of elements is not uncommon, studies have also indicated that the stratigraphic integrity of the chemical record in peat is maintained (Shotyk *et al.*, 1992). Even relatively mobile elements, such as P and K, are actively taken up and relatively concentrated in plant tissues and this may lead to a relative enrichment of these elements in plants compared to the porewater (Pakarinen and Tolonen, 1977). If so, the mobility of these elements will be restricted and the chronological record of these elements will have been preserved. However, studies have shown

that soluble inorganic nutrients and those held on exchange sites can be relocated by physicochemical processes, which may have influenced the chemical data in this study (Heathwaite and Göttlich, 1993). Notwithstanding this problem, the total concentrations shown in the chemical profiles, shown in Figure 4, should provide the most reliable chronological record of the nutrient status of the mire as it accumulated.

There does appear to be a correlation between pine macrofossils, pollen concentrations and percentages, and changes in nutrient concentrations. The tree remains, radiocarbon dated to between 4815 ± 40 and 4160 ± 50 years BP (equivalent to a depth of 75 cm to 60 cm in the peat monolith), are associated with higher P, Ca and K concentrations (Figure 5). Notwithstanding the occasional reversal, P increases from 84 cm to peak at 60 cm while K concentrations rise steadily from 70 cm to 60 cm. Ca concentrations increase from 79 cm and remain relatively high, above $2000 \mu\text{g g}^{-1}$ until 60 cm. In contrast, Na concentrations fall sharply at 74 cm and 45 cm, Mg from 75 to 59 cm, followed by Fe at 70 cm.

Several elements, including P, Fe, Mg, Ca and Cu, decrease in concentration between 62 and 58 cm. This decrease coincides with the youngest radiocarbon dated pine stump recorded in the peat (4170 ± 50 years BP) and a permanent decrease in pine pollen concentrations and percentages, c. 4160 ± 50 years BP (Figure 6). Another decrease in Ca, Zn, Na, K, P and a short-lived fall in Mg are recorded at between 48 and 45 cm (c. 3600 years BP) when pine concentrations are very low and pine pollen percentages have fallen to below 3% TLP. These changes also coincide with the highest stratigraphic position of tree remains in the peat stratigraphy (Table 3).

Although pine can tolerate a low level of nutrition, it has fairly high nutrient requirements, especially P, K, Ca, Mg, N and S, for maximum growth. Deficiencies can result in poor growth, retardation or mortality (McVean, 1963a, 1963b; Carlisle and Brown, 1968; O'Carroll and McCarthy, 1973; Malcolm and Cuttle, 1983a; 1983b; Paarlathi *et al.*, 1971; Beltman *et al.*, 1992; Wells and Miller 1994; Kaunisto *et al.*, 1999; Silfverberg and Hartman, 1999). Such an occurrence may account for the timing of the decline of pine from 62 cm and the absence of macrofossils above 45 cm at Cadogan's Bog because the peat became nutrient-deficient.

However, a closer examination of the data suggests that the relationship between the elements and pine is not straightforward. While the pine percentages fall throughout zone CB5, several elements increase between 53 and 45 cm, such as Ca, Cu, Mg and K, while P peaks at 50 cm. The peak in elements between 52 and 48 cm corresponds with a dramatic increase in *Sphagnum* spores (Figures 3 and 4), far in excess of any other level analysed. Görres and Frenzel (1997) suggest that elements such as Ca, Mn and K are strongly influenced by the nutrient cycling of mosses (Sphagnaceae). *Sphagnum* mosses are very efficient at accumulating elements passively as they have a porous structure, high content of polygalacturonic acids and high cation exchange capacities. Therefore, this sudden proliferation of *Sphagnum* may have created the element peak close to the sampling site and may not be a true reflection of the mineral status of the peat bog at that time.

The cause of the mid-Holocene pine decline at Cadogan's Bog

Human activity has been cited as a cause of the loss of pine around 4000 BP. In southwest Ireland, a continuous record of *Plantago lanceolata* begins between 4500 and 4000 years BP (Dodson, 1990) and coincides with the first records of sustained forest clearance, especially pine, at Ballinloghig Lake on the Dingle Peninsula (Barnosky, 1988) and close to Mount Gabriel (Mighall and Lagueard, 1999; Timpany, 2001). Evidence for human disturbance

in the pollen record is scant and microscopic charcoal concentrations are low at the start of the *Pinus* pollen decline (Figure 3). There is also little alteration in the pollen percentage of dryland trees, with only *Quercus* percentages falling during zone CB5 while pollen concentrations for *Quercus*, *Alnus*, *Betula* and to a lesser extent *Corylus avellana*-type, are relatively high. A small peak in *Plantago lanceolata*, *Rumex acetosacetosella* and *Pteridium* coincides with a rise in microscopic charcoal concentrations and small decreases in *Pinus* and *Quercus* pollen percentages at 46 cm. However, this disturbance is short-lived. It is, therefore, unlikely that human activity was wholly responsible for the decline in pine at Cadogan's Bog.

Increased mire surface wetness at Cadogan's Bog, suggested by higher concentrations and percentages of Poaceae, Cyperaceae, *Potentilla*-type (possibly *Potentilla palustris* (L.) Scop), *Succisa* and *Osmunda*, coincides with a decrease in *Pinus* concentrations and percentages during zone CB5. The sudden increase in *Calluna* percentages and concentrations in the middle of zone CB5 suggests that parts of the mire surface may have dried out. This shift to possible drier conditions is, however, short-lived. Anderson (1995) argues that a shift from a short period of unusually dry to wet conditions remains the most plausible explanation for the demise of pine c. 4000 years BP at Glen Torridon in northwestern Scotland. He suggests that pine trees growing in areas close to their distribution limits may have been sensitive to minor changes in moisture conditions. The rise in *Calluna* pollen at Cadogan's Bog coincides with a large increase in *Sphagnum* spores, which are often used to imply increased surface wetness. However, given the infrequent sporulation of *Sphagnum* and the differing tolerances of individual species to surface wetness, it is not always a reliable proxy for increased surface wetness.

Modern experiments have shown that drainage of peatland is necessary to promote good tree growth on ombrotrophic peats and fens (Burke, 1975; Malcolm and Cuttle, 1983a; 1983b; Brække, 1987; Kaunisto *et al.*, 1999). An increase in mire surface wetness is liable to lead to the waterlogging of roots and cause inadequate aeration. Such conditions can adversely check primary and secondary growth on pine seedlings and can prevent pine establishment and retard older seedlings (McVean, 1963a; Birks, 1975). The exact cause of increased surface mire wetness at Cadogan's Bog is not clear, although the lack of palynological evidence for human disturbance favours climatic change. In Ireland, Caseldine *et al.* (1998) suggest that increasing mire surface wetness at West Corlea, County Longford, was already occurring before the deposition of tephra from the Icelandic Hekla-4 volcanic eruption (2310 ± 20 BC), although wetter conditions may have been short-lived. There is evidence for a shift to wetter climatic conditions around 4000 years BP in ombrotrophic peat bogs found in the coastal regions of Britain, Holland and Norway (Dupont, 1986; Nilssen and Vorren, 1991; Barber *et al.*, 1994; Anderson, 1995; Anderson *et al.*, 1998). Birks (1975), Bennett (1984), Dubois and Ferguson (1985), Bradshaw and Browne (1987) and Dwyer and Mitchell (1997) all suggest that climatic wetness c. 4000 years BP prevented pine growth and regeneration. McNally and Doyle (1984) propose that pine trees colonizing raised bogs in Counties Offaly and Kildare between 4000 and 3500 years BP died because they were unable to produce viable seed owing to increased mire surface wetness.

Given that the timing of the loss of nutrients at Cadogan's Bog corresponds with periods of increased climatic wetness, it is likely that increased mire surface wetness and possibly nutrient depletion induced tree death. As well as impairing the ability of pine trees to take up nutrients, the increased water content is likely to have promoted greater leaching and depleted the upper peat of nutrients (Heathwaite, 1990). This process may account for the virtually simultaneous decline in most elements from 45 to 20 cm. Mörnsjö (1968) and Payette (1984) suggest that such changes

mark a change from minerotrophy to ombrotrophy in Swedish and Canadian mires.

Because a number of factors can influence the nutrient status of peat including the degree of aeration, the inputs from groundwater and bedrock weathering, the age of the peat, its flora and the degree of biological activity (Heathwaite and Göttlich, 1993), comparisons of chemical data must be treated with caution. Notwithstanding these factors, a comparison of the chemical status of the peat in Cadogan's Bog with other sites suggests that nutrient deficiency could have been a problem for pine growth. The concentrations of P, K, Ca, Mg and Fe at Cadogan's Bog are lower than peat samples collected from an undrained area of soligenous valley fen at West Sedgemoor (Heathwaite, 1990) and are comparable with total nutrient concentrations from a weakly minerotrophic peat in Newfoundland (Pollett, 1972). The Ca, P, Mg and Fe concentrations at Cadogan's Bog are much lower when compared to highly minerotrophic peats, and the differences are greatest during zones CB5 and CB6 when concentrations of P and Ca compare more favourably with ombrotrophic peat. P concentrations also regularly fall below concentrations of 600 to 750 $\mu\text{g g}^{-1}$, determined by Beltman *et al.* (1996) for fens in western Ireland and concentrations reported by Brække (1987) but are higher than those reported from blanket peats (Walsh and Barry, 1958).

Table 5 presents average nutrient concentrations for the Cadogan's Bog and the range of concentrations, based on experimental work, that can impair pine tree performance. P, K, and Mg concentrations analysed from the peat all occur within this range. Data derived from surface samples of Llyn Mire in mid-Wales, which currently supports Scots pine, are also shown. Concentrations of P are comparable with Cadogan's Bog while K concentrations are much higher. However, the concentrations for Cadogan's Bog are average concentrations for the whole sequence. Much lower concentrations occur between 50 and 20 cm and are within or below Ingestad's (1962) range for deficiency symptoms.

A direct comparison between total peat concentrations and foliar concentrations must be treated with caution. The total peat concentration does not always represent the amount of nutrients present in the soil or peat in a form available for plant uptake, that is, in the porewater or the exchangeable fraction. Available forms of Ca, P and Mg are all considerably lower than total concentrations in the Newfoundland peats (Pollett, 1972). Thus, it is plausible that the exchangeable fraction at Cadogan's Bog will only account for part of the total and therefore, if measured, would be lower than the average total concentrations shown in Table 5.

Table 5 A comparison of the average nutrient concentrations for Cadogan's Bog peat with foliar concentrations based on nutrient solution culture experiments expressed as % dry weight (after Ingestad, 1962, as reported by Carlisle and Brown, 1968)

Element	Peat	Optimum foliar nutrient concentration for maximum growth	Nutrient deficiency concentration ¹	Llyn Mire ²
P	0.047	0.15–0.4	0.06–0.1	0.044–0.067
K	0.034	0.9–1.6	0.3–0.4	0.24–0.35
Ca	0.237	0.04–0.3	0.05	NA
Mg	0.0725	0.12–0.18	0.06–0.09	NA

¹Levels at which nutrient deficiency symptoms become visually apparent and growth markedly reduced in Scots pine when foliar concentrations drop to or below the stated figures.

²Range of dry weight percentages for parts of the mire that currently support *Pinus sylvestris* L.

P is the main nutrient limiting the growth of forest trees in Ireland (Carey and Hendrick, 1986) and the decrease in P at Cadogan's Bog during the loss of pine *c.* 4000 years BP could have been critical. Waughman (1980) and Beltman *et al.* (1996) have demonstrated that P content in fens and bogs in western Ireland can be highly variable and that fen sites can suffer from P shortages especially in extractable P. Lower P availability in fens is thought to be the result of either bonding or the formation of Al, Ca and Fe phosphates (Doughty, 1930; Kaila, 1959; Waughman, 1980; Boyer and Wheeler, 1989; Nieminen and Jarva, 1996; Silfverberg and Hartman, 1999). Therefore the amount of extractable P can be as little as 2–8% of total P (Brække, 1987). Ca and Fe might be controlling P availability on Cadogan's Bog. It is also interesting to note that pollen taxa associated with minerotrophic peat, such as *Potentilla*-type, *Succisa* and *Osmunda*, also decrease in representation during zone CB6 and this might imply they are also responding to nutrient depletion. However, the mineral requirements of plants do vary (Malmer and Sjörs, 1955) and other parameters will also influence their presence.

K limitations can also affect Scots pine growth on mires including *Carex* rich, pine fens and other types of minerotrophic fens (Wells and Miller, 1994; Kaunisto *et al.*, 1999; Silfverberg and Hartman, 1999) and mild to moderate symptoms of K deficiency have been observed in forest crops from northwestern Irish blanket peats (O'Carroll and McCarthy, 1973). Its retention in peat is dependent upon the availability of exchange sites (Malcolm and Cuttle, 1983a; 1983b) but K and Ca are particularly prone to leaching as nearly all K is in an extractable form in peat while extractable Ca can be up to 83% of total Ca (Brække, 1987). Therefore the loss of K and Ca via increased leaching during zone CB5 might have helped to cause the loss of pine from the bog and the low concentrations of most of the elements measured during zone CB6 possibly helped to prevent new saplings from developing.

While the peat chemistry data suggest that Cadogan's Bog may have been sufficiently depleted in key elements to induce tree mortality and to prevent new saplings, one limitation of this study is the lack of data to establish more directly the nutritional status of the pine trees before their death. This is often gauged in modern stands by foliar analysis (Miller *et al.*, 1992; Silfverberg and Hartman, 1999). Unfortunately, an examination of the peat either side of the decline in pine pollen at Cadogan's Bog did not yield any pine needles.

Pine pollen representation, and therefore inferred woodland presence, does not recover at Cadogan's Bog. No pine macrofossils are recorded above 45 cm and pollen percentages fall below 9% and 3% TLP at 50 cm and 34 cm, respectively (Figure 3). The failure of many pine populations to re-establish themselves on mires has been well documented, although some outlier populations, mainly on mineral soils but also peat bogs, appear to have persisted well into the late Holocene in SW Ireland. In the Killarney valley, the results of pollen studies from small hollows in local woodlands suggest that pine survived until around 2000 years BP (Vokes, 1966; O'Sullivan, 1991; Mitchell, 1988; 1996; Cooney, 1996; Little *et al.*, 1996). However, close by on the Muckcross Peninsula the *Pinus* decline at Camillan Wood was dated to 3700 years BP and such variations suggest that the history of *Pinus* in the Killarney area is complex (Mitchell, 1988; 1996). Elsewhere, Dodson and Bradshaw (1987) note that a small resurgence of pine pollen occurs between 3100 and 2600 years BP and from 2400 to 2000 years BP, before probably disappearing at Slish Lake in Co. Sligo by *c.* 1700 BP. There is also evidence for pine stumps growing on mires during the later Holocene. In the Glenveagh National Park in County Donegal, pine stumps have been radiocarbon dated to 3880 ± 110 and 3850 ± 100 years BP (Telford, 1977), while radiocarbon dates of 1790 ± 95 and 1810 ± 95 years BP were determined from two pine stumps

in blanket bog at Ladies View, Killarney (Mitchell, 1996). A pine stump has also been dated to 1620 ± 130 BP at Clonsast Bog (Mitchell, 1956; McAulay and Watts, 1961).

The recovery and/or continued presence of mire-rooting pines is thought to have been largely controlled by mire hydrology and that pine populations persisted in areas remote from human activity or on dry land (McNally and Doyle, 1984; Bridge *et al.*, 1990) but the evidence presented here suggests that in certain areas increase mire surface wetness, possibly combined with mineral deficiency, could prevent the re-establishment of pine on peat bogs. Pine pollen concentrations and percentages only begin to recover in the uppermost part of zone CB7 and this pollen is probably derived from planting during the historic period.

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