

Lags in adjustment of vegetation to climate caused by the pace of soil development: Evidence from Britain*

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Abstract

In areas such as parts of Britain where many closely spaced sites have been investigated, between-site diversities prevent any simple correlation between vegetation response and climatic variables. These diversities reveal the influence of other factors in modulating this response. Analysis of profiles of allochthonous lake sediments has provided evidence for the importance of soil factors. The otherwise inexplicable spatial variation in the response of trees, in Britain and neighbouring parts of the European mainland, to the climatic warming (inferred from faunal evidence) at the most recent glacial termination, can be explained by the postulated spatial differentiation of raw skeletal soils. Differences in particle-size, composition and drainage, consistent with the spatial differentiation of pre-arboreal vegetation, would affect the water-retaining capacity of immature late-glacial soils and hence the reproductive success of tree birches. The lag in response of these to climatic amelioration appears to have varied from 500 to 1500 yr, and it seems likely that a similar lag may have characterised the early warming period of each interglacial. The conclusion must be that in this situation the degree of success of trees measured by pollen values is not a reliable indicator of palaeotemperatures. Secondly, it appears from evidence in northern Scotland that at an ecotone between forest types, the relation between vegetation and climate is likely to be obscured except in regions of uniform soils. In areas of differentiated bedrock, the vegetation pattern is likely to have been influenced most by the effects of soil maturation processes in developing a soil mosaic.

Introduction

The clear correlation between climatic variables and the major vegetation types, which is apparent on a global or continent-wide scale, declines and becomes obscured within the smaller-scale pattern of a region as geologically and topographically di-

verse as the British Isles. Here the differentiation of the remaining natural vegetation, and the distribution ranges of many species, show the strong influence of soil type. Much of the present pattern can be explained more readily in terms of the soil factor than by any feature of the climate (e.g. Tansley, 1939; Pearsall, 1950). Therefore in the interpretation of the palaeoenvironment from palynological data, it at once appears necessary to take into account the probable importance of soil factors in the past, and particularly their role in determining the degree of local success of newly arriving species – and hence the size of the plant populations. This introduces complications into attempts to relate the abundance of a species to climatic variables – e.g. temperature. Andersen (1957) and Iversen (1958)

* Nomenclature follows Tutin *et al.* (1964), *Flora Europaea*.

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developed the concept of soil dynamics through an interglacial cycle, outlining the progress through time at each site from immature (protocratic) to mature (mesocratic) soils, and hence to the impoverishment and acidification expected late in each cycle (terminocratic). Though basically controlled by the major climatic cycles (Milankovitch), the *rates* of soil changes must have been strongly influenced by the nature of the parent material and other local factors, so the soil cycle would be highly variable. Local variations in bedrock, substratum, topography and drainage must have determined the point in the transition from protocratic to terminocratic soils which had been reached at each site at the time of arrival of each migrating species. Assuming that each species was dispersing within the broad limits of its climatic tolerances, the initial degree of success of each would depend upon its reactions to the soils as it found them. If after critical examination of the data we agree that modern palynology can presume to assess the size of past populations (cf. Watts, 1973; Bennett, 1983) it remains a complex exercise to attempt to sort out the controlling variables.

The change from raw (*sensu* Iversen, 1973, p. 26 and immature to fertile and mature soils (protocratic to mesocratic) involves two independent processes, which both begin to operate at a climatically determined point, when freeze-thaw cycles cease to be seasonally regular. Soil stability then replaces the continuous disturbance associated with the periglacial environment. *Process 1* involves the accumulation of soil organic matter, with consequent increase in water-retaining capacity and in available nitrogen, and the establishment of a soil microflora, including mycorrhizal species. This represents soil improvement—upgrading. *Process 2* involves leaching — the removal by percolating rainwater of soluble mineral nutrients — and leads eventually to the acid soils of the terminocratic stage; this represents soil impoverishment—downgrading. It will be suggested in this paper that Process 1 (upgrading) would initially proceed slowly in the coarse-textured soils derived from fluvioglacial outwash or aeolian deposition, and more rapidly in areas — often nearer to the sources of ice-sheets — where the skeletal soils were tills deposited *in situ*, often derived from igneous or metamorphic bedrock and including a wide range of particle-size and a rich vari-

ety of mineral nutrients. Process 2 (downgrading) would be expected to proceed more rapidly in the areas of Palaeozoic uplands and high precipitation which had been areas of ice accumulation. The complex interaction of these processes in the British Isles has produced situations in which the response of terrestrial vegetation to climatic changes has inevitably been more complex than has that of other biota — e.g. the open-ocean plankton or the terrestrial insect assemblages.

Among the questions addressed by other contributors, it is Ritchie's (1986) No. 3 — to what extent is the vegetation response modulated by non-climatic factors? — with which I shall be concerned. My examples are drawn from western Britain, an area which has been investigated in close detail. Two of the 'independent measures of climatic change' seen as desirable by Ritchie are available for north-western Britain, in the results of 1) much work on fossil insect assemblages (Coope, 1970; 1977; Coope & Brophy, 1972; Bishop & Coope, 1977; Coope & Joachim, 1980) and 2) climatic reconstructions from the geomorphological evidence on Younger Dryas glaciers (Sissons, 1980).

The slow pace of Process 1 in all but exceptionally favored localities will be invoked to explain the lag of 500–1500 yr in the response of trees to climatic warming — deduced from the open-ocean plankton — 13500–13000 yr B.P. (Ruddiman *et al.*, 1977; Ruddiman & McIntyre, 1981). The rapid pace of Process 2 on the oceanic fringe of northern Europe will be invoked to explain a vegetation mosaic which bears no discernible relationship to any climatic variable; the mosaic can be explained on the supposition that certain soils were already inhospitable to the more demanding forest trees by the time these arrived.

The vegetation patterns to be reconstructed here are small-scale, based on a large number of investigated sites in an area of ca. 500 × 500 km. A small-scale consideration of these problems encourages agreement with Salisbury's warning (1926) that 'mere correspondence of the limits of distribution of a species or community with isothermal lines, or any other climatic limits, is at the best presumptive evidence and no proof of any causal connection between them.' Perring & Walters (1962) show similar caution.

The late glacial lag

Late-glacial vegetation in Britain; a lag in the adjustment of vegetation to climate explained by the slow pace of soil maturation

*a. The problem and its background: tree birches (*Betula spp.*) and the vegetation which preceded them*

The problem is why, in the words of Ruddiman *et al.* (1977) 'the British arboreal pollen response to an actual atmospheric climatic warming that occurred about 13500 [yr] B.P. lagged as much as 1500 yr or more behind the faster response of the insects (Coope, 1975), the aquatic pollen (Iversen, 1954), the coastal molluscs (Mangerud & Gulliksen, 1975) and the open-ocean planktonic foraminifera (Ruddiman & MacIntyre, 1973)'. The quoted figure of 1500 years refers to sites in Britain where the main expansion of percentage pollen values of *Betula* has been dated by ^{14}C to the years between 12000 and 11500 yr B.P. (e.g. Simpkins, 1974; Birks & Mathewes, 1978; Beckett, 1981). At these and at many undated sites (Fig. 1) the response of tree birches appears to have been similar in timing to that on the European mainland where – at an early stage in the development of the subject-percentage curves for *Betula* (e.g. Iversen, 1954) became transformed into temperature curves used to define the well-known sequence of interstadials and stadials (Andersen *et al.*, 1960, Van der Hammen *et al.*, 1967). The assumption here was

that the development of birch woodland (= discontinuous forest) was a valid index to climate. It has now been established in Britain that this assumption is not true.

Coope's work on fossil insect faunas has shown (Coope, 1970; 1975; 1977) that thermophilous faunas were present in abundance from some date between 13500 and 13000 yr B.P. Therefore Iversen's hypothesis (1954) that the tree birches must have lagged in response, behind the warmth-demanding water plants, must be expanded to accommodate a much longer lag than he envisaged. Critical ^{14}C dating is not possible in material as low in organic matter as these oldest deposits of the British late-glacial period (Sutherland, 1980), but the consistency of Coope's dates with those of Ruddiman

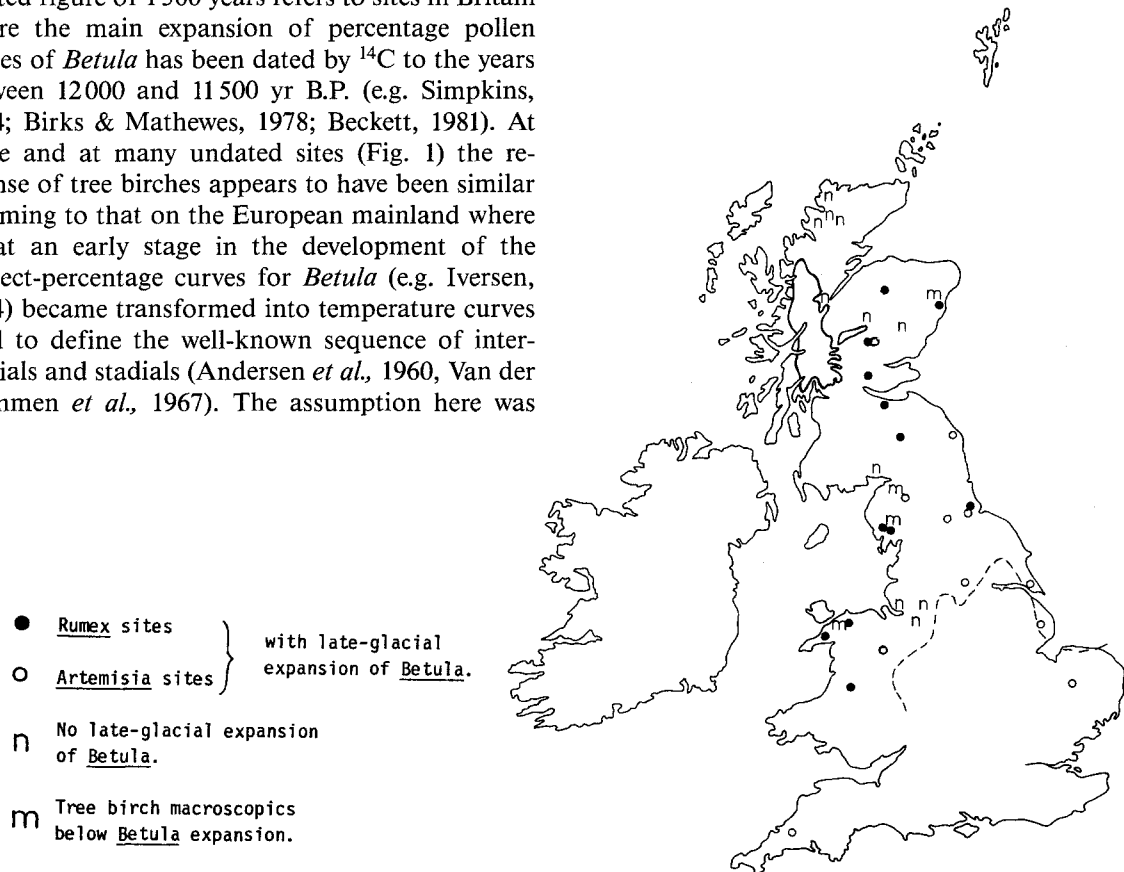


Fig. 1. Selected late-glacial sites in Britain; limits of last main glaciation (Devensian) (broken line) and Loch Lomond Advance (L.L.A.) glaciation (continuous line) are shown, with the exception of small cirque glaciers of L.L.A. age in the mountains of Scotland, N.W. England and N. Wales. References additional to those in text: Beales (1980), Hunt & Birks (1982), Pennington (1964; 1973), Suggate & West (1959), Walker (1966).

& McIntyre for the 'atmospheric climatic warming' is evidence that by 13 000 yr B.P., summer temperatures in Britain, as reconstructed from present ranges of many species of insects, must have been sufficiently high for tree birches. The difference in ^{14}C age between 13 000 yr B.P. and the date of the main increase in *Betula* pollen shows the length of the lag at each site (Fig. 2). Accumulating evidence from ^{14}C -dated profiles in Britain has demonstrated a spatial and temporal pattern of variation in the response of the tree birches – i.e. in the length of the lag – which cannot readily be explained in terms of any climatic variable. The lag is shortest at sites in north-west England (Pennington, 1975, 1977) and central Scotland (Lowe & Walker, 1977) where the expansion of *Betula* has been ^{14}C dated to 12 500 yr B.P. or soon after. The latest expansion of *Betula*, i.e. the longest lag, is found at sites near both the west coast of Wales (Simpkins, 1974) and the east coast of England (Beckett, 1981); cf. Fig. 2.

This lag cannot be explained by Iversen's interpretation of the record on the European mainland – that the rate of migration of trees would be slower than that of the water plants. Macroscopic remains of tree birches, including catkin-scales which are not transported to any distance (Great-Rex, 1983), have been found at widely separated sites below the late-glacial expansion of percentage pollen values of *Betula* (Fig. 1). This expansion – 'the British arboreal pollen response' of Ruddiman et al. (op cit.) – cannot therefore be related to the time of arrival of tree birches. The trees must have been present as individuals or small groups over a wide area (see the pollen map for Europe at 13 000 yr B.P. in Huntley & Birks (1983)). It has been inferred by the various authors that an expansion of these small units to form woodland is indicated by a sustained increase in *Betula* pollen percentages to form a well-defined maximum of more than 20% total pollen.

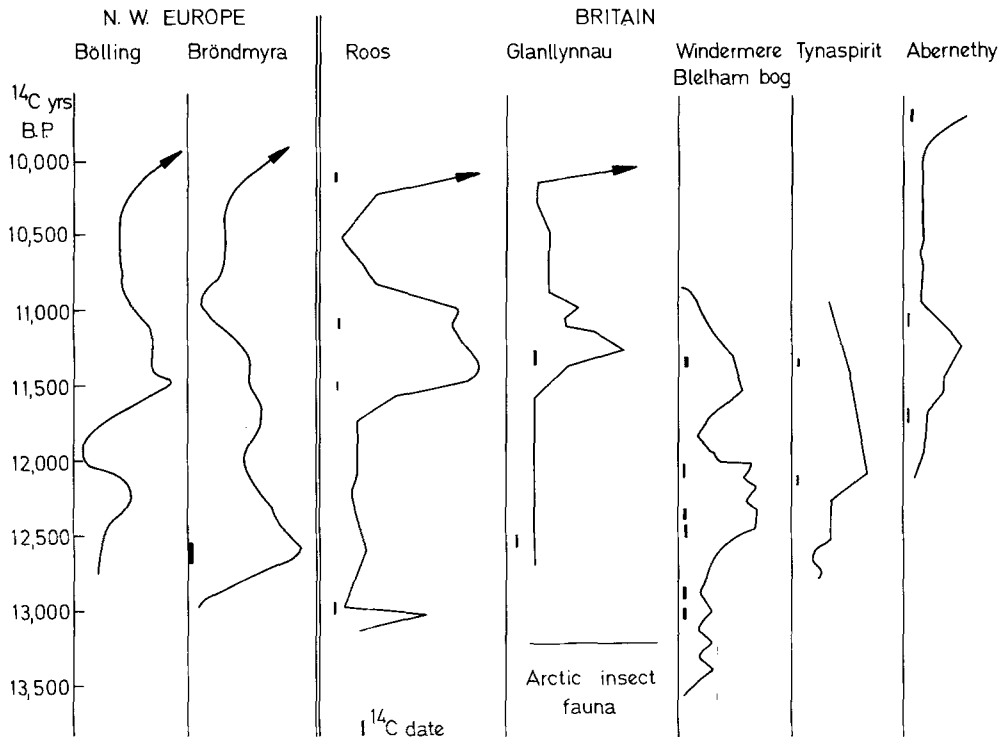


Fig. 2. Percentage curves for *Betula* pollen, 13 000–10 000 yr B.P., for ^{14}C dated sites in Britain, Roos (Beckett, 1981), Glanllynau (Simpkins, 1974), Windermere (Pennington, 1975, 1977), Tynaspirit (Lowe & Walker, 1977), and Abernethy (Birks & Mathewes, 1978); compared with those for two classical sites on the mainland of Europe: Bölling (Iversen, 1954) and Bröndmyra (Chanda, 1965).

The lowest (earliest) fruits and catkin-scales of tree birches in late-glacial deposits have been referred to *Betula pubescens* Ehr., on grounds which are listed by Godwin (1975, p. 254), e.g. Pennington, 1947. Macroscopic remains identified to *B. pendula* were found only at higher (younger) interstadial levels (e.g. Franks & Pennington, 1961). *Betula pubescens sensu lato*, or *B. pubescens* Ehr., coll., represents a circumpolar complex of which the taxonomy is much disputed (Hulten, 1971; Walters in Tutin et al., 1964), and it seems unlikely that the genotype of late-glacial tree birches will ever be known. At most sites from which macroscopic remains have been recovered, the dwarf birch *Betula nana* was present, and some fruits and catkin-scales have been referred to hybrids between it and the tree species. The well-known difficulty in quantitative separation between pollen of *B. nana* and that of the tree birches is recognised by the authors concerned, but the sustained increase in total *Betula* pollen to a well-defined maximum of more than 20% total pollen is, at the sites shown in Figs. 2 & 3, described by the authors as consisting mainly of grains of undoubted tree birch type. Fig. 2 shows the diversity in timing and amplitude of this expansion which makes it impossible to interpret it as a simple response to temperature.

Lack of information on the late-glacial genotype precludes exact comparisons with climatic requirements deduced from the ranges of modern populations, but Iversen's view that the presence of *B. pubescens* (together with its usual late-glacial associates) indicates 'a temperature in July a little above 10°C' (Iversen, 1954, p. 94), in conjunction with the July temperature inferred by Coope (op cit.), is consistent with the argument that summer temperatures were not the limiting factor in the expansion of scattered tree birches to form woodland.

Since 'the British arboreal pollen response' shows by its diversity an inability to relate to migration routes or patterns of summer temperatures, how can it be explained? The generally dry late-glacial climate in Britain postulated by Ruddiman & McIntyre (1981) makes it unlikely that precipitation gradients were involved. But in such a dry climate, the capacity of local soils to retain water is likely to have been critical to the success of *B. pubescens* coll.; modern populations have been shown to be susceptible to moisture stress.

The effect on the success of tree birches of the

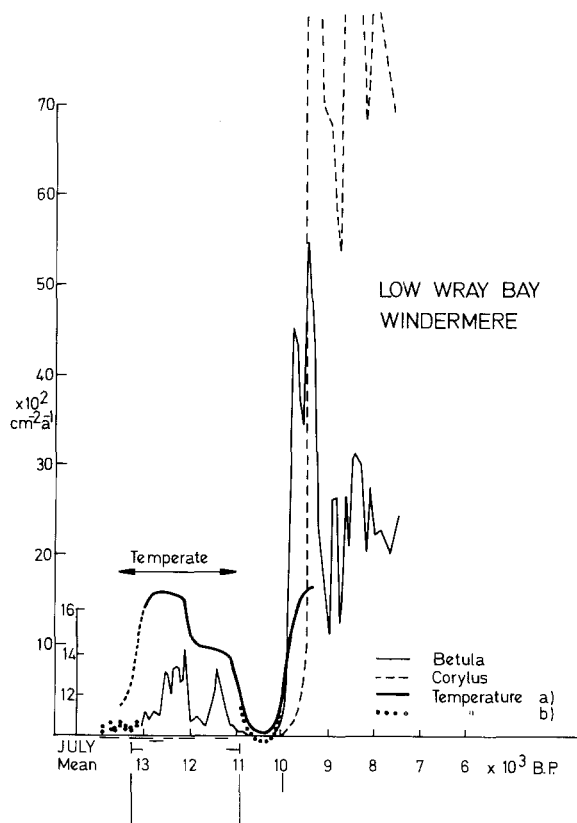


Fig. 3. Low Wray Bay, Windermere, i. (Pennington, 1977; Coope, 1977). Annual deposition of *Betula* pollen (cm^{-2}), compared with palaeotemperatures reconstructed from a) present distribution of fossil insect species and b) reconstructions of L.L.A. glaciers (Sissons, 1980). (No arctic insects at 14×10^3 B.P.; macroscopics from $13-11 \times 10^3$ B.P.; Windermere interstadial; Loch Lomond Stadial $11-10 \times 10^3$ B.P.).

raw late-glacial soils postulated by Iversen (1954) has been considered by Pennington (1977; 1981) and Coope & Joachim (1980). In the light of evidence from allochthonous lake sediments in Windermere, England, where the late-glacial sediment profile represents a time-series of late-glacial soil samples, I suggested in 1981 that 'one factor inhibiting the immediate expansion of *Betula pubescens* on its arrival was the almost completely immature state of the local soils.' Differentiation of soils would have taken place because of local differences in substratum, relief and drainage, affecting the rate at which soil organic matter accumulated, under Process 1. These can be invoked to explain spatial and temporal differences in the

pollen record of *Betula* populations which are impossible to explain in terms of climatic variables.

Some insight into late-glacial soil patterns can be obtained from the pattern of vegetation before the 'arboreal pollen response' – i.e. before the widely present but isolated birch trees increased to form areas of open woodland. The tundra vegetation was clearly differentiated. The shortest lag behind the atmospheric warming is found at sites where the lowest pollen zones are characterised by *Rumex*; these lie in or near the areas of ice accumulation in the west and north, and on the European mainland include Bröndmyra in south-west Norway (Faegri, 1953; Chanda, 1965). The longest lag in expansion of *Betula* is found at sites in the lowlands of Britain, in areas of glacial deposition by outwash, or aeolian sands, where the early pollen zones are characterised by *Artemisia*, as at the classical Continental sites including Bölling (Iversen, 1954). Huntley & Birks (1983) give pollen maps for Europe for *Rumex* and *Artemisia* at 13000 yr B.P. – based on selected sites – which bring out this pattern.

On the continent-wide scale this pattern could be related to a postulated pattern of precipitation – species of *Artemisia* being often associated with arid soils while species of *Rumex* are not (Huntley & Birks, 1983). However the British pattern of early late-glacial vegetation shows an intricate boundary between *Rumex* and *Artemisia* sites (Fig. 1) which corresponds quite closely with soil differences resulting from contrasts in the nature of the skeletal soils left on deglaciation. In certain parts of Britain, e.g. north-west England and the plain of Cheshire bordering N. Wales, the within-region differentiation between *Rumex* and *Artemisia* sites is related to the contrast between outwash sands and gravels on one hand (the *Artemisia* sites) and on the other, clay-rich tills deposited by ice which originated on mountains of igneous or metamorphic bedrock. It is postulated that these latter soils, which supported a rich vegetation of 'meadow' type characterised by *Rumex* (mainly *acetosa*) and grasses, were widespread in the glaciated north and west (Fig. 1) and matured more rapidly to a water-retaining capacity capable of supporting adequate success in reproduction by the tree birches. The shortest lag (c. 500 years) in the 'arboreal pollen response' behind the climatic warming shown by the change in insect assemblages is found at *Ru-*

mex sites, e.g. Windermere and Blelham Bog (Fig. 2), – though of course some *Rumex* sites in N.W. Scotland lay outside the area of any late-glacial expansion of tree birches (Pennington, 1975). In contrast, the long lag before the major expansion of tree birches found at sites in eastern England (Beckett, 1981) and at the classical sites in Denmark, coincides with lowland areas where the glacial deposits are base-poor coversands and outwash deposits: here the local presence of *Artemisia* shown by the pollen assemblages indicates open communities and suggests a slow rate of soil maturation under process 1.

b. The lag in tree response at Windermere (north-west England) – a Rumex site for which there are independent estimates of palaeotemperatures

It was at this site in England that ¹⁴C dating first revealed a surprisingly early late-glacial expansion of tree birches (Godwin, 1960; Pennington, 1970). The date has since been confirmed by a long series of ¹⁴C dates both here (Pennington, 1977) and at the neighbouring site Blelham Bog (Pennington, 1975). It is however apparent from results of detailed work on insect remains in this profile (Coope, 1977) that the summer temperatures reconstructed from present ranges of the fossil insects were suitable for tree birches for at least 500 yr before the first expansion of pollen percentages of *Betula*. Fig. 3 compares Coope's curve for mean July temperature at this site with annual deposition (influx) of *Betula* pollen, and the occurrence of macroscopic remains of tree birches. Percentage and absolute pollen values agree in showing that the main expansion of tree birches took place at c. 12500 yr B.P.

This initial lag in development of the birch populations contrasts with the closer relationship between them and the curve for summer temperatures through the period until 9000 B.P.: Fig. 3. This agrees with the hypothesis that the early situation – that of extensive barren regions carrying only raw mineral substrata – was unique. Once a maturing soil profile was established, there was then a close relationship between the success of tree birches and the fluctuating temperatures of the north European late-glacial period. These fluctuations include the falls in temperature at ca. 12000 and 11000 yr B.P., and the rapid rise at the opening of post-glacial (Holocene) time. The only dis-

crepancy after 12500 yr B.P. concerns the rise of *Betula* pollen to a second peak during Allerød time – as if the decline in pollen deposition at 12000 yr B.P. represented a temporary check to the birches, and was followed by recovery (Pennington, 1981). There is a clear and strong contrast between the initial lag of the birches behind rising temperatures, and the simultaneous steepest rise in deposition of birch pollen and summer temperatures (estimated from insect assemblages) after the cold period of deposition of glacial varves in Windermere. This can readily be explained in terms of soil processes; though during the first part of the Loch Lomond Stadial (Younger Dryas), temperatures fell below those required by trees, the areas of glaciation were limited to the mountain groups, and outside these, periglacial processes were not sufficiently disruptive to destroy late-glacial soil profiles and their accumulated humus content. In all lake sediments investigated in north-west Britain there is a rapid restoration of the organic content from 10000 B.P. – i.e. at the end of the Loch Lomond Stadial (Pennington & Lishman, 1971). This agrees with the rapid establishment of equilibrium between the rising temperatures and the increasing populations of tree birches.

Comparison with sites outside Britain can be made using Fig. 3, which summarises the information from the dated Windermere section on the relation between the annual influx of *Betula* pollen (considered to be the best quantitative index of local tree birches) and the curve for mean July temperatures, inferred from the insect evidence (Coope, 1977) and from local glacier reconstructions (Sissons, 1980). Confirmatory pollen evidence and ^{14}C dates are available from the neighbouring kettle-hole site of Blelham Bog (Pennington, 1975) but here the insect remains were too few to produce an insect diagram. In the Windermere section the deposit of ca. 500 annual glacial varves overlies the organic interstadial sediments, the stratigraphic boundary falling close to 11000 yr B.P. (Pennington, 1977), so the end of the period of mountain glaciation (the Loch Lomond Advance of Sissons) is dated to ca. 10500 yr B.P. The correlative stratigraphic boundary at Blelham Bog, between solifluction clay and overlying lake mud of low organic content, is bracketed by ^{14}C dates of 10650 ± 170 and 10490 ± 160 yr B.P. (Pennington, 1975). On stratigraphic evidence, therefore, a rise in tem-

perature at ca. 10500 yr B.P. has been postulated (Fig. 3). At both sites the sediments of ^{14}C age ca. 10500 – 10000 yr B.P. correspond with two pollen zones – a *Rumex*-Gramineae-*Empetrum* zone passing upwards into a juniper zone, within which percentages and annual influx of *Betula* begin a slow rise. This I interpret as an immediate response to rising temperatures by plants already present locally, and a slower response by tree birches which had been eliminated from this catchment of high relief by the severity of climate between 11000 and 10500 yr B.P. The steep rise in influx of *Betula* at ca. 10000 yr B.P. indicates the arrival and immediate rapid expansion locally of the tree birches; at this site this coincides with the most steeply rising portion of the temperature curve inferred from insect evidence. The lag of three to five centuries between the first rise of the temperature curve and the local expansion of post-glacial birch woodland is therefore explained by the time required for birches to return to this area. At this time there was no lag because of soil conditions.

This sequence seems analogous to the 'time lag for the response of the terrestrial vegetation which can be estimated to ab. 300 years' described by Berglund *et al.* (1984) from Håkulls Mosse in S.W. Sweden, though these authors have not yet published an analysis of the processes responsible for this lag.

Fig. 4 illustrates in the Windermere section the relationship between annual deposition of pollen per square centimetre (influx) – both *Betula* and total – and the curves for nitrogen and carbon (per cent dry weight) which are interpreted as an index to changing soil organic matter. The horizon of the climatic warming is placed at 45 cm, the boundary between a lower pollen zone characterised by *Salix herbacea*, and the *Rumex*-Gramineae pollen zone, in which are found macroscopic remains of *Betula cf. pubescens* and pollen of *Typha latifolia* (indicative of summer temperatures of 12–13 °C (Van Geel *et al.*, 1980)). From this horizon there is a simultaneous rise in annual deposition of *Betula* pollen and in carbon and nitrogen, but the increase in *Betula* is checked. This check represents a lag specific to the tree birches, since the increase in total annual pollen deposition is sustained. Since macroscopic remains are present, this check is interpreted as reflecting a limit to the local success of tree birches, until their main expansion at 12500 yr

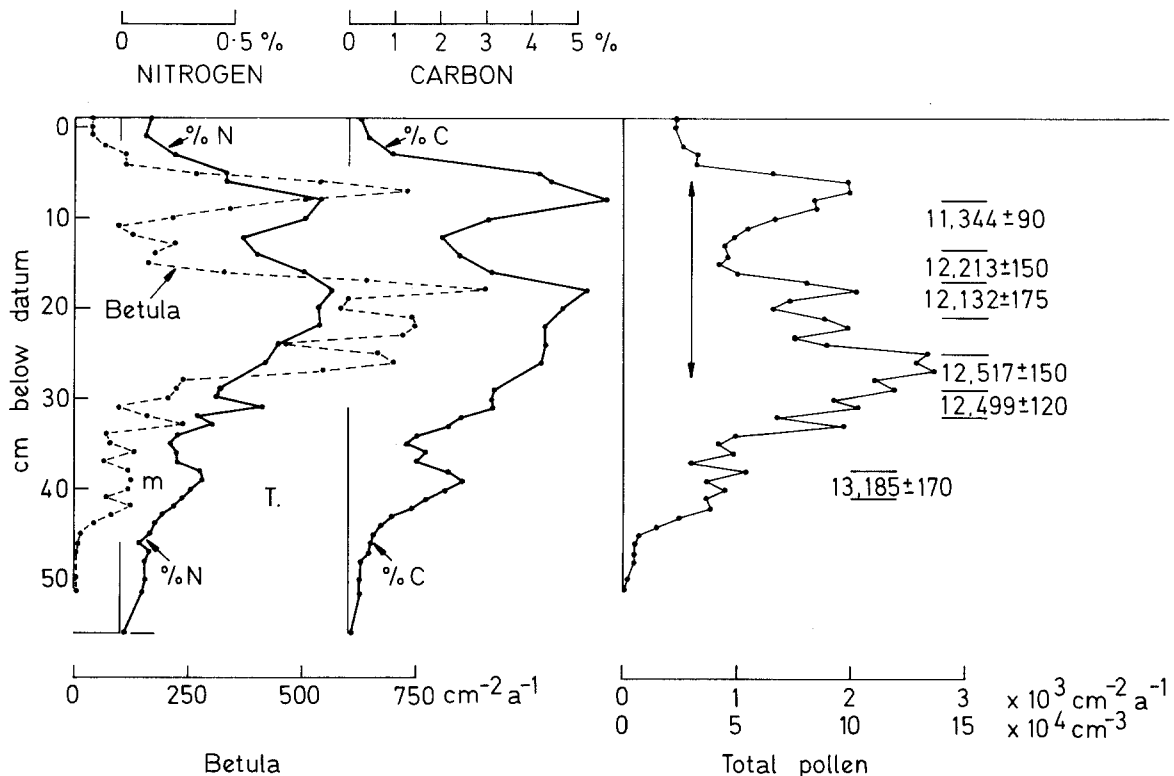


Fig. 4. Low Wray Bay, Windermere, ii. Annual deposition of *Betula* and of total pollen compared with the organic content of sediments – nitrogen and carbon as percentage of dry weight. ^{14}C dates are SRR-669, -670, -671, -673, -674 (Pennington, 1977). Lowest sample analysed represents upper boundary of lower varved clay (no pollen). Uppermost sample analysed represents lower boundary of upper varved clay (Loch Lomond Advance). Vertical arrow spans the section of maximum, and m=lowest, tree birch macroscopic remains. T=pollen of *Typha latifolia*.

B.P. The irregular rise in nitrogen and carbon continues until ca. 12000 yr B.P. From these data it is postulated that not until ca. 12500 yr B.P. were the soils in general sufficiently organic to provide adequately for the water requirements of an expanding population of tree birches.

The credibility of annual pollen deposition rates as a measure of the size of tree birch populations is supported for the Windermere site by comparison with the pollen record from three neighbouring but contrasted sites – Fig. 5. Details of the sites are given in the legend. Comparison of the influx diagrams suggests that at sites within 200 m of pollen sources, annual deposition of *Betula* pollen reached 500–1000 grains cm^{-2} at times during the late-glacial interstadial, but not before 12500 yr B.P. At site 4, in a large lake, annual deposition did not exceed 500 cm^{-2} . Site 3, in the upland near the

head of the Windermere catchment, shows a delayed maximum in deposition interpreted as the effect of higher altitude, and the persistence of high values after 11000 yr B.P. has been attributed to secondary deposition from soil disturbance at this altitude (Pennington (1973) and cf. Larsen *et al.* (1984)). These comparable values for pollen deposition rates in contrasted basins suggest some confidence in interpreting the sequential record from each basin as an index to plant populations.

c. Tree birches and soils – possible reasons for the initial lag

The question of what caused the initial check to the success of late-glacial tree birches cannot be answered by the use of modern analogues, since there is no modern equivalent of the late-glacial vegetation of northern Europe (Iversen, 1954). Iversen

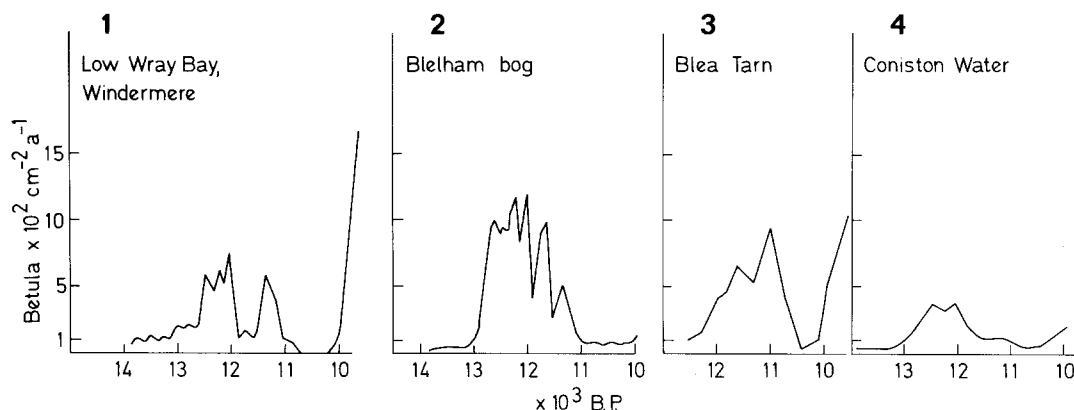


Fig. 5. Annual pollen deposition cm^{-2} of *Betula* at 4 neighbouring sites of contrasted size. Site 1 = 30 m from shore, lake water 3 m deep, in Windermere (area 14.8 km^2); 2 = enclosed kettlehole, 30 m diameter; 3 = small upland lake, 200 m diameter; 4 = 250 m from shore, midline of elongated lake of 4.9 km^2 .

compared the physiognomy of the discontinuous late-glacial birchwoods with that of the birch 'copses' of south-west Greenland, which are assumed to be growing at the climatic limit of *Betula pubescens* Ehr. coll. But lists of associated species in the Greenland copses (Elkington, 1973, 1974) bear little resemblance to late-glacial assemblages. The same applies to the pure birchwoods which remain in the extreme north of Britain today. The associated species are in general characteristic of the depauperate flora of poor and predominantly acid soils in a highly oceanic climate (McVean & Ratcliffe, 1962). They bear no relationship to late-glacial assemblages in which plants of high soil base-demand and comparatively high summer temperatures – e.g. *Hippophae*, *Helianthemum* – were conspicuous, and in which *Calluna* – an almost invariable associate today – was rare or absent (Pennington, 1977). In this situation of no analogues for the late-glacial pollen assemblages and uncertainty about the genotype of late-glacial tree birches, no exact comparisons can be made with distributions and physiological tolerances of modern plant populations.

Some general attributes of tree birches do however, offer clues to their degree of late-glacial success. In attempts to explain the apparent anomaly of thermophilous insect assemblages in a treeless landscape, Coope (in: Coope & Joachin, 1980) has stressed the susceptibility of birches to drought, and postulated that the development of birch

woodland was limited by the dry climate (cf. Iversen, 1954). Coope and others commented on the death of many birches in the exceptional drought of 1976 in Britain, especially those growing as pioneers on raw, freely-draining soils. The model of Ruddiman & McIntyre (1981) supports the idea of a dry late-glacial climate in Britain, by postulating that the surface waters of the North Atlantic were sufficiently chilled by melting icebergs to reduce 'moisture extraction by the atmosphere', though summer insolation was high. But in this situation of a cold ocean, it is difficult to postulate that any part of Britain was more 'oceanic' in climate, and hence it becomes impossible to explain spatial and temporal differences in success of the tree birches by supposed climatic gradients, as attempted by Pennington (1977) and Beckett (1981). It is however, possible that the late-glacial birches were particularly sensitive to soil conditions *because* of the prevailing dryness of the climate, and that a soil mosaic therefore imposed the pattern of spatial and temporal differentiation. The importance of the rate of accumulation of water-retaining humus is supported by the results of recent observations on tree birches in Britain.

If, as I suppose, at the time of the climatic warming between 13 500 and 13 000 yr B.P., tree birches in Britain were scattered (as individuals and small groups) within a tundra vegetation already differentiated according to soil type, then the problem of their response to the climatic warming was

not that of a moving forest-tundra ecotone, but rather that of what factors governed the local success in expansion of these scattered trees? Kinnaird (1974) studied the present regeneration success of *Betula pubescens* and *B. pendula* in northern Scotland, observing seedling density and survival to the sapling stage on different types of substrata, and concluded that moisture conditions 'seemed to be critical for the germination and establishment of young birch'. High seedling density was associated with flushed habitats and high seedling mortality with types of substrata which dried out rapidly (including moss carpets other than *Sphagnum*). The pattern of late-glacial success could therefore be explained by the probability that substrata would be more prone to drying out in the open communities characterised by *Artemisia*, supposedly on the coarser and more freely draining substrata, than on the more finetextured and more rapidly maturing soils of the *Rumex* province.

Under some conditions *Betula pubescens* shows a high rate of transpiration and a low efficiency of water-use (Davis & Pigott, 1982). The high rate of water absorption required is associated with its mycorrhizal roots. It may be supposed that the rate of spread of this tree into newly deglaciated regions and the neighbouring periglacial areas would be subject to a further lag until a normal soil microflora had been established.

d. Rates of soil maturation: modern evidence

The modern world cannot provide an analogue for ice-sheet decay at a glacial termination. Studies of the progressive changes in ground left bare by the recent retreat of ice fronts have suggested a lag of two to three centuries before trees became established (Faegri, 1933; Persson, 1964; Jacobson & Birks, 1980; Wright, 1984); this was under present conditions in Norway, Iceland and Alaska/Yukon respectively. It provides an estimate of the expected rate of Process 1 in the modern climate, at fairly short distances from sources of propagules for the various biota, and in the presence of plants – notably species of *Alnus* – which efficiently fix atmospheric nitrogen. However, Larsen et al., 1984, give reasons why the situation in recently deglaciated areas in front of modern glaciers 'is not a direct analog situation to Late Weichselian colonisation'. In comparison with late-glacial conditions in Britain, when sources of propagules would initially be

at much greater distance and these cold-tolerant species of *Alnus* were absent, this estimate of two to three centuries agrees reasonably well with the shortest lag in the late-glacial response of trees behind the climatic warming – 500 years. The longer lag found at other sites in Britain suggests that Process 1 proceeded much more slowly in areas of extensive fluvioglacial and aeolian deposition from an extensive and decaying ice-sheet.

Influence of soil factors on the post-glacial forest pattern

The early forest history of northern Scotland; birch, pine and oak

a. The problem and its background – the past and present forest mosaic

By 10000 yr B.P. the effects of Processes 1 and 2, acting on substrata of varied and contrasted composition, would be expected to have produced a soil mosaic sufficiently differentiated to have influenced the success of the migrating trees which followed the birches into northern Europe. Some migration patterns would be determined or modified by the influence of soil type on the success of a species in competition with those already established. An example from north-west Scotland at 58°N illustrates how the course of vegetation response to the rapid climatic improvement at 10000 yr B.P. was modulated to produce a pattern corresponding to the soil pattern. On the evidence of insect assemblages, summer temperatures rose rapidly after 10000 yr B.P. in all parts of Britain including western Scotland (Bishop & Coope, 1977). The forest patterns which then developed in N.W. Scotland reflected the competitive interactions between the successively arriving trees, birch, pine and oak; there is no independent evidence for climatic change during migration of these trees into northern Scotland. In north-west Scotland, at c. 58°N, there is no evidence for any expansion of birch woodland until some time between 9500 and 9000 yr B.P. (Lochs Sionascaig and Clair, Pennington et al., 1972), by which time local soils round Loch Sionascaig were already acid (op cit., Fig. 6). Though there are no macroscopic records of species of *Betula* from these sites, it seems likely that the species concerned was *B. pubescens* which has the

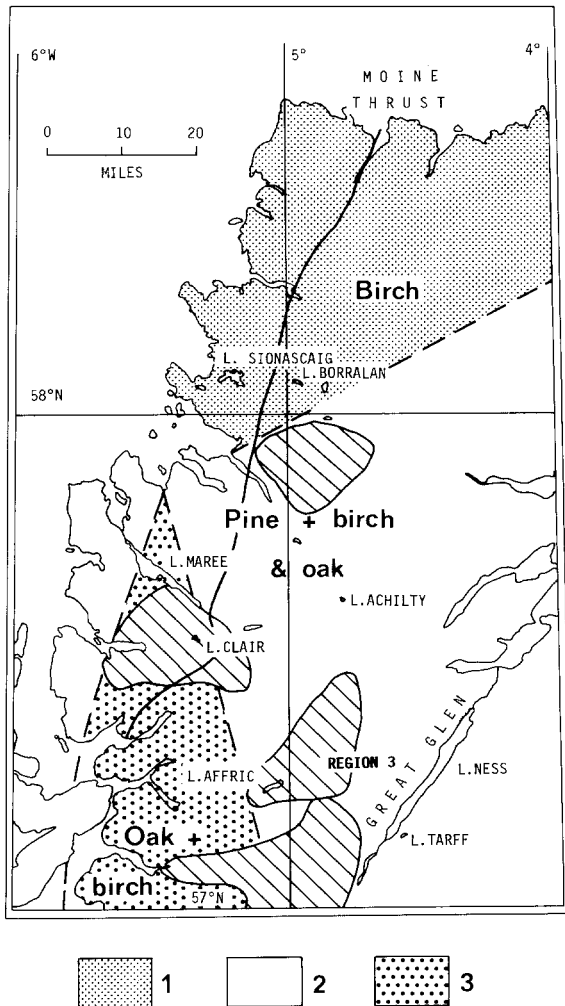


Fig. 6. Map of N.W. Scotland showing a) lakes investigated; b) boundaries of main 'tendencies of woodland distribution' (McVean, 1964); c) smaller areas (hatched) within which native pine forest fragments survive (Steven & Carlisle, 1959) and d) line of the Moine Thrust, west of which lie the base-poor rocks of the Scottish shield fragment. (1 = Birch, 2 = Pine + Birch & Oak, 3 = Oak + Birch).

more northerly range in Britain – *B. pendula* is rare in northern Scotland (Godwin, 1975). Pine, reaching this part of Scotland before 8000 yr B.P. from a postulated western refuge (Godwin, 1975; Huntley & Birks, 1983) was able to colonise such soils, to expand, and to maintain in this already 'terminocratic' situation the predominantly pine forest which represents the oceanic end of the boreal coniferous forest belt of the Eurasian continent,

here at more southerly latitudes than on the continental mainland. The post-glacial forest history of England and Wales shows that there, *Pinus* was largely displaced by *Quercus* and other deciduous trees within a short time of their arrival (Godwin, 1975). In parts of northern Scotland the persistence into later post-glacial time of pine-dominated forest can be related to the soil mosaic arising from contrasts in bedrock. In the area of north-west Scotland shown in Fig. 6, at the western sites, on the base-poor rocks of the Scottish shield-fragment, pollen values for *Quercus* show no expansion from bare 'presence'. East of the Moine Thrust (Fig. 6) the bedrock of Moine schists results in better and thicker soils in the lowlands, and there is more glacial drift. On the more favourable soils of these eastern catchments, the pollen values from Lochs Tarff and Achilty (Figs. 6 & 7) show that though the appearance of *Quercus* was later than at the poor acid sites in the west, its subsequent expansion indicates an ability to compete with pine, producing a mixed and probably altitudinally zoned forest (Pennington *et al.*, 1972; unpubl.).

b. Evidence from lakes on contrasted soils (Figs. 6 & 7)

McVean & Ratcliffe (1962) used the composition of the remaining fragments of Scottish forests and the distribution of plant communities to delimit regions of Scotland on the basis of 'natural' forest type – what would be expected in the present climate were it not for the effects of man: cf. Fig. 6. McVean (1964) considered that the present distribution of *Quercus* within its range reflects mainly edaphic factors. The pollen record of *Pinus* and *Quercus* from 3 sites within the Pine area (Fig. 7) supports this. (Percentage values only are available, but since the post-glacial rates of sediment accumulation seem to have been almost constant, and there are no obvious differences in pollen concentration, it is unlikely that influx values would change the interpretation). Fig. 7A gives these pollen values.

At *Loch Sionascaig* (see Pennington *et al.*, 1972, Figs. 4 & 6, for full diagrams) the pollen record shows only minimal traces of human influence: from the earliest times its soils must have been too poor and acid to attract settlement. Between 8000 and 4000 yr B.P. *Pinus* pollen made up to 50% of the total; from ca. 4000 B.P. *Pinus* and *Betula* were largely replaced by the taxa of blanket bog commu-

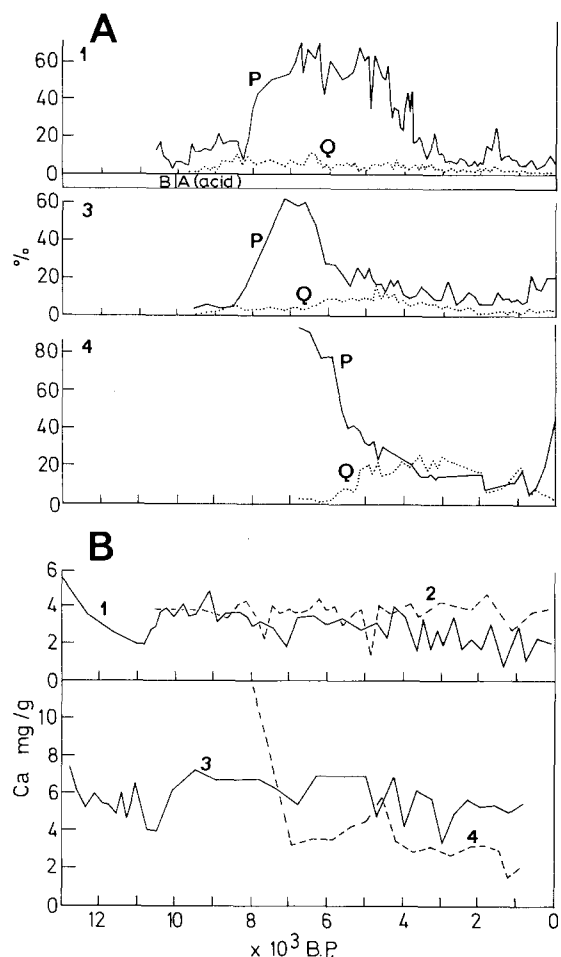


Fig. 7. Selected data from percentage curves for *Pinus* (P) and *Quercus* (Q); Scottish sites. (A) 1, Loch Sionascaig; 3, Loch Tarff; 4, Loch Achilty (see Fig. 6); (B) Calcium in sediment, % dry weight; Site 2 = Loch Clair. Note the change in humus type from B (circumneutral) to A (acid) at Loch Sionascaig.

nities. The *Quercus* curve suggests a very minor establishment by ca. 8000 B.P. and no subsequent expansion; this is interpreted as indicative of few and isolated occurrences of oak in edaphically favourable placed, comparable with its history at Loch Maree (Birks, 1972). At a horizon corresponding to a ¹⁴C date of between 10000 and 9500 yr B.P., before the local expansion of tree birches, the organic component of the Sionascaig sediment shows a transition from circumneutral to acid humus in the source material – i.e. the soils – since the ESR spectra of the humic acids change in type (Atherton *et al.*, 1967). This evidence for soil acidification ex-

plains the lack of success on the part of the oaks in competition with the pine. The geochemical analyses included total calcium (mg g^{-1} dry wt) – Fig. 7B; values for calcium were lower at the acid western sites than at Lochs Tarff and Achilty, reaching their minimal levels in the last 4000 years (when bog had replaced forest) on the Sionascaig catchment.

Lochs Tarff and Achilty lie east of the main watershed, in areas where some oak remains in the valleys – i.e. they are on the southeastern and eastern margins of the main area of surviving pine woods (Fig. 6). The profile from Loch Achilty covers only the time since 7000 yr B.P. – before that the sediments of this small lake were mainly fluvial and contained only broken pollen grains. A series of 11 ¹⁴C dates has shown that after 7000 yr B.P., organic sediment accumulated conformably and at a constant rate. This lake is still surrounded by forest, but much modified by forestry and not included in Steven & Carlisle's survey of native fragments. Pollen analysis showed however, that the oak woodland on one side of the lake is of long ancestry, and hence the site is on or near the ecotone between pine-birch and oak-birch. The well-grown oaks and rich herbaceous flora indicate a more favourable soil than at any of the western sites; this agrees with the higher pollen values for oak, ca. 5000–2000 yr ago, than at any other of these sites. At Loch Tarff the pollen values indicate a limited expansion from ca. 6000 yr B.P. – limited probably by the altitude (289 m), and at the lower altitudes competing successfully with pine. The calcium values for Lochs Tarff and Achilty are higher by up to $\times 2$ than at the western sites.

Synthesis of the pollen diagrams from sites shown in Fig. 6 suggests therefore that the early arrival of pine from a western refuge established a predominantly coniferous forest type; that oak then arrived first in the west, where it got as far north as Loch Sionascaig but was unable to expand because of prevailing acid soils already in the terminocratic stage of soil development, but that on the less degraded soils of the Great Glen lowlands to the east (Fig. 6), the oak was able to migrate north-eastward and compete on equal terms with pine and birch in the eastern lowlands and valleys.

The evidence from pollen, diatoms and sediment composition at Loch Sionascaig shows the existence of circumneutral soils and waters in early

late-glacial time, when freshly pulverised mineral substrate originating from Lewisian gneiss were available – but a rapid change from this situation under a non-forest vegetation, so that soils had become acid within 2000–3000 yr, by 9500 yr B.P. There are few estimates of the present rate of soil acidification by leaching (process 2) in an oceanic situation, but a comparable time-scale – of up to 4000 yr to podsol formation – was suggested by Burges & Drover (1953) for soil maturation on sand ridges formed as progressive beach fronts in New South Wales. The more rapid progress of soil acidification demonstrated for the post-deglaciation period at Loch Sionascaig (and assumed for the other western sites) explains the differentiation of vegetation for which a climatic cause might otherwise have been postulated. Synthesis of all the evidence, from sites on acid and on less acid soils with the estimates of summer temperatures provided by fossil insect assemblages, indicates that here the *time* of arrival of birch, pine and oak was related to migration-distance from sources, and the degree of *expansion* to edaphic factors.

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