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The Late Devensian Flora and Vegetation of Britain [and Discussion]

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The Late Devensian flora and vegetation of Britain

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[Pullout 1]

For the period *ca.* 15000–10000 years ago, which spans the interval between the latest presence of lowland ice and the final disappearance of mountain glaciers from Britain, so many botanical data are now available that it is possible to analyse plant distributions and vegetation composition in detail not yet possible for earlier periods. Species lists, provided by identification of pollen and of macroscopic remains, show a combination of diverse phytogeographic elements into an assemblage characteristic of the period – an admixture of apparently thermophilous plants with those now found in northern and arctic situations, and of oceanic and steppe elements. Ordination of data on floras has revealed much similarity between the regions of Britain, but pollen analysis continues to emphasize how strong must have been the regional differentiation of vegetation.

A comparison of pollen diagrams published since 1970, from sites lying on a broad north–south transect of western Britain, shows much variety in the pollen assemblage zones which have been distinguished, and in the vegetation interpreted from the pollen data by comparison with surface samples and modern vegetation. Sufficient ^{14}C dating is now available, however, to permit chronostratigraphic correlation of these pollen zones, and to show that there is consistent evidence for climatic amelioration at about 13000 B.P., and rapid deterioration at about 11000 B.P., leading to conditions of incomplete vegetation cover and universal soil disturbance which can be correlated with geomorphological evidence for the recrudescence of mountain glaciation in western Scotland, the Lake District, and North Wales, in the period called Younger Dryas on the continental mainland. Between 13000 and 11000 there is in western Britain evidence for a woodland biozone, or palaeobotanical interstadial, equivalent to Bølling plus Allerød of continental stratigraphers (Mangerud, Andersen, Berglund & Donner 1974), and divided by a very minor regression of vegetation during Older Dryas time (*ca.* 12000–11800). The now closely ^{14}C-dated site at Low Wray Bay, Windermere, is described in detail, and suggested as a reference site for this interstadial.

INTRODUCTION

A gap in the British plant record follows the deposition of an arctic moss flora at Dimlington *ca.* 18500 years ago. On lithostratigraphic evidence, this gap is assumed to correspond with the glacial stadial during which ice covered most of the area within the limits of Devensian till. Unfortunately there is as yet no evidence, from that part of Britain south of the ice margin, as to how much of the Middle Devensian flora survived within Britain the presumably severe conditions of this glacial maximum. The earliest post-Dimlington plant remains as yet discovered in Britain, with ^{14}C dates of *ca.* 14500, come from inside the limits of glaciation, from lake deposits accumulated within basins on the surface of Devensian gravels and till. From this time onwards there is an increasing volume of evidence on Late Devensian flora and vegetation, from both macroscopic remains and from pollen analysis, which demands more intensive comparison and analytical treatment than is possible for the sparser data from earlier periods.

From the time of the earliest investigations of the Late Quaternary deposits of northern Europe (summarized by Iversen (1973)) plant remains have been used to characterize the

Late-glacial environment. The threefold division of Late Weichselian deposits was first made in south Scandinavia on the evidence of plants identified from macroscopic remains, e.g. *Dryas octopetala*: this plant evidence agreed with lithostratigraphic divisions to indicate a threefold sequence of cold–temperate–cold environments. Pollen analysis of profiles from south Scandinavia subsequently identified the temperate substage, named for the type site at Allerød, with the zone of maximum percentages of arboreal pollen (mainly *Betula*) which became Pollen Zone II in a zone sequence I, II and III. Since then, the pattern of the percentage curve for *Betula* in pollen profiles from south Scandinavia has been widely adopted as a Late Weichselian temperature curve (see, for example, Van der Hammen, Maarleveld, Vogel & Zagwijn 1967), on the grounds, which were ably argued by Iversen (1954) that trees constitute the most reliable indicators of macroclimate and summer temperatures. Late Weichselian pollen diagrams have customarily been divided (zoned) into Pollen Zones I, II, III and their subdivisions on changes in proportions of *Betula* pollen, interpreted as showing the direct results of local responses of tree birches to the major climatic changes which independent evidence shows were included in this period.

In their Correlation of Quaternary Deposits in the British Isles, Mitchell, Penny, Shotton & West (1973) used Pollen Zones I, II and III for subdivision of the most recent Devensian deposits. Godwin (1975), in his recently published authoritative account of the history of the British flora, has continued to use these zones as the only practicable framework within which to order the great volume of Late-glacial plant records (from both macroscopic remains and pollen grains identified to species level) now lodged in the Data Bank of the Cambridge Botany School. But from 1963 onwards it had become clear that this could not be a *generally* adequate basis for division of the Late-glacial (Late Devensian) deposits of the British Isles without some further definition of Zone II. Watts (1963) showed that in some Irish profiles there is no expansion of percentages of *Betula* pollen, and Kirk & Godwin (1963) published analyses of a profile from Loch Droma in the NW Highlands of Scotland, in which there was no significant expansion of the curve for percentages of *Betula*, though macroscopic remains of tree birch indicated its presence within the Late-glacial period. Since then many published Late Devensian profiles from western Britain have shown an absence of any significant expansion of *Betula* (see, for example, Moar 1969; Pennington 1970, Fig. 6*c*, for high altitudes in the Lake District; Pennington, Haworth, Bonny & Lishman 1972, for northern mainland Scotland; Birks 1973, for parts of the Isle of Skye).

These discoveries point to an absence of any Late Devensian woodland from much of western Britain, and to pronounced differences between pollen zones from one part of Britain to another. In addition, radiocarbon dating has shown that at sites in western Britain where significant expansion of woodland (more than 20 % *Betula* pollen) has been found, the zone of maximum development of birch woodland must have been non-synchronous, falling within the period 12500–12000 ^{14}C a B.P. in the southern Lake District (Pennington & Bonny 1970; Pennington 1975, confirmed by hitherto unpublished dating) and within the period 11900–11000^{14}C a B.P. in North Wales (Simpkins 1974; Burrows 1974, 1975). It therefore seems well established that not only was there much regional differentiation within the Late Devensian vegetation of Britain, but that there is no generally applicable pollen chronology. This raises questions about interpretation of pollen data in terms of climate.

In the last five years it has become usual to describe Late Devensian pollen profiles in terms of pollen assemblage zones, and to refer these as far as possible to a ^{14}C chronology, as advocated

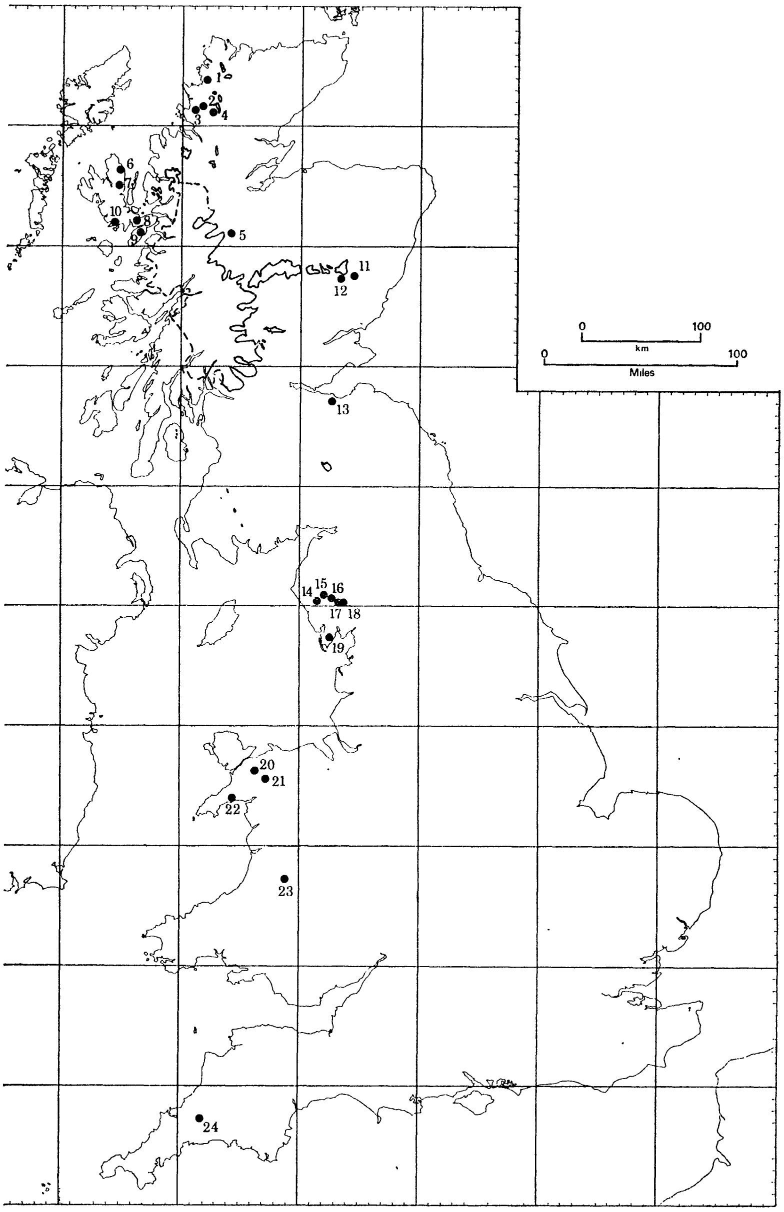


FIGURE 1. Map, showing (i) sites discussed in the text, and (ii) boundaries of the Loch Lomond Readvance (Sissons 1974) in Scotland. Sites of corrie glaciers of the same period in the mountains of Cumbria (Manley 1959) and North Wales (Seddon 1962) are not shown. Sites are: 1, Lochan an Smuraich (Pennington 1977); 2, Cam Loch (Pennington 1975); 3, Loch Sionascaig; 4, Loch Borralan; 5, Loch Tarff (all Pennington *et al.* 1972); 6, Loch Mealt; 7, Loch Fada; 8, Loch Cill Chriosd; 9, Loch Meodal; 10, Lochan Coir'a'Ghobhainn (all Birks 1973); 11, Blackness; 12, Roineach Mhor (both Walker 1975); 13, Corstorphine (Newey 1970); 14, Burnmoor Tarn (Pennington 1970); 15, Sty Head Tarn (Pennington, unpublished); 16, Blea Tarn, Langdale (Pennington 1970, 1973); 17, Blelham Bog (Pennington 1970; Pennington & Bonny 1970); 18, Low Wray Bay, Windermere (Pennington 1947, 1973; Godwin 1960, 1975); 19, Dalton-in-Furness (Johnson *et al.* 1972); 20, Nant Ffrancon (Seddon 1962; Burrows 1974, 1975); 21, Capel Curig (Crabtree 1972); 22, Glanllynnau (Coope & Brophy 1972; Simpkins 1974); 23, Elan valley (Moore 1970); 24, Hawks Tor, Bodmin Moor (Conolly, Godwin & Megaw 1950; Brown 1977).

by West (1970). Lithostratigraphic and biostratigraphic evidence alike has firmly established that the course of amelioration from the Devensian glacial maximum to the temperate environment of the Flandrian was interrupted by a temporary return to conditions sufficiently cold to re-establish mountain glaciers in Britain in Younger Dryas time (figures 1 and 2). The period of Late Devensian plant records therefore covers a very wide range of environments. In any discussion of the biota of the period it is necessary first to recognize the diversity of included environments (climates) and secondly, to find a clearly defined system for subdivision of Late Devensian profiles which can be generally applied in Britain. Scandinavian stratigraphers have now established a chronostratigraphic subdivision of the Late Weichselian period (Mangerud *et al.* 1974), and I have shown how this can be applied to two closely ^{14}C-dated profiles from western Britain (Pennington 1975). Figure 2 shows how use of this chronostratigraphy makes it possible to define the familiar Late Weichselian subdivisions (Allerød, etc.) as chronozones, and to correlate these with Late Devensian chronozones in dated British profiles.

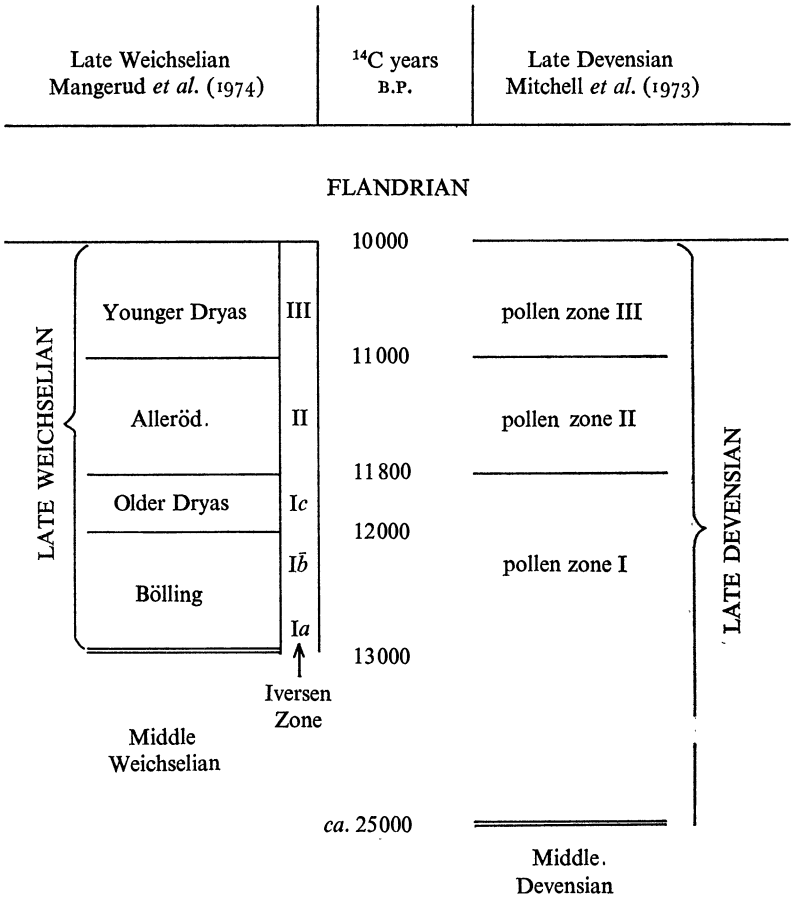


FIGURE 2. Late Devensian and Late Weichselian subdivisions.

FLORA

Little can be added to the comprehensive account of the Late Devensian flora which is presented in the second edition (1975) of Godwin's *History of the British flora*. This incorporates all the records for each taxon (from each of Pollen Zones I, II and III) which had been entered in the Data Bank of the Cambridge University Botany School by 1970. Godwin's discussion emphasizes and enlarges upon, with long species lists, the picture of the rich and varied Late-glacial flora of northwest Europe which has been consistently developed and expanded since the pioneer work of himself, Jessen and Iversen in the 1940s. The Cambridge records show that about half of the total number of species in the British flora has now been recorded from Late Quaternary deposits, and of these about 60 % were already in the country by the end of Late Devensian time.

Since it is unlikely that existing records of the Middle Devensian flora (see, for example, Bell 1969) represent more than chance-preserved samples, and since there are no plant records at all from the period of the Devensian ice maximum, it will probably remain impossible to decide how many of the Late Devensian records represent species which had survived within Britain from earlier periods. Taxa recorded from both Middle and Late Devensian deposits, and therefore among those most likely to have persisted in Britain, include, together with those of sub-arctic or montane distribution today, such as *Betula nana*, *Salix herbacea* and *Oxyria digyna*, a large number of weeds and ruderals whose primary requirement appears to have been for open habitats, aquatics such as *Groenlandia densa*, steppe elements such as *Helianthemum canum* and *Artemisia* spp., and species of predominantly southern distribution today such as *Lycopus europaeus* and *Onobrychis viciifolia* (cf. Godwin 1975, Tabs 37–41).

A large number of relatively warmth-demanding plants including the tree birches and *Populus tremula*, which are absent from all Middle Devensian records, must be supposed to have entered Britain in response to ameliorating conditions after the glacial maximum was past, across wide land bridges with the Continent which were then exposed by low Late-glacial sea levels. This low sea level would also have left exposed land areas to the west of Britain, and Godwin's suggestion that these could have provided glacial refuges for trees and other taxa receives support from the evidence, to be presented in the next section of this paper, for early immigration of tree birches into parts of western Britain after the Devensian ice maximum. The distribution of *Pinus sylvestris*, which appears confined to the Late Devensian woodland of eastern and southern England, indicates a very different immigration route for this tree – as Godwin comments, its Late-glacial distribution would appear to have been continuous, across the dry bed of the North Sea, with the mainland pine-birch region, in Allerød time.

The outstanding difference between the Late Devensian flora and the modern flora of Britain is the absence from the former of a large group of thermophilous trees and shrubs – including *Corylus*, *Ulmus*, *Quercus*, *Alnus*, *Tilia*, *Hedera*, *Ilex*, etc. The conventional interpretation of this absence in terms of low Late-glacial summer temperatures and slow dispersal from distant refuges may be questioned with respect to *Corylus* in western Britain. Birks (1973) shows that reconstruction of the Late Devensian environment of the Isle of Skye by detailed consideration of evidence from other plant data leads to the conclusion 'it seems inconceivable that conditions were not suitable for the germination, growth and flowering of *Corylus avellana*'. The rapid expansion of this species at the opening of Flandrian time in western Britain suggests that it must have been present at no great distance, yet some as yet unidentified factor inhibited its expansion during the Late Devensian period.

Late Devensian flora – phytogeography

Godwin (1975, pp. 446–450) presents a 'phytogeographic synopsis' which includes the results of numerical analysis of past and present British floras by Birks & Deacon (1973). Late Devensian sites from which data had been published by 1970 were allocated to 10 geographic regions of Britain (Birks & Deacon, Fig. 2), and for each region the percentage of plant records falling into each of five aggregate phytogeographic groups was calculated for (*a*) the Late Devensian flora and (*b*) the present flora. The phytogeographic groups include the following floristic elements:

(*a*) Arctic–alpine, Arctic–sub-arctic, Alpine;
(*b*) Northern montane, Continental northern;
(*c*) Continental northern, Continental southern, Continental widespread;
(*d*) Sub-atlantic northern, Sub-atlantic southern, Sub-atlantic widespread, Atlantic northern, Atlantic southern, Atlantic widespread, Mediterranean Atlantic;
(*e*) Continental southern, Sub-atlantic southern, Atlantic southern.

Table 5 in Birks & Deacon (1973) gives the percentages for each floristic element in each geographic region, and Figure 159 in Godwin (1975) presents the results in the form of histograms, in which the values for floristic elements are aggregated into the above five phytogeographic groups.

The conclusions were:

(i) Late Devensian plant records, considered as a whole for each of the ten regions, indicate a phytogeographical diversity as great as that found in the present British flora.

(ii) These ten regions of Britain differ less from each other with respect to the phytogeographical affinities of their Late Devensian floras than they do with respect to these affinities of their modern floras. This is shown by the histograms but was further demonstrated by numerical analysis by Birks & Deacon. By two-dimensional plots of the geographical regions, resulting from non-metric multi-dimensional scaling of the dissimilarity coefficients matrix, these authors were able to demonstrate a clear north–south gradient in the present British flora which cannot be found in the Late Devensian flora. Their conclusion for the Late Devensian was that 'there was little floristic differentiation within Britain at this time'.

(iii) The preponderant elements in the Late Devensian flora were those included in groups (*b*) and (*c*) – northern and continental – and these showed little geographic variation throughout Britain.

(iv) In so far as floristic differentiation can be recognized in the Late Devensian flora, it is found mostly with respect to the aggregate groups (*a*) and (*d*). Even at that time the effect of altitude is perceptible, in the higher values for group (*a*) in regions which include high mountains.

This elegant demonstration emphasizes the contraction of range of many species since Late Devensian time – a contraction which has differentiated those regions where they have survived from those in which they have been extinguished. The causes of extinction must include:

(i) The direct effects of temperature, as argued for arctic–alpine species by Conolly & Dahl (1970). Many species in this group now survive only in areas where summer temperatures do not exceed a certain maximum.

(ii) The reduction of habitats open to species of high light requirements or low competitive ability by the post-glacial spread of forest – cf. the example of the Upper Teesdale refugium for such species (Godwin 1956).

(iii) The decline in soil base-status from the generally high level characteristic of a Late-glacial stage, with subsequent limitation of many species to areas of calcareous bedrock (cf. Iversen 1954, 1973), e.g. the wider northward range in Late Devensian time of *Polemonium caeruleum* and *Scabiosa columbaria*.

Though it is convenient for some purposes to consider the Late Devensian period as a whole, aggregating floral records from all its subdivisions, it is salutory to remember that for many sites the aggregate species record covers a period of more than 3000 years, which included strong contrasts in climate. The apparent uniformity in geographical distribution within Britain of most of the components of the Late Devensian flora may reflect to some extent the consequences of combining data from cold periods (with expansion southwards of arctic–alpine and montane species) and more temperate periods (with northward expansion of more thermophilous species). As knowledge of Late Devensian chronology increases, we may look forward to more critical comparisons, restricted to a few centuries of Late Devensian time, which might well reveal stronger north–south gradients in the fossil floras.

Late Devensian flora – interpretation in terms of climate

The simultaneous presence in plant assemblages of species of such widely contrasted modern affinities that their present geographical ranges do not overlap, which is one result of the wider ranges of many plants in Late Devensian time than today, presents obstacles to interpretation of Late Devensian climate in terms of the present ranges of species. Iversen (1954) discussed one aspect of this problem, postulating that the primary factor which controls the present distribution of many light-demanding plants (heliophytes) is competition from other species which cast shade, so the presence of heliophytes in Late-glacial deposits gives no information about temperature, to which many of them appear indifferent. Bell (1969) discussed difficulties of reconstruction of the Middle Devensian environment, because of the presence in many plant assemblages of species of southern and steppe distributions today, together with northern elements. Godwin (1975, pp. 432–3) made the point that the absence of trees from a flora does not of itself indicate low summer temperatures, because there are features of the extreme continental type of climate which are adverse to trees irrespective of summer temperatures – very cold winters, severe wind exposure, severe spring thaw and floods, or highly unstable soils. Persistence of any one of these features may have limited the establishment and expansion of trees in any region of Britain in Late Devensian time, which would explain to some extent the accumulating evidence that the development of tree birches was not always in equilibrium with temperature, as deduced from the present ranges of other species present.

Bell (1969) discusses the question of the extent to which the present distribution limits of plant species reflect their physiological tolerances and are in equilibrium with climate. Perring & Walters (1962), discussing distribution maps of the present British flora, comment: 'The effect of climate upon different species varies widely, and it may take years of research to determine what is the critical factor which has limited a particular species to its present range.' Botanists have therefore accepted for some time that until this critical factor is determined by experiment, climatic interpretations based on the present range of a species represent hypothesis rather than fact.

Vegetation

Godwin (1975) described in detail the pattern of change in Late Devensian vegetation shown by results, published up to 1970, from sites where the profile had been divided by the author into Pollen Zones I, II and III on the basis of the *Betula* curve, or on the lithostratigraphic sequence in which organic sediment sandwiched between two minerogenic deposits was correlated with Zone II. Figure 156 in Godwin presents comparative percentage pollen spectra, in the form of sectorial diagrams, for each of these zones at a number of British sites; these demonstrate clearly the contrasted pollen spectra found (*a*) at the same site within successive periods of Late Devensian time, and (*b*) from one site to another within Britain during the periods of time represented by each zone. In his text Godwin discusses fully the composition of the plant communities represented by Late Devensian pollen spectra and reconstructed from assemblages of macroscopic remains – communities of woodland – which in southern and eastern England included *Pinus* as well as the more widespread tree birches and *Populus tremula*, aquatic, marsh, shrub and heath, grassland and other terrestrial habitats, together with the records of the many plants found today by waysides and in arable fields as weeds, and in open montane habitats.

In this paper I shall consider work on the Late Devensian vegetation of western Britain, published in 1970 or subsequently, in which definition and correlation of pollen zones have followed the principles advocated by West (1970) and some attempt has been made to correlate pollen zones to a chronostratigraphical framework. Figure 1 shows the position of these sites, which lie on a broad north–south transect from north Sutherland to Cornwall, and gives references in the legend. Table 1 sets out the pollen assemblage zones, correlated to the chronostratigraphic subdivisions shown in figure 2 by the available ^{14}C dating. In three areas it has been possible to prepare a synthesis of regional vegetation history by correlation of pollen assemblage zones from at least 5 sites: namely, (i) the English Lake District (Pennington 1970, 1973), table 1*a*(i); (ii) the mainland of Scotland from the Great Glen north to Sutherland (Pennington *et al.* 1972; Pennington 1975, 1977), table 1*a*(ii), and (iii) the Isle of Skye (Birks 1973), table 1*b*(ii). In (i) and (ii) the chronostratigraphy was established by detailed ^{14}C dating at one or two sites, and parallel changes in pollen stratigraphy and lithostratigraphy at *ca.* 13000, 12000 and 11000 B.P. were interpreted as evidence for climatic changes at these dates, justifying correlation with similar horizons in the undated profiles (table 1). In (iii) Birks adopted a different plan, assuming constant rates of sediment accumulation at each site (determined from early Flandrian ^{14}C dates) and using these to calculate dates for Late Devensian pollen zone boundaries and demonstrate their non-synchroneity (Birks 1973, Fig. 27). Pollen assemblage zones from these three regions have been compared firstly, within western Britain from the Lake District northwards, and secondly with sites from the Grampian Highlands, from North and Central Wales, and from Cornwall (table 1*b*).

In the synthesis of vegetation history which follows some attempt will be made to interpret pollen data objectively, avoiding the 'intuitive' European approach criticized by Livingstone (1968). Sufficient evidence is available to show that the pollen spectra of each zone are likely to include contributions from several different plant communities (Kirk & Godwin 1963; Birks 1973). In reconstruction of palaeoenvironments from pollen data, the assumed relationships between pollen spectra and vegetation and between vegetation and climate can be tested by comparison with spectra currently being produced by a variety of vegetation types. It will be shown how such methods have demonstrated that, whereas most of the Late Devensian pollen spectra found by Birks on Skye can be interpreted in terms of the present vegetation of that island, between sea level and the mountain summits, many Late Devensian pollen spectra from the British mainland can either be matched only by those now accumulating at higher latitudes or altitudes than are found in Britain, or cannot be matched in northern Europe today.

SYNTHESIS OF LATE DEVENSIAN VEGETATION HISTORY

(*a*) *Before* 13000 B.P.

Lake deposits containing plant remains have been dated to well before 13000 at several sites near the coasts of the Irish Sea (see Pennington 1975), indicating that ice had withdrawn from that area before 14500. The basal sediments in a kettlehole basin sectioned by coastal erosion at Glanllynnau (figure 1) contained seeds of the family Caryophyllaceae and moss fragments, together with remains of an arctic beetle assemblage, and the seeds yielded a date of 14468 ± 300 which is unlikely to be erroneous (Coope & Brophy 1972). The earliest organic matter to be deposited in Lake District lake basins, which contains pollen spectra and annual pollen deposition rates indicative of treeless tundra, has been dated to 14330 ± 230 at Blelham Bog (Godwin & Willis 1964; Pennington & Bonny 1970) and to 14557 ± 280 and 14623 ± 360 (SRR-681 and 682 – figure 3) in the littoral sediments of Windermere. Though these lake sediments of the Lake District may contain ^{14}C-deficient carbon from aquatic photosynthesis, the close agreement between dates from these two contrasted environments (a small kettle hole and a large lake with an extensive mountain catchment) suggests that an unlikely combination of errors would have been required to produce this result. It may therefore be concluded that a sparse vegetation was developing by *ca.* 14500 on newly deglaciated land, at a time when faunal remains indicate low temperatures, as at Glanllynnau (Coope & Brophy 1972 – Coleoptera) and Blelham Bog (Harmsworth 1968 – Cladocera).

(i) *Salix herbacea*–Cyperaceae–*Lycopodium selago* pollen assemblage zone (p.a.z.): before *ca.* 14000

In Windermere this correlates broadly with the sample dated to 14557 ± 280 (figure 3) and with such low pollen concentration that annual deposition rates cannot have exceeded 100 grains/cm^2 per year, a figure low even for tundra (Davis, Brubaker & Webb 1973). In the correlated zone at Blea Tarn, higher in the same catchment, annual deposition of most taxa in this p.a.z. compares closely with that estimated for present deposition in a lake at 1400 m in Jotunheim, S. Norway, surrounded by *Salix herbacea*-dominated snowbeds of the middle alpine region (Pennington 1973). Faegri (1953) suggested that this assemblage, which he found at the base of two Late-glacial profiles from southwest Norway, represents chionophilous communities likely to have characterized the periglacial vegetation of oceanic Europe.

Birks (1973) compared with this p.a.z. at Blea Tarn his *Lycopodium*–Cyperaceae p.a.z. at the base of three profiles from Skye, but *Salix* percentages are lower on Skye than in the Lake District. He found within this zone combinations of taxa which indicated at one site chionophilous communities, and at other sites communities now found on exposed summit heath and fell-field. At Cam Loch in Sutherland the lowest p.a.z., dated to well before 13000 by the overlying ^{14}C date, contains *Oxyria*–*Rumex* type pollen together with *Salix herbacea* (Pennington 1975). This p.a.z. is not recorded from other sites; it may represent a type of environment during which only in certain lake basins was pollen recruited to the accumulating sediment.

(ii) *Rumex*–Gramineae p.a.z.: *ca.* 14000–13000

Figure 3 shows how a pollen zone dominated by 20 % *Rumex* (predominantly *R. acetosa*) and 25 % grass pollen is in Windermere dated to *ca.* 13000–13800. Pollen concentration is ten times that of the underlying zone; division by the mean Late-glacial rate of sediment accumulation

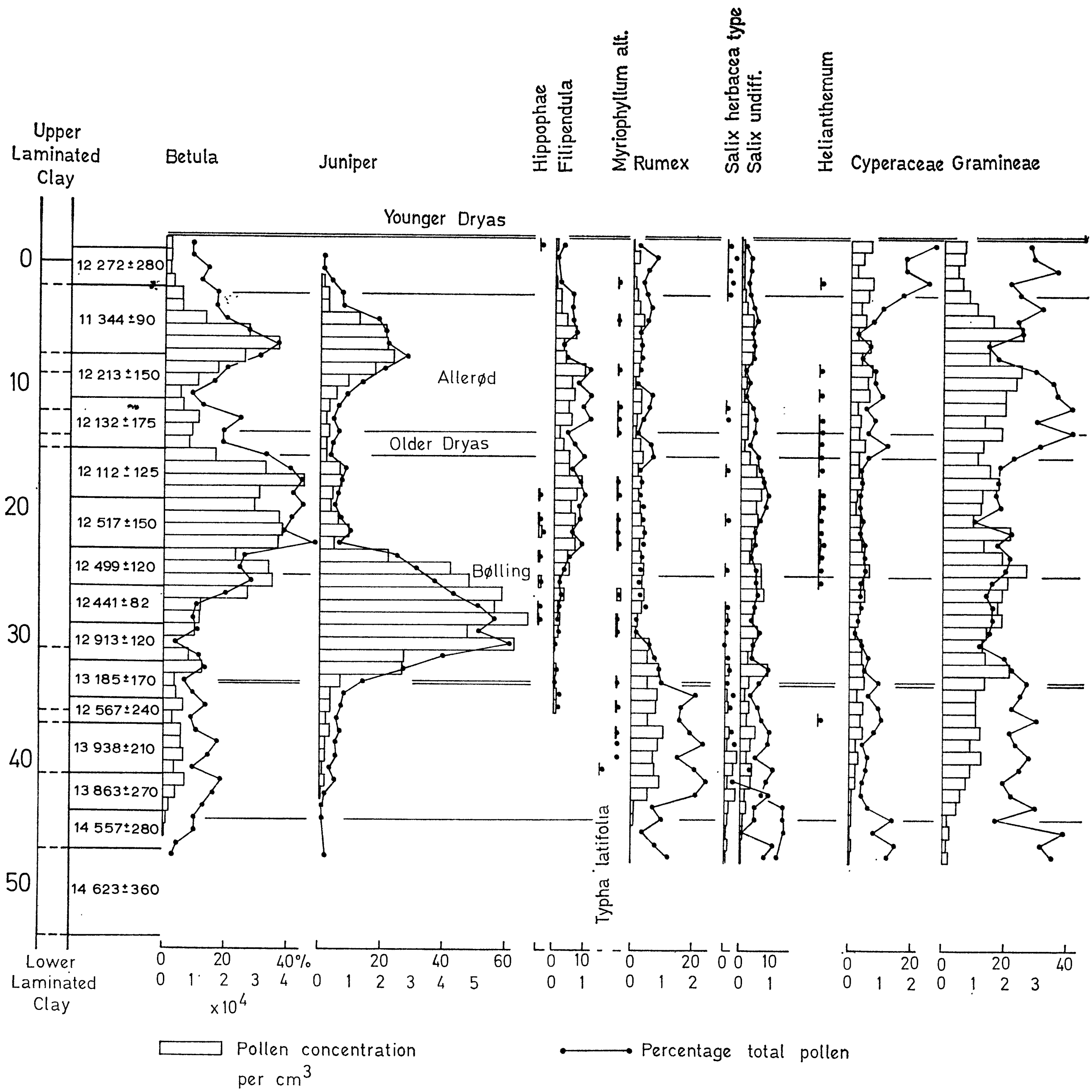
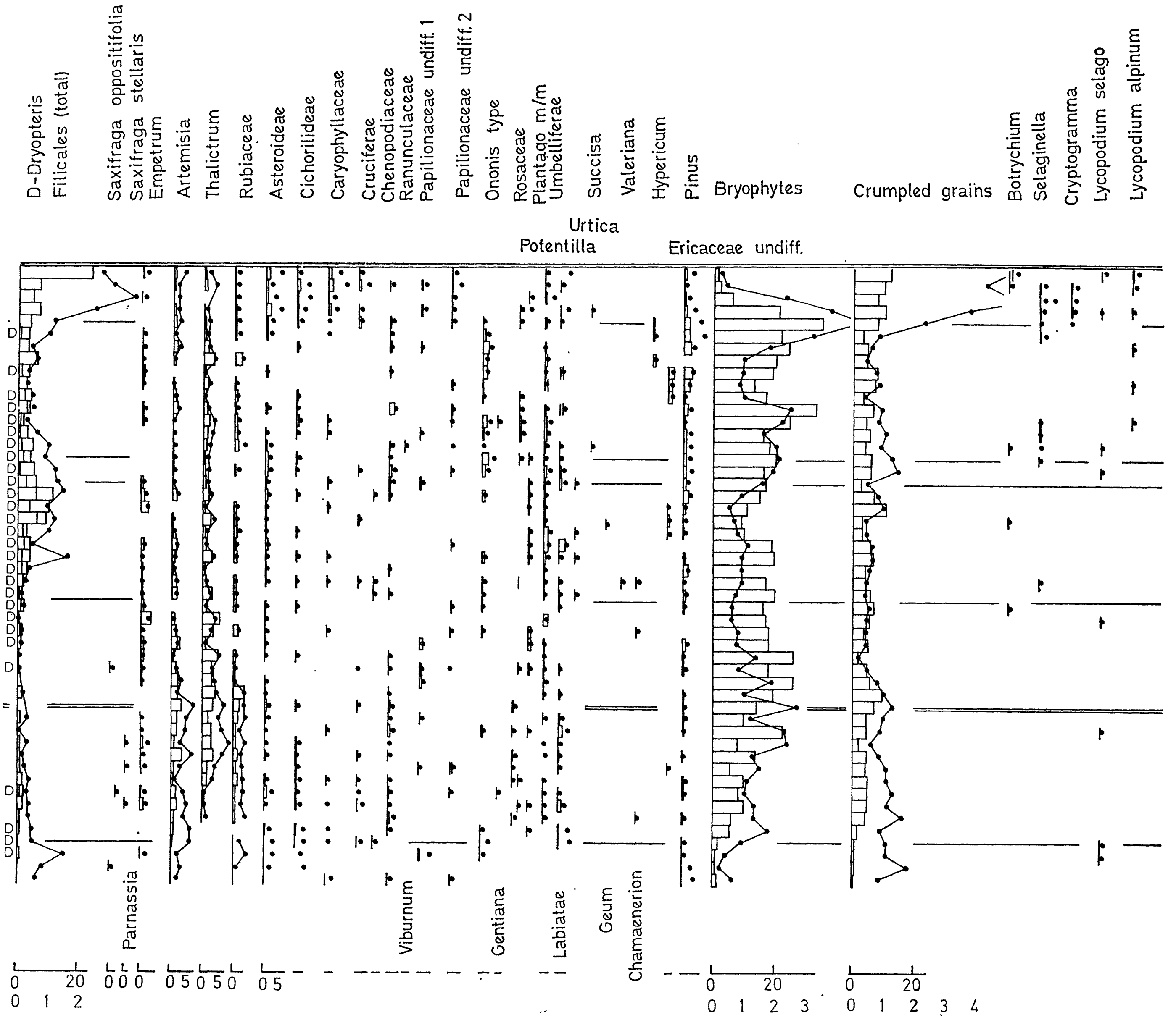


FIGURE 3. For description see opposite.

indicates an annual influx of *ca.* 1000 grains/cm^2. Within this zone appear many taxa suggestive of climatic amelioration, e.g. *Filipendula*, *Hippophae*, *Typha latifolia*, together with, at the base of the zone, a significant increase in percentage and absolute values for juniper and tree birch pollen. Through this zone *Salix herbacea* declines, Cyperaceae values remain low, and *Lycopodium selago* disappears. Some undoubted *Betula nana* pollen is present, together with that of *Empetrum*, *Thalictrum* and Rubiaceae. A rich assemblage of herbaceous taxa is represented by occasional grains (see figure 3); this includes *Helianthemum* and *Artemisia*.

A comparable zone is found at the base of many profiles from western Britain (see table 1*b*).



anal. W. Pennington

Figure 3. A percentage and absolute pollen diagram from Low Wray Bay, Windermere. This represents more detailed and absolute analysis of the profile previously investigated (Pennington 1943, 1947, Figs. 3 and 14, Godwin 1960, Fig. 1). This core was taken with a 12.5 cm diameter corer (Mackereth, Gilson & Findley, unpublished) which permitted ^{14}C dating of 15 samples. The line of best fit to these samples (figure 5) indicates a mean rate of sediment accumulation between 11000 and *ca.* 14000 of *ca.* 1 cm in 50 years. Division of the scale for pollen concentration (per cm^3) by 50 therefore converts concentration figures to grains deposited cm^{-2} a^{-1}. The pollen diagram covers the organic silts between lower and upper laminated (varved) clays (Pennington 1947).

It is interpreted by Birks, on the basis of surface samples from high-altitude vegetation, as the product of communities of species-rich grassland and tall herb communities, but *Rumex* percentages are lower on Skye than at mainland sites (never more than 10, often less than 5). I have found the high values for *Rumex* (up to 45 %) encountered at mainland sites in only one type of surface sample – that from the pioneer communities, rich in *Rumex acetosa* and *Oxyria digyna*, of ground recently exposed by the retreat of glacier tongues in the valleys of Jostedalsbre, S. Norway (cf. Faegri 1933): comparisons with typical spectra from the *Rumex*–Gramineae zone in NW Scotland are given in table 2 of Pennington (1977). I would therefore suggest that on the British mainland this zone represents primarily those communities which were able to colonize and develop on immature soils, at a time when the length of snow-lie in the lowlands had been reduced, and solifluxion had become less intense. The presence of taxa indicative of tall herb communities and of dwarf-shrub heath (*Betula nana*, *Empetrum*) shows that a vegetation mosaic, representative of unstable and of stabilized habitats, must have been present.

It seems likely that within the time represented by the *Rumex*–Gramineae zone in western Britain, full expression was found of those characteristics which make the Late-glacial vegetation of northern Europe unique. Godwin (1956, 1975) stressed the vigour with which species were able to expand into newly available habitats under the influence of an ameliorating climate; Iversen (1954, 1973) laid emphasis on the special effects of lime-rich and humus-deficient immature soils. Both authorities discussed the importance of the initial lack of competition, both from the dominating species of closed communities and from the continuous woodland whose shade would inhibit light-demanding species. Both have drawn attention to the fact that it is impossible to make climatic interpretations depending on modern ranges of species, when present distributions are controlled by intolerance of shade or by other forms of intolerance of competition, such as those which cause ruderal and weed species to depend on anthropogenically disturbed habitats.

What was happening to trees during the time represented by the *Rumex*–Gramineae zone? In Windermere, within the limits of ^{14}C sample SRR-680, dated to 13863 ± 270 but shown by its δ^{13}C value to incorporate hardwater error (Harkness, in prep.), there is a steady increase in percentage and absolute values for *Betula* pollen of predominantly tree birch type, up to 20 % and 200–400 grains $cm^{-2}\ a^{-1}$. Comparison with modern samples suggests that this represents the local arrival of tree birches – the 'establishment' of *Betula pubescens* (cf. Godwin 1975, p. 489). In moss polsters from open birch woodland, Birks (1973) found that 20 % of total pollen represents the lower limit of *Betula* percentages, while Fredskild (1973) found an annual *Betula* influx of 200–400 grains/cm^2 in the recent sediments of Comarum Sø, S. Greenland, within a vegetation of shrub tundra which includes small copses of *Betula pubescens* in sheltered places and appears to approximate to the 'park-tundra' postulated by Iversen (Degerbøl & Iversen 1945). This conclusion from pollen data is supported by the presence of fruits and catkin-scales of *Betula pubescens* at a horizon in Windermere now identified as *ca.* 4 cm above the base of the *Rumex*–Gramineae p.a.z. (compare figure 3 with Fig. 14 of Pennington 1947). It seems necessary to conclude that the local arrival of tree birches in the southern Lake District took place before 13000 B.P., and that some factor delayed the expansion of the species until *ca.* 12500. The factor could have been climatic or edaphic. For this site it is not, however, possible to explain the presence of a thermophilous insect fauna below the main *Betula* zone in terms of delayed immigration of tree birches (Coope & Brophy 1972; Coope 1976).

A sample of the vegetation of southeastern England, during the time represented by the

Rumex–Gramineae p.a.z. in the west, came from Colney Heath (Godwin 1964, 1975) where peat erratics in river deposits gave a date of 13560 ± 210. The long list of herbaceous taxa identified, regarded as highly characteristic of late-glacial plant assemblages, contains most of those found in the *Rumex*–Gramineae zone in Windermere, together with leaves of *Salix herbacea* and wood which was probably of juniper. Godwin's view, that the Colney Heath flora was most likely to represent that of the later part of the glacial period in southern Britain, is now confirmed, by ^{14}C correlation with the period of declining snow cover and new exposure of skeletal soils at sites within the limits of Devensian glaciation.

At Nant Ffrancon (figure 1), though critical ^{14}C dating is as yet unfortunately lacking, synthesis of the work of Seddon (1962) and Burrows (1974, 1975) suggests a situation there similar to that at Windermere, in that near the base of the organic deposits, a pollen zone containing a *Rumex*–Gramineae assemblage and some *Betula* and *Filipendula* pollen appears to correspond with the horizon where Burrows found the earliest macroscopic remains of *Betula pubescens*.

In northern mainland Scotland there is a contrast, in that the p.a.z. defined by maximum *Rumex* percentages is not a clearly defined *Rumex*–Gramineae zone, but overlaps with *Lycopodium selago* below and with *Juniperus*, or *Empetrum*, above (table 1*b* (i), (ii)). This can be interpreted as the effect of prolongation in higher latitudes, first of conditions favouring the chionophilous *Lycopodium selago*, and second of conditions favouring the preservation of disturbed habitats occupied by *Rumex acetosa* and other pioneer species. In the Grampian Highlands, the pollen zone in Walker's (1975) two sites which appears to correlate with the *Rumex*–Gramineae zone at other sites (table 1*b* (iii)) contains so much *Pinus* pollen that it is most readily interpreted as the result of secondary deposition of pollen from melting ice. A similar effect is seen at the base of this p.a.z. in profiles from higher altitudes in the Lake District (table 1*a* (i)).

Small percentage increases in *Betula* within this zone, which were found in several cores from Blelham Bog (Pennington 1970; Evans 1970) have been shown by absolute pollen analysis to represent statistical artefacts rather than any real increase in *Betula* (Pennington & Bonny 1970). The analysis of contiguous cm samples in the Windermere profile has confirmed this (see figure 3). Chance selection of certain samples on the percentage *Betula* curve could have produced an appearance of a fluctuation, but analysis of contiguous samples has shown no consistent trend in percentage or absolute values for *Betula* above the rise already described. Johnson, Tallis & Pearson (1972) incline towards the same explanation of the *Betula* curve within the lowest zone of their profile from Dalton-in-Furness, 30 km south of Windermere.

(*b*) 13000–11000 B.P.

(i) *Juniperus* p.a.z.: 13000–12500 in the Lake District; 13000–? elsewhere

Figure 3 shows the steep percentage and absolute rise in *Juniperus* which at Windermere coincides with the upper boundary of the *Rumex*–Gramineae p.a.z., and Fig. 2 in Pennington & Bonny (1970) shows an exact parallel at Blelham Bog. At both sites this zone boundary is dated to 13000, and in the Windermere ^{14}C samples the $\delta\,^{13}$C values show no evidence of hardwater error. A p.a.z. of high values for *Juniperus* has been widely recognized below the main *Betula* zone at western sites (table 1*b*) and absolute pollen analysis has shown how a very significant increase in pollen deposition rates coincides with this first major expansion of juniper at 13000 (Pennington 1975, and figure 3). There is a date of 12556 ± 230 for the correlative zone at

Glanllynnau (Coope & Brophy 1972; Simpkins 1974) and inferred dates of just after 13000 for the base of the Gramineae–*Rumex–Juniperus* subzone at Loch Meodal on Skye (Birks 1973). At Cam Loch the base of the *Rumex–Juniperus* p.a.z. coincides with the mean position of the ^{14}C sample dated to 12956 ± 240 (SRR-253). There is therefore a body of evidence from western Britain to show that a widespread increase in pollen production by juniper coincided with the date of 13000, suggesting a climatic amelioration correlated with that used to define the base of the Bølling chronozone. Nevertheless a clear expansion of juniper has not been found at all sites in western Britain, and the distribution of this plant would appear to have been far from uniform; compare three neighbouring sites in northern Scotland, Lochs Sionascaig & Borralan (Pennington *et al.* 1972) and Cam Loch (Pennington 1975).

In these papers I have interpreted the sudden increase in pollen production by juniper where present, as a response to climatic amelioration by a species already present, as Iversen (1960) interpreted the later juniper maximum at the late-glacial/post-glacial boundary. At the Windermere site, where the evidence already quoted shows that tree birches must have been present before 13000, it remains to be explained what factor favoured expansion of juniper rather than birch at 13000. Godwin (1975) discussing the ecology of juniper, which is very imperfectly understood, gives the evidence for its present status as a dominant above the present tree-line in northern Britain, a habitat which suggests that in some respects it is less exacting than birch. The data presented by Birks (1973) on modern pollen rain within juniper communities shows, however, that the high percentages found within this *Juniperus* p.a.z. at many sites can only be matched in tall dense thickets of *Juniperus communis* ssp. *communis* in Britain today, and not by the more prostrate forms found at higher altitudes.

(ii) *Betula* p.a.z.: 12500–12000 in the Lake District, ? elsewhere

A clearly defined p.a.z. of maximum Late Devensian percentages of *Betula* is found immediately above the juniper zone at Loch Meodal on Skye (Birks 1973) and in Lake District lowland profiles (figure 3). Detailed regional studies by Dr Birks in Skye and by myself in the Lake District have shown first, that there is much variation between sites with respect to *Betula* percentages reached in this zone, these declining at the less edaphically and climatically favoured sites on Skye and with increasing altitude in the Lake District, and secondly that all the evidence points to 'an uninterrupted succession on stable soils, through a juniper phase . . . to birch woodland' (Pennington 1970) or 'a progressive unidirectional vegetation succession . . . presumably in response to climatic amelioration' (Birks 1973). Comparisons already made with modern samples suggest that 20 % of *Betula* pollen may approximate to a tree cover somewhere between the scattered birch copses of parts of southern Greenland (equivalent to 'park-tundra') and a canopy cover of 25–30 % (Birks 1973, Fig. 25), while the 30 % or more of *Betula*, found throughout this zone in the Lake District lowlands and corresponding with an annual influx of 800–1000 grains $\mathrm{cm^{-2}\,a^{-1}}$ at two sites, exceeds by a factor of 4 the present deposition from park-tundra, and on a Birks regression line corresponds with a canopy cover of at least 50 %.

^{14}C dates from Blelham Bog and from Windermere (figure 3) agree to show that the lower boundary of the *Betula* p.a.z. in the Lake District falls at *ca.* 12500. It is postulated that this boundary, equivalent to that of the biostratigraphic zone which Iversen called Ib (Mangerud *et al.* 1974) does not represent a synchronous and climatically determined horizon such as those used as boundaries for Late Weichselian chronozones by Mangerud *et al.*, but the result of local vegetation development at each site.

The characteristic Late-glacial assemblage of *Helianthemum*, *Hippophae* and *Artemisia*, which Iversen noted as quite absent from arctic and sub-arctic regions today (in Degerbøl & Iversen 1945), reaches its maximum development in the Windermere profile within the zone of maximum *Betula* – i.e. the chronozone 12500–12000. This assemblage, which has not been found in Scotland, has not been recognized in modern vegetation but must represent a community of unshaded habitats. It seems probable that some local factor continued to inhibit the growth of tree birches on particular types of terrain, so that a mosaic of woodland and of open areas with unstable soils was present.

(iii) *Rumex–Empetrum* ± *Juniperus* p.a.z. Northern Scotland only: *ca.* 13000–12000

This pollen zone has been found at five sites in northern Scotland, is correlated at Cam Loch with the chronozone 13000–12000 (Pennington 1975) and is correlated with the biostratigraphic zone A2 of Pennington *et al.* (1972). A correlative zone can be recognized at Blackness in the Grampians (Walker 1975). Juniper values vary from site to site, reaching a maximum (20%) at Loch Sionascaig, the westernmost site. Pollen deposition rates at Cam Loch during this chronozone resemble those found by Fredskild in two lakes, Isoetes Sø and Kløftsø, situated in dwarf-shrub tundra dominated by *Empetrum hermaphroditum* plus some juniper, near the coast of SW Greenland (Fredskild 1973). Percentages of those taxa present are also in fair agreement with Fredskild's data (Pennington 1977, Tab. 2). The absence of *Calluna* from the Late Devensian pollen spectra distinguishes them from all modern samples from dwarf-shrub heath in Britain or Norway today. I postulate that the *Empetrum*-rich deposits at Loch Droma, ^{14}C dated to 12810 ± 155 (Kirk & Godwin 1963) correlate with this zone. The evidence is that dwarf-shrub tundra, similar in pollen productivity though not in species composition to that found on the outer coasts of SW Greenland today, was the prevailing vegetation of the northern Scottish mainland during the Bølling chronozone.

(iv) *Betula–Rumex* p.a.z.: 12000–11800 in the Lake District

At many sites, including Loch Meodal (Birks 1973) the *Betula* zone is narrow and only a few samples were analysed. The longer profiles (indicative of more rapid sediment accumulation) from Blelham Bog and Windermere have shown that the *Betula* zone as a whole is divided by a narrow zone of reduced annual deposition of the pollen of the more thermophilous taxa, which at both sites is correlated with the chronozone *ca.* 12000–11800 and so with the Late Weichselian Older Dryas chronozone (Pennington 1975; and figure 3). Comparison of the pollen data with geochemical data (figure 4) shows that on both criteria this narrow zone represents partial regression towards the composition of pre-13000 deposits. A rather small percentage increase in *Rumex* defines the p.a.z. Confirmation of this interpretation of climatic deterioration at this horizon comes from the insect fauna of the Windermere profile (Coope 1977).

(v) *Rumex–Artemisia* p.a.z.: *ca.* 12000–*ca.* 11800 in northern Scotland

This p.a.z. is found at the five sites from NW Scotland, is correlated with a distinct paler lithostratigraphic unit, and with a distinct diatom zone which includes taxa of sub-aerial habitats (Haworth 1976). It represents zone A3 of Pennington *et al.* (1972) and is approximately dated at Cam Loch. This p.a.z. represents a regression to conditions of an incomplete plant cover (favouring *Artemisia*) and increased soil erosion interpreted as due to an increased incidence of freeze-thaw cycles, during the Older Dryas chronozone. At the most northerly site, Lochan an Smuraich, this zone contains increased percentage values for undoubted *Betula nana* pollen (Pennington 1977).

(vi) *Betula–Juniperus* p.a.z.: 11800–11000 in the Lake District

This represents the upper part of the overall *Betula* zone in the Lake District, is correlated by ^{14}C dating with the Allerød chronozone (figure 2) and appears to be correlative with what the authors regard as Zone II deposits at Glanllynnau (date of 11300 from within the zone, Simpkins 1974) and Nant Ffrancon (date of 11500 ± 400 from within the zone of *Betula pubescens* macroscopics, Burrows 1975). In both Lake District sites the higher percentages of grass, sedge and *Empetrum* pollen, together with increased values for *Dryopteris* and unidentifiable fern spores, distinguish the spectra of this zone from the earlier *Betula* p.a.z. The fluctuating values for *Betula* and *Juniperus* firstly provide a basis for division of the zone in agreement with Iversen's division of Allerød deposits (Iversen 1954) and secondly suggest an interaction between birch and juniper which represents breakdown of the ecological equilibrium established before

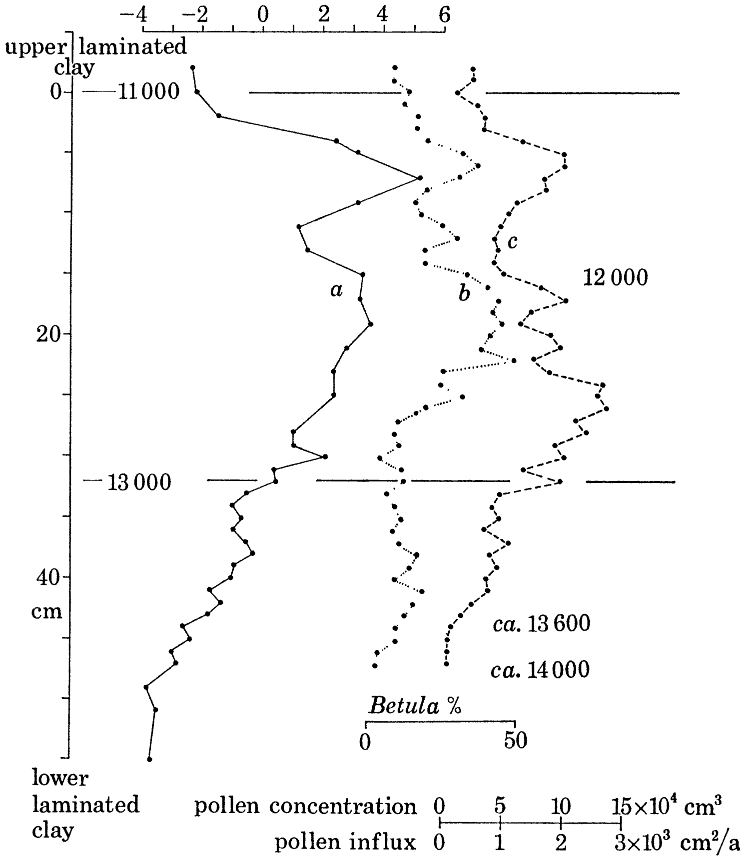


FIGURE 4. Geochemistry compared with pollen stratigraphy in the same profile as in figure 3. (*a*) stratigraphic plot of the sample scores on component 1 of a principal components analysis of the data for distribution within the profile of the elements C, H, N, Fe, Mn, Ca, K and Na; this component includes 68 % of total variance in the chemical data; (*b*) *Betula* pollen as a percentage of total pollen; (*c*) pollen concentration, per cm^3. The position of the boundaries of the Windermere Interstadial at 13000 and 11000 is indicated by horizontal lines, which divide the profile into: (1) a pre-interstadial period of progressively ameliorating environment; (2) the interstadial, divided by a regression at *ca.* 12000 and (3) a regression at *ca.* 11000 to an approach to the glacial environment of before 14000.

12000. Maximum percentage and absolute values for *Pinus* are found in this zone, and are attributed to an increased representation in the regional pollen rain during Allerød time, when pine was present in the woodlands of southern and eastern England.

A local subzone of Cyperaceae–*Selaginella*, distinguished in the Windermere profile (p. 266), is interpreted as indicative of deterioration in conditions towards the close of this chronozone. At Blea Tarn, higher in the same catchment, intensified erosion of mineral soils at this time led to a complete lithostratigraphic reversion to minerogenic sediment within a correlative *Betula–Empetrum* zone (Pennington 1970, 1973).

(vii) *Empetrum*–Cyperaceae–*Juniperus* p.a.z.: 11800–11000, in northern Scotland

This p.a.z. correlates with zone B of Pennington *et al.* (1972), there called 'interstadial'; ^{14}C dating at Cam Loch identified it with the Allerød chronozone. At no site in this region do *Betula* percentages exceed 10, and at neither Cam Loch nor Lochan an Smuraich do annual deposition rates reach the Greenland values for 'park-tundra' (Pennington 1977), so no local expansion of birch can have taken place. The increased absolute values for *Betula* in this zone are attributed to an increase in the regional pollen rain of NW Europe during Allerød time. Pollen spectra and annual deposition rates resemble in general those of the earlier *Rumex–Empetrum–Juniperus* zone, except for lower values for *Rumex*, and a continuation of *Empetrum*–juniper heath is supposed. Juniper maxima at Loch Tarff (figure 1) and Blackness in the Grampians (table 1*b* (iii)) in the later part of this zone may result from a late-Allerød warmer period such as that interpreted by Iversen (1954) from the *Betula* curve in Denmark.

(*c*) 11000–10000

(i) *Rumex–Artemisia*, *Artemisia–Rumex*, *Artemisia*—Caryophyllaceae p.a.zs: 11000–*ca.* 10500, most parts of the British mainland

Pollen assemblage zones distinguished by maximum values for the profile of *Artemisia* pollen, including *A. norvegica* at Scottish sites but including also much pollen which is not that of *A. norvegica*, have been widely recognized in Britain and correlated with Jessen/Godwin zone III. ^{14}C dating at Blelham Bog, Windermere and Cam Loch has identified the *Artemisia*-dominated pollen zones with the first half of Younger Dryas time, *ca.* 11000–10500, and this must have been the period during which 400–500 paired laminations (varves) were laid down in Windermere from deposition from corrie glaciers in the mountains (figure 5). In almost all profiles the *Artemisia* pollen zones coincide with a distinct lithostratigraphic unit of lower organic content, indicative of soil movements consequent on increased incidence of freeze-thaw cycles, and often identifiable geochemically with the unweathered products of intense periglacial erosion (Pennington 1970, 1973).

It has not so far been possible to find comparable pollen spectra in modern samples. Species of *Artemisia* are associated with dry habitats and do not in general tolerate much snow cover (Iversen 1954); the genus is associated rather with the continuously frost-heaved soils of a continental periglacial environment. The pollen spectra of the Younger Dryas *Artemisia* pollen zones in Britain do not resemble at all closely those of deposits older than 13000, as demonstrated by numerical analysis of data from Blea Tarn and Cam Loch (Pennington & Sackin 1975), but resemble rather the characteristic spectra from unglaciated parts of Europe during the last glacial maximum (Menéndez-Amor & Florschütz 1964; Lang 1970), in the prominence of *Artemisia*, of *Pinus* as a percentage of the total, and in the frequent presence of Chenopodiaceae.

Salix values in the Younger Dryas deposits of Britain are usually much lower than in early Late Devensian deposits.

The absolute increase in pollen deposition of *Artemisia* over much of Britain during Younger Dryas time is surprising, in view of the amount of precipitation as snow which must have been required to re-establish glaciers on the mountains of western Scotland (Sissons 1974), the Lake District (Manley 1959) and North Wales (Seddon 1962), and suggests that strong differentiation with respect to snow cover must have been present in Britain at this time.

In lakes which lie within the limits of Younger Dryas ice (figure 1) most of the Late Devensian deposit consists of coarse minerogenic material, but in some of these lakes a narrow *Artemisia* pollen zone can be found, indicating that some lake sites had become open and were recruiting pollen within the time represented by the *Artemisia* pollen zone.

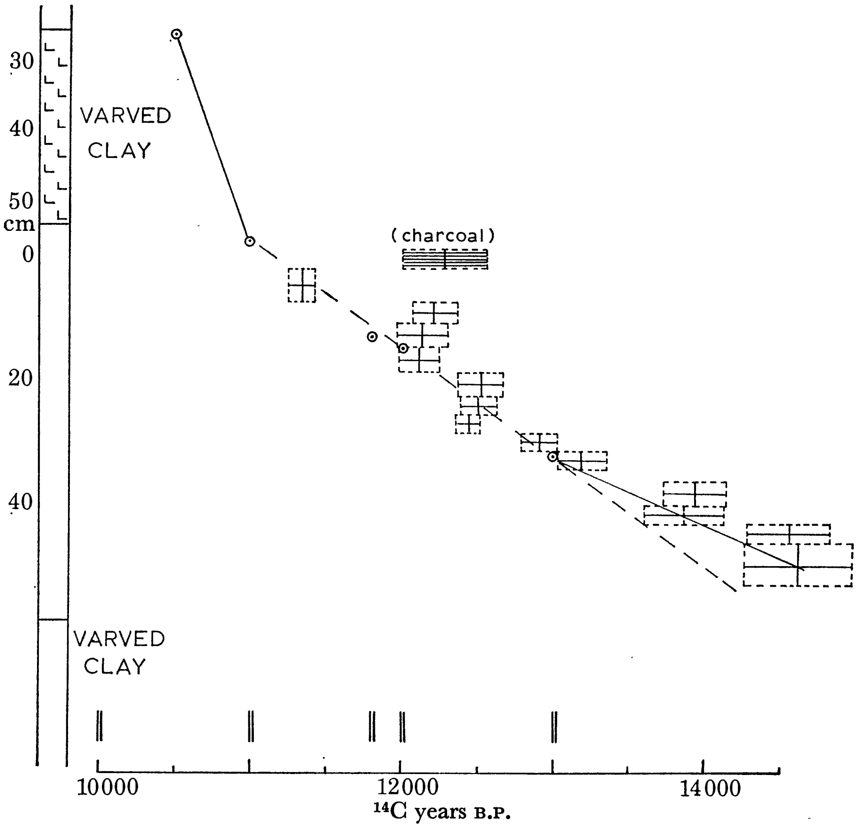


FIGURE 5. ^{14}C dates from the profile in figure 3, plotted to show sample depth and one standard deviation. The dated samples are: SRR-668, -1 to 2 cm, 12272 ± 280, δ^{13}C = -26.6‰; SRR-669, 2–7.5 cm, 11344 ± 90, δ^{13}C = -24.1‰; SRR-670, 7.5–11 cm, 12213 ± 150, δ^{13}C = -25.0‰; SRR-671, 11–15 cm, 12132 ± 175, δ^{13}C = -21.1‰; SRR-672, 15–19 cm, 12112 ± 125, δ^{13}C = -26.1‰; SRR-673, 19–23 cm, 12517 ± 150, δ^{13}C = -23.9‰; SRR-674, 23–26 cm, 12499 ± 120, δ^{13}C = -26.6‰; SRR-675, 26–29 cm, 12441 ± 82, δ^{13}C = -26.9‰; SRR-676, 29–32 cm, 12913 ± 120, δ^{13}C = -26.9‰; SRR-677, 32–35 cm, 13185 ± 170, δ^{13}C = -24.7‰; SRR-678, 35–37 cm, 12567 ± 240, δ^{13}C = -24.2‰; SRR-679, 37–41 cm, 13938 ± 210, δ^{13}C = -10.2‰; SRR-680, 41–44 cm, 13863 ± 270, δ^{13}C = -17.0‰; SRR-681, 44–47 cm, 14557 ± 280, δ^{13}C = -25.1‰; SRR-682, 47–54 cm, 14623 ± 360, δ^{13}C = -23.4‰. The position on the depth–time-scale of chronozone boundaries, determined from the pollen diagram and shown on the time axis by double lines, is indicated by the symbol ⊙. The date of SRR-678 is unacceptable and this sample is not plotted. The sample which contains micro-charcoal, of ^{14}C age greater than the time of deposition in the lake, is hatched. A line fitted to the other samples and the positions of chronozone boundaries, projected backwards, suggests that if deposition was approximately constant there is a hardwater error of up to 500 years in the four lowest dates.

(ii) Gramineae-*Rumex–Betula nana* subzone (Birks, 1973), Gramineae–Cyperaceae p.a.z., *Salix*–Cyperaceae p.a.z. (Walker 1975), Gramineae–Cyperaceae p.a.z. (Brown 1977): undated, but correlated Zone III

These as yet undated pollen zones, which in each instance appear on stratigraphy to represent the Younger Dryas chronozone, lie between deposits containing raised percentages of *Betula* which are correlated with the Late Devensian interstadial, and the base of the Flandrian sequence. These pollen zones are of great interest in that they demonstrate how the environment associated with the *Artemisia* pollen zones was not continuous over Britain in Younger Dryas time. Their existence suggests that a different vegetation (associated by Walker with much snow cover) was present in parts of the Highland zone of Britain – Skye, the Grampian Highlands, Bodmin Moor. Birks (1973) discusses the difficulty of precise interpretation of the vegetation represented by this zone on Skye and of the associated climate. The site at Lochan an Smuraich (Pennington, 1977) in the north of Sutherland, represents a link between the vegetation of mainland Scotland and of Skye during this period, in that the percentage rise in *Artemisia* is not accompanied by any absolute rise in Lochan an Smuraich (cf. table 1*b*(ii)).

(iii) Herb-dominated p.a.zs containing much grass, sedge and *Rumex* pollen, *ca.* 10500–10000

These p.a.zs (table 1) are found, throughout western Britain, in sediment of increasing organic content, and are interpreted as representative of the pioneer vegetation which colonized and stabilized soils, as climatic amelioration brought to an end, after 10500, the processes of glacial and periglacial erosion. The ^{14}C dates from Blelham Bog and Cam Loch correlate these p.a.zs with the second half of the Younger Dryas chronozone of Mangerud *et al.* (1974). To some extent the sequence of pollen zones resembles that found at the base of Late Devensian deposits (e.g. in northern Scotland (table 1*a*(ii)) but the succession must have occupied a much shorter period of time. In most regions the period of primarily herbaceous vegetation was followed by successive maxima of *Empetrum* and of *Juniperus*, the latter marking the transition to the Flandrian. In Skye, though juniper subzones were distinguished at some sites, there was a rather rapid transition to the basal *Betula–Corylus* zone of the Flandrian.

(*d*) *Synthesis of Late Devensian environmental history, ca.* 14500–10000, *at Windermere; the Windermere Interstadial, ca.* 13000–11000

The site at Low Wray Bay, Windermere, to be more fully described elsewhere, is chosen for a final synthesis for three reasons – (1) it embraces maximum contrast in Late Devensian environments, including both laminated (varved) clays and a woodland biozone, (2) it has been investigated by multidisciplinary Quaternary research over the last 30 years and (3) it has now been more fully dated by ^{14}C than any other Late Devensian site.

Before 14500, coarsely laminated clay was deposited from seasonal melt from valley glaciers fed by a remnant ice cap on the Lake District mountains, and vegetation was so sparse as to have left no records.

ca. 14500–13000; ^{14}C results (figure 5, legend) show that before 13000 there is evidence in δ ^{13}C values for hardwater error due to aquatic photosynthesis, and the true dates probably lie nearer to the backward projection of the linear depth–time-scale fitted to dates (figure 5) between 13000 and 11000. On this, the *Salix herbacea* p.a.z. falls at *ca.* 14000–13600, changes in sediment composition indicative of soil maturation (figure 4, curve *a*) begin at 14000 and continue without regression until *ca.* 12000, and the *Rumex*–Gramineae p.a.z., within which is found evidence for the arrival and establishment of *Betula pubescens*, is dated to *ca.* 13600–13000. Within this period, therefore, the evidence points to continuous climatic amelioration, unaccompanied however by any significant expansion of woody plants. It can be postulated that while summer temperatures were high enough for the moderately thermophilous insect fauna found by Dr Coope (1977), some other factor remained inimical to trees except in particularly favoured (sheltered?) habitats, until *ca.* 13000.

13000–11000; the Windermere Interstadial. This section of the Windermere profile is clearly distinguished on both sediment composition and pollen concentration (figure 4); on percentage composition of pollen spectra it constitutes a woodland biozone or palaeobotanical interstadial, correlated chronostratigraphically with the Bølling–Allerød Late Weichselian Interstadial, and similarly divided by a minor regression between *ca.* 12000 and 11800. The evidence from Blelham Bog (Pennington 1975) confirms that from the Windermere site (1.2 km distant) in showing that maximum rates of annual pollen deposition, interpreted as indicative of maximum pollen productivity of the vegetation, distinguish this interstadial.

Five p.a.zs are distinguished within the Windermere Interstadial in the ^{14}C dated pollen diagram – figure 3. They are:

(1) The *Juniperus* zone, 13000–12500, in which maximum Late Devensian pollen deposition rates are recorded; cf. Watts (1977) for Irish sites. Percentages of juniper indicate tall thickets of the shrub.

(2) The *Betula* zone, 12500–12000, in which pollen deposition rates are almost as high and pollen data suggest a 50% tree cover of *Betula*; the absolute fall in juniper in this zone may represent the results of unsuccessful competition with birch for restricted habitats favourable for shrubs and trees, or of some other factor as yet unidentified.

(3) The *Betula–Rumex* p.a.z., *ca.* 12000–11800, within which annual pollen deposition by *Betula* is significantly reduced and there is a small percentage and absolute rise in *Rumex*. This zone appears to represent the results of an environmental change (regression) of small amplitude, which however destroyed permanently the ecological equilibrium attained between 12500 and 12000. Within and above this zone, percentages of grass, sedge and herbaceous pollens are higher than in the earlier part of the interstadial, but this is to some extent the result of an absolute decline in deposition rates of *Betula*.

(4) The *Betula–Juniperus* p.a.z., *ca.* 11800– just before 11000, in which values for both *Betula* and *Juniperus* rise again to percentage and absolute maxima, and in which a great variety of herbaceous taxa is recorded. High values for *Dryopteris* and unidentified fern spores in this *Betula–Juniperus* zone suggest that the later interstadial (Allerød) birch woodland was more fern-rich than the earlier, and higher values for grass pollen suggest a more open woodland. Maximum percentages of *Pinus* are found in this p.a.z., though the percentages, which do not exceed 3 (total pollen), do not suggest local presence of pine.

(5) The Cyperaceae–*Selaginella* p.a.z., distinguished by low values for *Betula* and *Juniperus* and by the presence of spores of *Selaginella*, *Lycopodium* spp. and *Cryptogramma*. High percentages of sedge pollen result from constant deposition rates during a period of rapid fall in deposition rates of other taxa (figure 3). It is possible to interpret this pollen zone as indicative of increased snowfall during the period of break-up of Allerød vegetation (cf. Birks 1973, on chionophilous vegetation). The anomalous ^{14}C date, SRR-668, is attributed to the effect of the micro-charcoal common in the sediments of this zone and presumed to have originated with eroding soils; Burrows (1974) noted similar charcoal in correlative sediments at Nant Ffrancon.

11000–10500. The first half of the Younger Dryas chronozone is represented in Windermere (and in the other large lakes of the Lake District) by 400–500 paired microvarves which show strongly graded bedding (Pennington 1947) – indicating that between *ca.* 11000 and 10500 the lake must have been turbid with clay and silt produced by active ice in the high corries of the mountain catchment (Manley 1959). Pollen is extremely sparse in the laminated sediment, which I have explained by demonstrating low rates of pollen deposition at the present time in a Norwegian lake sediment, similarly laminated, where there is a rapid throughput of water from seasonal meltwater from mountain glaciers (Pennington 1973). In Windermere the proportional composition of the sparse pollen is comparable with that found in the correlative solifluxion clay at Blelham Bog (Pennington & Bonny 1970; Pennington 1973, Table 4), but the necessarily laborious analysis was not pursued above the base of this zone.

Conclusions

(*a*) *Late Devensian flora*

The Late Devensian flora was rich and varied and is likely to have included *ca.* 60 % of the species of the present flora. Species assemblages show that (*a*) for all regions of Britain the phytogeographical affinities of the Late Devensian flora were as varied as in the present flora, and (*b*) plants of contrasted modern ranges (e.g. northern, southern, oceanic and steppe) appear to have coexisted in a vegetation different from that of the preceding and following periods. Problems arise in relation to attempted climatic reconstructions based on present geographical ranges of plant species, and raise the question of to what extent the modern distribution of a species is governed by its physiological tolerances, and how far it depends on interaction with other species.

(*b*) *Late Devensian vegetation*

The great diversity in Late Devensian pollen spectra shown by this analysis of results from profiles on a broad north–south transect of western Britain can only be explained in terms of strong regional differentiation of Late Devensian vegetation. Climatic differentiation may be invoked to account for some of these differences in vegetation, but it seems unlikely that any simple explanation in climatic terms can be devised. It must be accepted that the facts of vegetation history in western Britain do not fit the simple model of uniform response by trees to changing temperatures which was developed from work on neighbouring parts of the continental mainland. However, at sites which have been adequately dated by radiocarbon, the profiles can be divided into a series of chronozones whose boundaries coincide with those of recently defined Late Weichselian chronozones, and, like these, appear from interpretation of the pollen data to have been climatically conditioned.

Pollen evidence from western Britain, supported by lithological and geochemical evidence, indicates a continuous and uninterrupted development of plant communities and soils, interpreted as a response to climatic amelioration, from before 14000 B.P. until *ca.* 12000 B.P. Snow-bed communities (postulated by Faegri to be the characteristic periglacial vegetation of the oceanic fringe of Europe), and the tolerant plants of exposed summit-heath today, were followed by pioneer species of immature soils, and by species-rich communities including plants which now demand high base-status. Into these communities dispersed the shrubs and tree birches whose subsequent development varied so greatly with aspect, altitude and soil that it cannot have been controlled primarily by temperature. A widespread and synchronous increase in pollen production by juniper at 13000 is interpreted as the consequence of the general climatic amelioration which has been used to define the lower boundary of the Late Weichselian substage (Mangerud *et al.* 1974). This rapid expansion of juniper defines the base of the Windermere Interstadial. Throughout Bølling time (13000–12000) tree birches must have been present in most of western Britain, dispersed in edaphically favoured and locally sheltered conditions as postulated by Godwin (1975, pp. 488–9), and forming up to 50 % cover in the most favoured areas by the end of the period. In Scotland these favourable areas appear to have been few, and in northern Scotland the *Empetrum–Juniperus* heath, which had succeeded the pioneer vegetation at 13000, persisted. If this was primarily a climatic effect, reflecting cool and cloudy conditions in northern Scotland (cf. Brown 1971) it is difficult to explain the scarcity of *Empetrum* in Skye, and some edaphic factor is almost certainly involved. On the western hills of Skye and the Lake District a species-rich grassland persisted, producing pollen spectra which show no significant expansion of *Betula*, and a comparable vegetation with some juniper is recorded from *ca.* 13000 from Bodmin Moor (Brown 1977).

This highly differentiated interstadial vegetation with a spatially uneven distribution of woody plants appears to have suffered only minor regression during the climatic deterioration of Older Dryas time (*ca.* 12000–11800) – because changes in the pollen spectra are small, e.g. the *Rumex–Artemisia* zone in northern Scotland, and most easily seen in the long and closely sampled profiles from the southern Lake District. In the second part of the interstadial, the Allerød chronozone, 11800–11000, fluctuating curves for *Betula* and *Juniperus* could be explained by the irregularly declining temperatures postulated by Coope & Brophy (1972) on faunal evidence. In parts of Wales and on Bodmin Moor, maximum percentages of birch were reached during Allerød time, as in southern and eastern England. In general, the evidence from western sites suggests an interstadial vegetation type containing varying proportions of *Betula*, *Juniperus* and *Empetrum*, which both developed earlier, and represented a different vegetation type, when compared with the birch-pine p.a.z. of eastern England, which reached its maximum development in Allerød time and correlates on both chronostratigraphy and pollen spectra with the Late Weichselian Zone II. Since this western interstadial has been investigated fully in the sediments of Windermere, it may be termed provisionally the Windermere Interstadial.

The major regression in Late Devensian vegetation in Younger Dryas time, which is characteristic of northern Europe and now explicable in terms of sea temperatures in the North Atlantic (Ruddiman *et al.* 1977), correlates with lithostratigraphic and geomorphological evidence for recrudescence of mountain glaciation in western Highland Britain. Periglacial soil disturbance must have been general outside the limits of glaciation (Watson 1977; Mitchell 1977) and this agrees with vegetational evidence – the widespread occurrence of pollen spectra characterized by *Artemisia* – in suggesting that snow cover was localized to those upland areas of the north and west where the pollen spectra indicate a more snow-tolerant vegetation.

I am greatly indebted to Mr H. C. Gilson, Mr W. Findley and Mr I. Haig for the design, construction and operation of a 12.5 cm corer, which made possible the detailed ^{14}C dating of the Windermere profile, and to Dr D. D. Harkness of S.U.R.R.C., East Kilbride, for his patience in dating these samples, many of which contained only small amounts of organic matter. Mrs J. P. Lishman was responsible for geochemical analyses, and Mr M. J. Sackin, of Leicester University, carried out the computer analysis of the geochemical data. I thank Dr H. J. B. Birks for many discussions of late-glacial problems, and Dr A. P. Brown for access to his as yet unpublished data.

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Discussion

D. M. Bertie (*Department of Geography, University of Reading, 2 Earley Gate, Whiteknights Road, Reading RG6 2AU*). It is interesting to note that the latest work on the Late Devensian flora of Britain and Ireland appears to be lending support to the results obtained by G. R. Coope with beetles regarding palaeotemperature curves for the British Late-glacial. It is disappointing, therefore, to see that Dr Pennington continues to fix the new British pollen zones to the Scandinavian zones (the dates for the boundaries of the zones are obviously derived from Mangerud *et al.* 1974, p. 119). Dr Pennington appears to have arbitrarily used the dates for the Scandinavian zones for obtaining the boundaries of the new British pollen zones, with rather dubious results. For example, the Older Dryas *Betula–Rumex* zone seems to have no justifiable existence, the zone's boundaries not being marked by emergence or decline of a plant species, other than that it lies between ^{14}C dates 12000–11800 a B.P. It would have been far better to have used Dr Coope's Late-glacial Interstadial ('Windermere' Interstadial), 13000–11000 a B.P., as a framework to work within, thereby bringing the new pollen work into line with current thought on the British Late-glacial. An excellent opportunity for comparative work between plants and beetles in the British Late-glacial has been lost here.

Reference

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W. Pennington. The zonation of the Windermere Interstadial, based on synthesis of the evidence from pollen and beetles, is discussed by Dr Coope and myself later in this volume (pp. 337–339 and table 1). All forms of evidence agree to indicate a temporary deterioration at *ca.* 12000 B.P. on the Windermere ^{14}C dates.

hil. *Trans. R. Soc. Lond. B*, *volume* 280

ABLE 1. CORRELATION OF POLLEN ASSEMBLAGE ZONES FROM THE SITES SHOWN IN FIGURE 1. FOR SITES WHERE THE AUTHOR DID NOT NAME POLLEN ASSEMBLAGES, NAMES HAVE BEEN APPLIED FROM INSPECTION OF THE PUBLISHED POLLEN DIAGRAMS

(*a*) (i)

ENGLISH LAKE DISTRICT

Blelham Bog and L.W.B., Windermere 436 m O.D.	Burnmoor 254 m O.D.	Blea Tarn 186 m O.D.	Sty Head Tarn 436 m O.D.	Chronozone Flandrian	S Loch Tarff
				10000	*Juniperus*
uniperus ramineae–herbs 10490	*Juniperus*	*Juniperus* Gramineae–Cyperaceae	unconformity		*Empetrum*
				Younger	
rtemisia–Rumex	*Artemisia–Empetrum–*Compositae	*Artemisia*	(barren clay)	Dryas	*Artemisia–Rumex*
umex–Artemisia	*Rumex–Artemisia*	*Rumex–Artemisia*	*Artemisia–*Caryophyllaceae		
				11000	
yperaceae–*Selaginella*	Cyperaceae–*Rumex*	*Betula–Empetrum*	Cyperaceae–Caryoph.		*Juniperus*
etula– 11450 *Juniperus–Filipendula*	*Betula–Juniperus–Filipendula*	*Betula–Rumex–Lycopodium selago*	*Betula–*Compositae	Allerød	Cyperaceae–*Empetrum*
			Juniperus–Filipendula		
		Juniperus – ferns		11800 O.D.	
etula–Rumex	*Betula–Rumex–Empetrum*	*Betula nana–*Cyperac. – *L. sel.*	*Rumex–Lyc. selago*		*Rumex* – herbs
				12000–	
etula 12050	*Betula*	*Juniperus–Salix* spp.	*Betula*	Bølling	*Rumex–Empetrum*
12500					
uniperus 12913	*Juniperus–Rumex*		*Rumex–Artemisia*		
				13000	
umex– 13185 Gramineae–Rubiaceae–*Artemisia*	*Rumex–Salix* spp.	*Salix herbacea–Lycopodium selago*	*Rumex–*Gramineae + secondary pollen + *Pinus*		*Rumex–Salix herbacea–Lycop. selago*
13900 *alix herbacea–* yperaceae 14600	secondary pollen + *Pinus*	clay	clay		
aminated clay	laminated clay				

(*a*) (ii)

NORTHWEST SCOTLAND			N	LAKE DISTRICT			
Loch Sionascaig	Cam Loch		Lochan an Smuraich	Blelham Bog		L.W.B., Windermere	
Juniperus	*Juniperus*		*Juniperus*				
Empetrum	*Empetrum*	10 226	*Empetrum*	*Juniperus* Gramineae–herbs			
			Cyperaceae		10 490	upper laminated clay	
	Cyperaceae–*Rumex*	10 585					
Cyperaceae–*Rumex*	*Artemisia*–			*Artemisia*–*Rumex*			
Artemisia–		10 698	*Artemisia*–				
Caryoph–	Caryoph–		*Betula nana*	*Rumex*–*Artemisia*			
Lyc. selago	*Lycop. selago*					*Rumex*–*Artemisia*	
Cyperaceae–	Cyperaceae–		*Empetrum*–			Cyperaceae–	
Juniperus	*Selaginella* (+*Betula*)		*Lycop. selago*	*Betula*–		*Selaginella*	
							11 344
					11 450	*Betula*–	
Cyperaceae–	Cyperaceae–		*Empetrum*–				
Empetrum	*Empetrum* (+*Betula*)		Cyperaceae	*Juniperus*		–*Juniperus*	
		11 900					
Rumex–*Artemisia*	*Rumex*–*Artemisia*		*Rumex*–*B. nana*	*Betula*–*Junip.*–*Rumex*		*Betula*–*Rumex*–*Gram*	
					12 050		
							12 120
Rumex–	*Rumex*–		*Rumex*–	*Betula*	12 460	*Betula*	
Juniperus	*Juniperus*		*Empetrum*				12 500
					12 650		
				Juniperus		*Juniperus*	
							12 913
		12 956					
Rumex–	*Rumex*–		*Rumex*–	*Rumex*–		*Rumex*–	13 185
Salix herbacea–	*Salix herbacea*–		*Salix herbacea*–		13 450	Gramineae–	
Lycop. selago	*Lycop. selago*		*Lycop. selago*	Gramineae–		Rubiaceae–	
	Salix herbacea–			Rubiaceae		*Artemisia*	
	Oxyria						
							13 900
						Salix herbacea–	
						Cyperaceae	
							14 600
				GRAVEL			

b (i)

(*b*) (ii)

NORTHWEST SCOTLAND Cam Loch			SKYE Loch Cill Chriosd	SKYE Loch Mealt	SKYE Loch Meodal	NORTHWEST MAINLAND SCOTLAND Lochan an Smuraich	
Juniperus–		10000				*Juniperus*	10000
			Gramineae–*Rumex*–*Juniperus*	Gramineae–*Rumex*–*Juniperus*			
Empetrum Cyperaceae–*Rumex*	10226 10585				Gramineae–*Rumex*–	*Empetrum* Cyperaceae	
Artemisia–Caryoph–*Lycop. selago*	10698	mountain glaciation	*Lycopodium*–Cyperaceae	Gramineae–*Rumex*–*Betula nana*	*Betula nana*	*Artemisia*–*Betula nana*	
		11000			(11000)		11000
Cyperaceae–*Selaginella* (+*Betula*)						*Empetrum*–*Lycop. selago*	
Cyperaceae–*Empetrum* (+*Betula*)	11900	11800	Gramineae–*Rumex*–*Betula*	Gramineae–*Rumex*–*Betula*	*Betula*	*Empetrum*–Cyperaceae	11800
Rumex–*Artemisia*		12000			(12000)	*Rumex*–*B. nana*	12000
Rumex–*Juniperus*			Gramineae–*Rumex*–*Juniperus*	Gramineae–*Rumex*–*Juniperus*	Gramineae–*Rumex*–*Juniperus*	*Rumex*–*Empetrum*	
	12956	13000			(13000)		13000
Rumex–*Salix herbacea*–*Lycop. selago* *Salix herbacea*–*Oxyria*			*Lycopodium*–Cyperaceae	Gramineae–*Rumex*–*Selaginella* *Lycopodium*–Cyperaceae	Gramineae–*Rumex*–*Selaginella*	*Rumex*–*Salix herbacea*–*Lycop. selago*	

(*b*) (iii)

GRAMPIANS (Walker 1975)		NORTHWEST SCOTLAND		NORTH WALES		
Blackness	Roineach Mhor	Loch Tarff		+ Glanllynnau (Simpkins 1974)		Nant Ffranc (Seddon 196
		Juniperus *Empetrum*	10000	*Juniperus*		*Juniperus*
						Rumex–Empet *Artemisia–* Caryoph.–
Gramineae– Cyperaceae	*Salix–* Cyperaceae	*Artemisia–Rumex*		*Artemisia–* Caryophyllaceae– Compositae		*selago–Emp*
			11000			
Betula–Juniperus				*Betula–Juniperus*		*Betula–*
		Juniperus (24 %)		*Betula*	Gc	*Juniperus*
					11300 (G)	
		Cyperaceae– *Empetrum*				*Betula*–Gram
			11800			
	Betula–Salix–	*Rumex* – herbs				
			12000			
					12050 (G) 12556 (B)	
Betula (max.)–*Salix–* Gramineae	*Rumex*	*Rumex–* *Empetrum*		*Rumex–* *Juniperus*	Gb	*Betula* *Juniperus*
Empetrum–Rumex						
			13000			
Gramineae–*Rumex* (+*Pinus*, and secondary pollen)	*Rumex–Artemisia–* Gramineae (+*Pinus* and secondary pollen)	*Rumex–Salix herbacea–* *Lycop. selago*		Gramineae– Cyperaceae–*Artemisia*	Ga	*Rumex*–Gram Rubiacea
				seeds of Caryophyllaceae†	14468	

† Coope & Brophy 1972

***ut* 1**

*

con

52)

trum

–Lycop.

petrum

nineae

mineae–

ae–*Salix*

(*b*) (iv) (b) (v)

LAKE DISTRICT		CORNWALL (Brown 1977)		WALES			
Blelham Bog & Windermere		Hawks Tor 3	Bodmin Moor regional p.a.z.	Central Elan valley (Moore 1970)		North Cors Gevallt (Crabtree 1973)	
	10000						
Juniperus Gramineae – herbs *Artemisia–Rumex*			sedge – grass	*Juniperus* *Rumex*	III–IV	*Juniper* *Empetrum*	III–IV
						Rumex *Artemisia*	III
Rumex–Artemisia				*Artemisia*–· Gramineae	III		
	11000		11069				
Betula– *Juniperus*			*Betula*– *Empetrum*	*Juniperus*– Cyperaceae	II–III	*Betula–Juniperus*	
		Betula–Umbelliferae– *Juniperus*					
Betula–Rumex– Gramineae	11800		11553	*Betula*	II	*Betula*–Gram– *Rumex*	II
	12000	Umbelliferae– *Juniperus*	Grass– sedge –			*Betula*	
Betula		12635 ± 300	herb				
Juniperus		Cyperaceae–		*Juniperus*–	I–II	*Juniperus*	
		Ranunculus acris		*Betula nana*			
	13000	13088 ± 300					I
Rumex-Gramineae– Rubiaceae–*Artemisia*				*Rumex*– Gramineae	I	*Rumex*–Gramineae– Rubiaceae– *Artemisia* + secondary pollen and *Pinus*	
13900 *Salix herbacea*– Cyperaceae							
14500 lower laminated clay							

Table 1. Correlation of pollen assemblage zones from the sites shown in figure 1. For sites where the author did not name pollen assemblages, names have been applied from inspection of the published pollen diagrams

(*a*) (i) ENGLISH LAKE DISTRICT — (*a*) (ii) NORTHWEST SCOTLAND

ENGLISH LAKE DISTRICT					NORTHWEST SCOTLAND			
Blelham Bog and L.W.B., Windermere 436 m o.d.	Burnmoor 254 m o.d.	Blea Tarn 180 m o.d.	Sty Head Tarn 436 m o.d.	Chronozone	S Loch Tarff	Loch Sionascaig	Cam Loch	Lochan an Smeraich N
uniperus ramineae herbs 10490 *rtemisia Rumex* *umex–Artemisia*	*Juniperus* *Artemisia*– *Empetrum*– Compositae *Rumex–Artemisia*	*Juniperus* Gramineae– Cyperaceae *Artemisia* *Rumex–Artemisia*	unconformity (barren clay) *Artemisia*– Caryophyllaceae	Flandrian 10000 Younger Dryas 11000	*Juniperus* *Empetrum* *Artemisia–Rumex*	*Juniperus* *Empetrum* Cyperaceae–*Rumex* *Artemisia* Caryoph– *Lyc. selago*	*Juniperus* *Empetrum* 10228 Cyperaceae–*Rumex* 10366 *Artemisia*– 10606 Caryoph– *Lycop. selago*	*Juniperus* *Empetrum* Cyperaceae *Artemisia*– *Betula nana*
yperaceae– *Selaginella* *etula*– 11450 *Juniperus*– *Filipendula* *etula–Rumex* *etula* 12050 12600 *uniperus* 12913	Cyperaceae– *Rumex* *Betula*– *Juniperus*– *Filipendula* *Betula–Rumex*– *Empetrum* *Betula* *Juniperus*– *Rumex*	*Betula*– *Empetrum* *Betula–Rumex* *Lycopodium* *selago* *Juniperus* – Ferns *Betula nana* Cyperac. – *L. sel.* *Juniperus*– *Salix* spp.	Cyperaceae– Caryoph. *Betula* Filipendula Compositae *Rumex*– *Lyc. selago* *Betula* Juniperus *Rumex* *Artemisia*	Allerød 11800 o.b. 12000 Bolling 13000	*Juniperus* Cyperaceae *Empetrum* *Rumex*–herbs *Rumex*– *Empetrum*	Cyperaceae– *Juniperus* Cyperaceae *Empetrum* *Rumex–Artemisia* *Rumex*– *Juniperus*	Cyperaceae– *Selaginella* (+*Betula*) Cyperaceae *Empetrum* (–*Betula*) 11800 *Rumex–Artemisia* *Rumex*– *Juniperus* 12956	*Empetrum* *Lycop. selago* *Empetrum*– Cyperaceae *Rumex–B. nana* *Rumex* *Empetrum*
umex 13165 Gramineae– Rubiaceae– *Artemisia* 13900 *alix herbacea* yperaceae 14600 aminated clay	*Rumex*– *Salix* spp. secondary pollen + *Pinus* laminated clay	*Salix herbacea*– *Lycopodium* *selago* clay	*Rumex* Gramineae + secondary pollen + *Pinus* clay		*Rumex*– *Salix herbacea*– *Lycop. selago*	*Rumex*– *Salix herbacea*– *Lycop. selago*	*Rumex*– *Salix herbacea*– *Lycop. selago* *Salix herbacea*– *Oxyria*	*Rumex*– *Salix herbacea*– *Lycop. selago*

b (i)

LAKE DISTRICT		NORTHWEST SCOTLAND	
Blelham Bog	L.W.B., Windermere	Cam Loch	
Juniperus Gramineae herbs 10490 *Artemisia–Rumex* *Rumex–Artemisia*	upper laminated clay *Rumex–Artemisia*	*Juniperus*– *Empetrum* 10228 Cyperaceae–*Rumex* 10585 *Artemisia*– Caryoph.– 10608 *Lycop. selago*	10000 mountain glaciation 11000
Betula 11450 *Juniperus* *Betula–Junip.–Rumex* 12050 *Betula* 12460 12650 *Juniperus*	Cyperaceae– *Selaginella* 11344 *Betula*– *Juniperus* *Betula–Rumex*–Gram. 12120 *Betula* 12500 *Juniperus* 12913	Cyperaceae– *Selaginella* (–*Betula*) Cyperaceae– *Empetrum* (–*Betula*) 11900 *Rumex–Artemisia* *Rumex*– *Juniperus* 12956	11800 12000 13000
Rumex 13450 Gramineae– Rubiaceae GRAVEL	*Rumex*– 13165 Gramineae Rubiaceae– *Artemisia* 13900 *Salix herbacea*– Cyperaceae 14600	*Rumex*– *Salix herbacea* *Lycop. selago* *Salix herbacea*– *Oxyria*	

(*b*) (ii)

SKYE			NORTHWEST MAINLAND SCOTLAND	
Loch Cill Chriosd	Loch Mealt	Loch Meodal	Lochan an Smeraich	
Gramineae– *Rumex*– *Juniperus* *Lycopodium*– Cyperaceae	Gramineae– *Rumex*– *Juniperus* Gramineae– *Rumex*– *Betula nana*	Gramineae *Rumex*– *Betula nana* (11000)	*Juniperus* *Empetrum* Cyperaceae *Artemisia*– *Betula nana*	10000 11000
Gramineae– *Rumex*– *Betula* Gramineae– *Rumex*– *Juniperus*	Gramineae– *Rumex* *Betula* Gramineae– *Rumex*– *Juniperus*	*Betula* (12000) Gramineae– *Rumex* *Juniperus*	*Empetrum*– *Lycop. selago* *Empetrum*– Cyperaceae *Rumex–B. nana* *Rumex* *Empetrum*	11800 12000 13000
Lycopodium– Cyperaceae	Gramineae– *Rumex*– *Selaginella* *Lycopodium*– Cyperaceae	(13000) Gramineae– *Rumex*– *Selaginella*	*Rumex*– *Salix herbacea* *Lycop. selago*	

(*b*) (iii)

GRAMPIANS (Walker 1975)		NORTHWEST SCOTLAND		NORTH WALES	
Blackness	Roineach Mhor	Loch Tarff		Glanllynnau (Simpkins 1974)	Nant Ffrancon (Seddon 1962)
Gramineae– Cyperaceae	*Salix*– Cyperaceae	*Juniperus* *Empetrum* *Artemisia–Rumex*	10000 11000	*Juniperus* *Artemisia*– Caryophyllaceae– Compositae	*Juniperus* *Rumex–Empetrum* *Artemisia*– Caryoph.–*Lycop.* *selago–Empetrum*
Betula–Juniperus *Betula* (max.)–*Salix*– Gramineae *Empetrum–Rumex*	*Betula–Salix*– *Rumex*	*Juniperus* (34%) Cyperaceae– *Empetrum* *Rumex* – herbs *Rumex*– *Empetrum*	11800 12000 13000	*Betula–Juniperus* *Betula* Gc 11300 (G) 12050 (C) 12056 (B) *Rumex*– Gb *Juniperus*	*Betula*– *Juniperus* *Betula*–Gramineae *Betula* *Juniperus*
Gramineae–*Rumex* (+ *Pinus*, and secondary pollen)	*Rumex–Artemisia*– Gramineae (+ *Pinus* and secondary pollen)	*Rumex–Salix* *herbacea*– *Lycop. selago*		Ga Gramineae– Cyperaceae–*Artemisia* seeds of Caryophyllaceae† 11468	*Rumex*–Gramineae– Rubiaceae–*Salix*

† Coope & Brophy 1972