PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Early and Middle Devensian Flora and Vegetation [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1977 **280**, 229-246
doi: 10.1098/rstb.1977.0108

Phil. Trans. R. Soc. Lond. B. **280**, 229–246 (1977)
Printed in Great Britain

FLORA AND FAUNA

Early and Middle Devensian flora and vegetation

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The record of palaeobotanical data from the Early and Middle Devensian (to 18000 B.P.) is reviewed, with additional pollen data from the Devensian type site at Four Ashes presented. Pollen and macrofossil assemblages derive principally from herb vegetation, but woodland episodes are known from the Early Devensian. Correlations of herb and woodland biozones are made with events in the Weichselian sequences of the Netherlands and north central Europe, and comparisons are made with the north American Wisconsin interstadial sequence and events in the North Atlantic cores. The environment of the herb and woodland biozones is discussed. The effect of a cool Atlantic as a modifying factor affecting the longitudinal zonation of Middle Weichselian vegetation across north central Europe is considered. The relation between environmental evidence based on flora/vegetation and that on fauna is discussed. Apparent discrepancies result from inadequate solutions of the problems associated with interpreting palaeoclimates from fossil assemblages. An interpretation of the data in the context of variation of assemblages of the same age across north Europe may offer better solutions for these problems.

1. Introduction

We will be concerned here with flora and vegetation of the period from the beginning of the Devensian to 18000 B.P. This period may cover *ca.* 60000–80000 years, depending on the placing of the Ipswichian/Devensian boundary. It precedes the period of major Devensian ice expansion, which took place in the east of England a few thousand years after 18000 B.P. The stratigraphical relations of the many sites which show Early and Middle Devensian fossil floras are difficult to determine. The sites are isolated from one another and are usually associated with low terraces of rivers, which often have a complex stratigraphy themselves. In the latter half of the period we are considering (to *ca.* 45000 a B.P.) the prime method of determining the sequence of fossil floras has been by radiocarbon dating, applied with due regard to the difficulties of dating material with very low radiocarbon content. Beyond that, biostratigraphy plays a certain role, particularly the alteration of woodland and herb biozones in the pollen record. Sufficient is known of the outline sequence of such biozones in northwest Europe to use them as a basis for biostratigraphy. For example, Amersfoort, Brørup and Odderade (pollen-based) interstadials have been described in the Early Weichselian, all with woodland, and each separated by herb biozones. No woodland biozones have yet been identified from the radiocarbon dated part of the sequence (later than *ca.* 45000 a B.P.) in northwest Europe, and Early Devensian woodland biozones in Britain have been correlated with these Early Weichselian woodland biozones of the continent. The absolute age of these woodland biozones has not yet been satisfactorily determined.

With this background of dating we can now consider the fossil floras in more detail.

2. The fossil record

Table 1 lists sites with Early and Middle Devensian floras, indicating analyses of pollen and macrofossil floras, the presence of herb or woodland biozones, and the relation of these to insect assemblages. Figure 1 shows the location of these sites. It will be noted that most sites are in the Midlands of England, and only one is in Ireland. They thus cover a rather limited area of the British Isles.

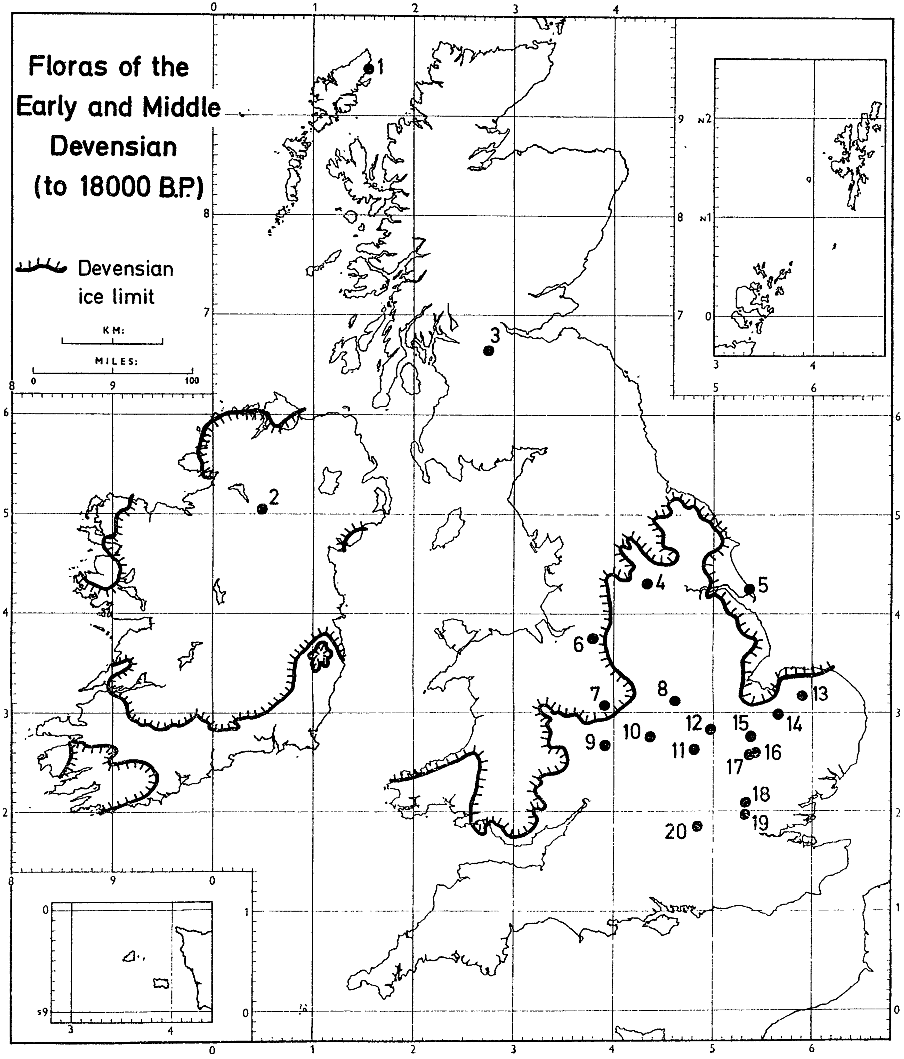

Figure 1. Location of sites with Early and Middle Devensian floras. Site numbers refer to the list in table 1.

Table 1. Fossil floras of the Early and Middle Devensian

site no. in figure 1	site	age (^{14}C B.P.)		author	flora		biozone	fauna (insect)
					pollen	macro		
	1. ^{14}C-dated sites							
5	Dimlington, Yorks.	18500 ± 400 18240 ± 250	I 3372 Birm 108	Penny, Coope & Catt 1969; Bell 1968	.	+	h	post-UW, cold
16	Barnwell Station, Cambs	19500 ± 600	Q 590	Bell & Dickson 1971; Coope 1968	.	+	h	post-UW, cold
1	Tolsta Head, Lewis	27333 ± 240	SSR 87	von Weymarn & Edwards 1973	+	.	h	
18	Broxbourne/Nazeing, Herts	28000 ± 1500	Q 25	Godwin & Willis 1960	.	+	h	
12	Great Billing, Northants	28225 ± 330	Birm 75	A. Morgan 1969	.	+	h	post-UW, cold
2	Derryvree, Co. Fermanagh	30500 ± 1170	Birm 166	Colhoun, Dickson, McCabe & Shotton 1972	(+)	+	h	post-UW, cold
7	Four Ashes, Staffs (45)	30500 ± 440	Birm 195	A. Morgan 1973	+†	.	h	post-UW, cold
7	Four Ashes, Staffs (2)	30655 + 765 − 700	Birm 25	A. Morgan 1973	+†	.	h	post-UW, cold
10	Brandon, Warwicks	30766 + 537 − 520 32270 + 1029 − 971	Birm 27 Birm 10	Shotton 1968; Kelly 1968	.	+	h	post-UW, cold
7	Four Ashes, Staffs (3)	36340 + 770 − 900	Birm 24	A. Morgan 1973	+†	.	h	post-UW, cold
8	Syston, Leics	37420 + 1670 − 1390	Birm 78	Bell, Coope, Rice & Riley 1972	.	+	h	post-UW, cold
4	Oxbow, Yorks	38600 + 1720 − 1420	NPL 163B	Gaunt, Coope & Franks 1970	+	+	j	post-UW, cold
7	Four Ashes, Staffs (34)	40000 + 1400 − 1200	Birm 196	A. Morgan 1973	+†	.	h	UW
9	Upton Warren, Worcs (Band 2)	42520 ± 1300 42100 ± 800	GRN 595 GRN 1245	Coope, Shotton & Strachan 1961	+	+	h	UW
15	Earith, Hunts (E7)	42140 + 1890 − 1530	Birm 88	Bell 1970	.	+	h	UW
7	Four Ashes, Staffs (4)	42530 + 1345 − 1115	Birm 56	A. Morgan 1973	+†	.	h	UW
7	Four Ashes, Staffs (20)	> 43500	Birm 74	A. Morgan 1973	+†	.	h	pre-UW, cold
15	Earith, Hunts (E9)	> 45000	Birm 86	Bell 1970	+	+	h	pre-UW, cold
6	Chelford, Cheshire	60800 ± 1500	GRN 1475 (enriched)	Simpson & West 1958	+	+	w	Ch
	2. Sites relatively dated							
7	Four Ashes, Staffs (19)	post-UW		A. Morgan 1973	+†	.	h	post-UW, cold
20	Marlow, Bucks	> 31000 UW		Bell 1969; Shotton & Williams 1971	+	+	h	UW
7	Four Ashes, Staffs (10)	Chelford ws		A. Morgan 1973	+†	.	w	Ch

TABLE 1 (*cont.*)

site no. in figure 1	site	age (^{14}C B.P.)	author	flora: pollen	flora: macro	biozone	fauna (insect)
14	Wretton, Norfolk	herb s III	West *et al.* 1974	+	+	h	cool
		Chelford ws		+	+	w	tundra
		herb s II		+	+	h	
		Wretton ws		+	+	w	
		herb s I		+	+	h	cool
13	Beetley, Norfolk	herb s II	Phillips 1976	+	+	h	
		Beetley ws (= Chelford ws?)		+	+	w	
		herb s I		+	+	h	
	Sidgwick Avenue, Cambridge	Early Devensian	Lambert, Pearson & Sparks 1963	.	+	h	+
		3. Other sites					
11	Thrapston, Northants	Middle Devensian in part	Bell 1968	+	+	h	
19	Barrowell Green, Middx	Middle Devensian	Reid & Chandler 1923	.	+	h	
3	Airdrie, Lanark	Devensian	Reid 1899; Coope 1962	.	+	.	+

Abbreviations: h, herb; w, woodland; s, substage; ws, woodland substage; UW, acme biozone of Upton Warren beetle-based interstadial; Ch, Chelford pollen or beetle interstadial. †, see appendix for pollen analyses.

(*a*) *Sediments and environments represented*

Early and Middle Devensian floras have been found mainly in organic infills of channels in fluviatile environments depositing sands and gravels. The channels are of varying size and contain sediment of varying organic content. Cut and fill processes may result in the redeposition of fragments of such channel fillings as 'erratics'. Floras have also been found in infills of hollows formed by the melting of ground ice, as at Beetley, Norfolk.

Observation of the sedimentary regime is important for the interpretation of these fossil floras. Most Devensian macrofossil floras derive from communities growing in situations close to braided river systems, while the pollen floras are derived from local and regional vegetation. A comparison of macroflora, pollen flora and sediment is therefore needed to analyse the provenance of the fossils, and to determine local and regional components (West *et al.* 1974, p. 391). The studies reported here do not all give the same degree of consideration to provenance. Nevertheless, the floras of the herb biozones have a considerable uniformity over a wide area, indicating local diversity within a regional vegetation of tundra physiognomy, probably predominantly grassland.

(*b*) *Pollen floras*

Pollen floras from the Early and Middle Devensian are broadly divisible into two categories, those dominated by tree pollen (a.p.) and those dominated by non-tree pollen (n.a.p.). The former give pollen assemblage biozones denoting regional woodland (woodland biozones), the latter give biozones denoting regional herb communities (herb biozones). The existence of a woodland biozone gives a basis for describing an interval as a pollen-based interstadial.‡

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‡ The use of the term interstadial based on differing lines of evidence leads to confusion (see West *et al.* 1974, p. 398).

(i) *Woodland biozones*

High a.p. pollen spectra have been recorded at Chelford (site 6), Four Ashes (site 7), Wretton (site 14) and Beetley (site 13). All show high frequencies of *Pinus*, lesser frequencies of *Betula*, and low frequencies of *Picea*. The Chelford assemblage was compared with *Pinus–Betula–Picea* forest of northern Fennoscandia by Simpson & West (1958). The macroscopic remains recorded at Chelford and Beetley indicate the species concerned were *Pinus sylvestris* L., *Betula pubescens* Ehrh. and/or *Betula pendula* Roth., and *Picea abies* (L.) Karst. cf. ssp. *obovata* (Ledeb.) Hulten (Phillips 1976). An interesting taxon represented in the pollen flora is pollen referable to that of the dwarf shrub *Bruckenthalia spiculifolia* (Salisb.) Reichb., a calcifuge species of woods and subalpine pastures in the Balkan mountains (Phillips 1976). This has also been recorded from Early Weichselian woodland biozones in northwest Europe (Behre 1974).

High a.p. biozones from Four Ashes, Wretton and Beetley have been correlated with that from the earlier-described site at Chelford, and all have been grouped to a substage which may be called the Chelford pollen-based interstadial. The Beetley pollen diagram shows the most complete expression of this substage. At Wretton earlier biozones with *Betula–Pinus* and *Betula–Pinus–Alnus*–Gramineae–*Calluna* assemblages occur. These appear to represent an older woodland substage, named the Wretton pollen-based interstadial, separated from the younger interstadial by a herb biozone. Both are placed in the Early Devensian. In the light of the difficulties of stratigraphy and correlation of the Early Devensian, this grouping of sites into interstadials can obviously be only provisional, and further biostratigraphical studies will certainly modify the present arrangement.

(ii) *Herb biozones*

High n.a.p. biozones have been recorded (table 1) at Wretton from before the Wretton pollen-based interstadial, between this and the Chelford Interstadial, and after this interstadial. At other sites high n.a.p. spectra have been recorded at the following radiocarbon ages B.P. (site numbers refer to figure 1): > 45000 (site 15, E9), > 43500 (site 7), > 31000 (site 20), 42530 (site 7), 42140 (site 15, E7), 42100/42520 (site 9), 40000 (site 7), 38600 (site 4), 36340 (site 7), 30655 (site 7), 30500 (site 7), and 27333 (site 1). Other sites, undated, with high n.a.p. spectra are at Four Ashes (Middle Devensian, site 7) and Earith (Middle Devensian, site 15, E1, E2, E4, E5).

All these pollen spectra show above 80 % n.a.p., many above 95 % (% total land pollen). A discussion of the interpretation of such pollen spectra in terms of regional vegetation was given by West *et al.* (1974). Much information is now available on pollen rain in areas of herb vegetation (arctic, alpine (Birks 1973); steppe (Levkovskaya (1973)) and it seems clear that these high n.a.p. spectra derive from herb vegetation, dominated probably by Gramineae and with a tundra physiognomy. There is no evidence for widespread vegetation with shrubs, though at Tolsta Head *Juniperus* and *Salix* pollen frequencies indicate shrub vegetation. In most spectra Gramineae and Cyperaceae pollen make up a high percentage of total pollen, but the provenance of Cyperaceae varies. At many sites high frequencies of Cyperaceae pollen are accompanied by Cyperaceae macroscopic remains and thus are probably of local origin. The spectra may show considerable variety in kind and number of herb taxa. Occasional high frequencies of *Armeria*, Compositae, Cruciferae and *Plantago* occur. These variations reflect the variety of plant communities associated with braided river plains and of the neighbouring uplands, and the changes of provenance associated with changes of sedimentary régime.

As will be discussed later, pollen spectra from sites with insect faunas indicating the acme of the beetle-based Upton Warren interstadial (sites 7, 9, 20) show no increase of tree pollen frequencies. The pollen spectra so far obtained from this period appear to show no variation in regional vegetation that is not seen in the other herb-rich parts of the Middle and Early Devensian.

(*c*) *Macrofossil floras*

There is a long history of the study of plant macrofossils in last glaciation deposits. Clement Reid (1899) and E. M. Reid (1949) made substantial contributions to the 'full-glacial' flora. More recently, C. A. Dickson (1970) and F. G. Bell (1969, 1970) have, through careful taxonomic work, made great improvements in standards of identification. As a result, there is a considerable body of evidence of species of the Early and Middle Devensian flora, adding substance to the evidence given by the pollen flora.

Macroscopic floras (table 1) are known from both the woodland biozones (e.g. Chelford (Simpson & West 1958); Beetley (Phillips 1976)) and from the herb biozones. It is the assemblages from the herb biozones which have been more frequently found and which are of particular interest. These floras have been found in varying sediment types, ranging from 'drift-muds' or leaf beds, to laminated silts and clays and detritus muds. The taphonomy of the floras may thus differ considerably (West *et al.* 1974). Nevertheless, there is a considerable uniformity of the flora, as there is with the pollen spectra of the herb biozones. The absence of woodland is borne out by the macrofossil flora, but there is evidence for local dwarf shrub communities at certain sites (e.g. Earith), recorded by the sediment (leaf-beds) and the species lists, which include *Betula nana* L., *Salix herbacea* L., *S. polaris* Wahlenb., *S. phylicifolia* L. and *S. viminalis* L. However, these communities do not seem to have been very extensive since they have not been recorded substantially in the pollen spectra. Various habitat and vegetation categories have been identified in the macrofossil flora, including aquatic and marsh communities, tall herb communities, ruderal and weed species associated with disturbed and open ground (related to freeze-thaw phenomena and floodplain processes) and grassland (Beetley, Wretton). These components of the Devensian flora have been discussed in detail by Bell (1970) and Godwin (1975).

Three phytogeographical or ecological elements have merited particular attention. These are the southern, steppe and halophyte elements in the macrofossil floras. Their occurrence has been fully discussed by Bell (1969). Bell concluded the southern element, a heterogeneous group (including true thermophiles, and some species southern because of habitat availability), indicated summer (July) temperatures near to 16 °C, with a continental type of climate, since many of the southern species have a continental distribution in Europe as a whole. A number of taxa are characteristic of the steppe region of the southwest of the U.S.S.R. They may not be members of steppe communities as such, but their presence may indicate a xeromorphic situation with grasses, other herbs and dry mineral soils. Species considered both as obligate halophytes (e.g. *Glaux maritima* L.) and facultative halophytes are of widespread occurrence in these macrofossil floras. Their presence may indicate saline soils, which are likely to have been induced by evaporation (which may be related to wind and insulation) and low precipitation in the summer, associated with impeded drainage. Such soils can be associated with permafrost in northern Eurasia. It is notable that floras with halophytes are found at Earith and Wretton in association with ice-wedge casts, though the stratigraphical evidence cannot prove contemporaneity. Thus at Wretton (site WUB) a high frequency of halophyte macrofossils occurred in a sediment very rich in terrestrial flora penetrated by an ice-wedge cast.

We have seen that it is not possible yet to separate different categories of herb biozone on the basis of pollen assemblages. It seems that it is also difficult to show that different macrofossil floras indicate differing vegetational conditions of substance (Bell 1970, p. 374). Variations in taphonomy and habitat, together with phytosociological variation of open plant communities, represent a multivariate situation which has not yet been analysed in detail, and which requires, for analysis, the combined evidence of stratigraphical context, sediment, macrofossils and pollen.

(*d*) *Continuity of the record*

The record of Early and Middle Devensian fossil floras, as shown in table 1, covers in outline the period of time involved, but there are considerable gaps of time in which there is no knowledge of the flora. We may expect these gaps to be filled as new records accumulate. The present record indicates the probability of survival of a large flora during the Devensian in the area south of the ice limit, and such a conclusion is supported by records of floras closely related in time to glacial advance (Dimlington) and to structures indicating permafrost (Wretton). We may note that the pollen record of the Weichselian in the Netherlands (Zagwijn 1961, 1974) is more complete, but on the basis of lack of organic deposits in certain periods, especially 13000–27000 B.P., a polar desert environment has been postulated. This point is discussed in § 4.

3. CORRELATIONS

(*a*) *Netherlands*

The most detailed and best dated sequences from the last glaciation come from the Weichselian of the Netherlands (van der Hammen & Wijmstra 1971; Zagwijn 1961, 1974). The sequence from this area is summarized in figure 2. A correlation of the Chelford woodland substage with the Odderade or Brørup interstadials of northwest Europe was suggested by West *et al.* (1974), with the latter correlation being the more likely. A correlation of the Wretton woodland substage with the Amersfoort Interstadial was made by the same authors. These correlations are indicated in figure 2. There is no clear evidence from the flora or vegetation in the herb biozones of pollen-based interstadials which might be correlated with the Moershoofd, Hengelo and Denekamp interstadials of the Netherlands. This raises the important problem of the interpretation of high n.a.p. spectra in terms of vegetation and climate, especially since it has now been amply demonstrated that climatic regimes with a parameter of warmth indicated by beetle faunas are not evident so far from changes within high n.a.p. spectra. From the palaeobotanical point of view, the best interpretation will be obtained from studies of pollen, macroscopic remains, and sedimentary conditions and environment.

(*b*) *North central Europe*

A number of Middle Weichselian floras are known from southern Poland (Srodon 1968). These are of particular interest in showing forest-tundra with coniferous forest. For example at Dobra (Srodon 1968, ^{14}C age 32500 a B.P. (GrN 5111), *Pinus cembra*, *P. sylvestris*, *Picea abies* and

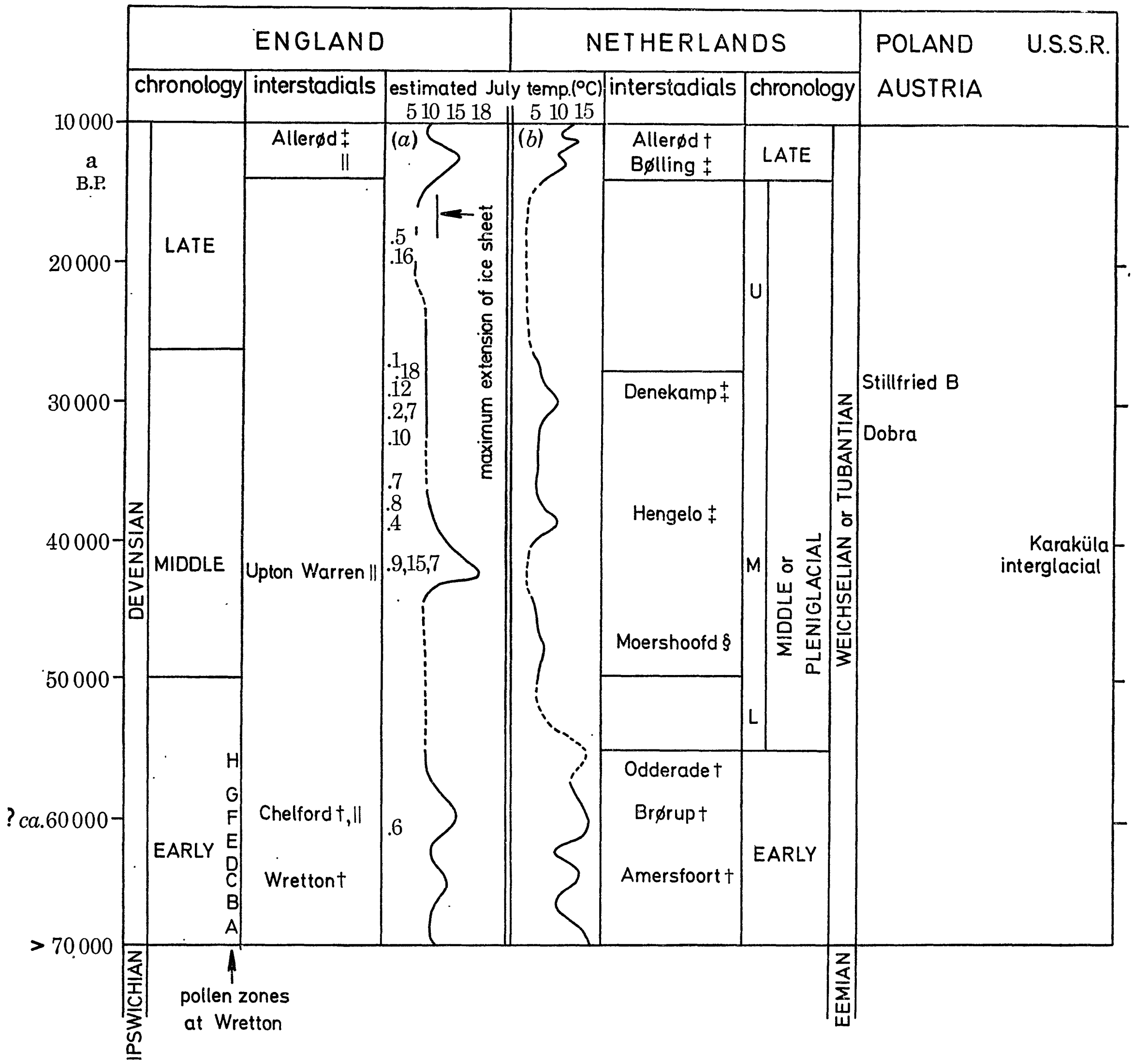

Figure 2. A classification of the Devensian, showing the age of dated (absolute and relative) Early and Middle Devensian floras. Correlation with the Netherlands and with some central and north European sites are shown. The figure shows the position of interstadials and the basis for their definition: †, pollen-based interstadial, woodland; ‡, pollen-based interstadial, shrub-tundra; §, pollen-based interstadial, tundra; ||, beetle-based interstadial. *a*, curve based on beetles back to Chelford Interstadial (Coope, Shotton & Strachan 1971; Coope 1975*a*) and below this on palaeobotany; *b*, curve based on palaeobotany.

Larix occur, together with a rich herbaceous flora recalling that of the alpine meadows in the Tatra Mountains. Srodon (1968) points out that this difference from the flora and vegetation of northwest Europe is paralleled in the Late-glacial and in the Early Weichselian interstadials, in both of which periods the flora and vegetation in south Poland showed a warmer climate than that indicated by floras and vegetation of northwest Europe. The Polish Middle Weichselian interstadials are correlated with the 'Paudorf' of central Europe and Stillfried 'B' soil complex of Austria (location in figure 3).

When we go further east we find evidence reported of forest interglacial conditions in the mid-Weichselian. This interglacial, the Karaküla interglacial of the Russian Plain

(Serebryanny, Raukas & Punning 1970), has ^{14}C dates from its sediments, indicating an age *ca.* 50000–25000 a B.P., and shows a vegetational history with high *Picea* values and low frequencies of *Tilia*, *Ulmus*, *Quercus* and *Corylus*.

This apparent longitudinal zonation of vegetation in north central Europe deserves further study from botanical and climatic viewpoints, especially since it appears that the Middle Weichselian vegetational history of north central and eastern Europe shows a complexity of change not so far found in the British Middle Devensian.

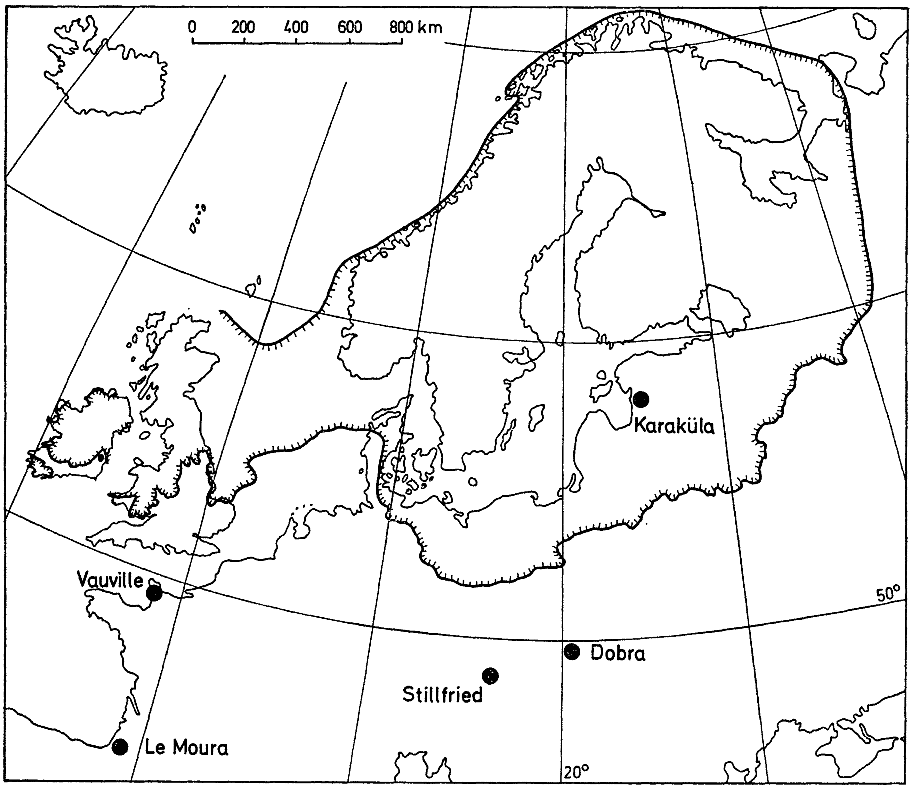

FIGURE 3. Map of western Europe showing areas and sites considered in text, with margin of Devensian/Weichselian ice.

(*c*) *North Atlantic and North America*

A further consideration of this last point leads to the conclusion that the cold water masses present in the northeast Atlantic in Middle and Early Devensian time (McIntyre & Ruddiman 1972, depression of annual temperature of NE Atlantic surface water by 5 °C; see also Manley 1951) had a cooling effect in northwest Europe and gave a climate which affected the vegetation zonation. This effect may be paralleled by mid-continent and (east) coast differences in north America, where Late-glacial mid-continent coniferous forest and east coast herb vegetation present a contrast (Davis 1967), mirrored in northwest Europe by Late-glacial herb vegetation in the west and coniferous forest in European U.S.S.R. (West 1961). In the Middle Wisconsin, in the eastern Great Lakes region (Berti 1975), the Port Talbot and Plum Point interstadials (Port Talbot I, 55000–50000 a B.P.; Port Talbot II and Plum Point interstadials 48000–23000 a B.P.) show coniferous forest with *Quercus* and forest-tundra with *Pinus* and *Picea* respectively.

The situation is comparable to that in southern Poland, and again offers a great contrast to the situation in northwest Europe.

A further point in relation to the ocean record is the discrepancy between the age of Early Devensian (Weichselian) interstadials as determined by radiocarbon dating (*ca.* 60000 a B.P.) and the ages of possible correlative fluctuations in the palaeotemperature curve (Emiliani stages 5 a–d) dated at *ca.* 75000–115000 a B.P. (Shackleton & Opdyke 1973). Difficulties of dating both organic terrestrial material and marine cores prevent a resolution of this problem at present.

4. ENVIRONMENT INDICATED BY FLORA AND VEGETATION

The interpretation of past environments from biological evidence is notoriously difficult. We have to start from the principles of the Huttonian approach through 'actualism', with the limitations that insufficient is known of the relation between species and their environment and that the extent and nature of biotypic differentiation within species is usually unknown. We have to take present distributions, consider their relation to environmental parameters, draw conclusions and apply the results to fossil assemblages. But 'actualism' can be a trap, since the responses of terrestrial organisms to changing climate, biotic and edaphic factors can rarely be evaluated in terms of width of tolerance to the parameters concerned. Any final interpretation of environmental history must then rest on evidence from geology, geochemistry, flora and fauna.

The climate of the Chelford Interstadial was discussed by Simpson & West (1958). The fossil flora indicated a mean annual temperature of 2 to −3 °C, with average January temperatures of −10 to −15 °C, and average July temperature 16–12 °C. These deductions, based on present distribution of similar vegetation, are perhaps too precise. But a continental climate is suggested with summers warm and wet enough for boreal forest growth. Climatic inferences about the Wretton pollen-based interstadial are based on scanty evidence. Woodland spread at this time, suggesting a summer temperature higher than 10 °C in July. The strong rise of *Calluna* pollen and the frequencies of *Alnus* perhaps suggest a more oceanic climate than in the later Chelford Interstadial.

The interpretation of the climate of the herb biozones is extremely difficult. Bell (1970) considered that the presence of thermophile species at Earith indicated July temperatures approaching 16 °C, with winters very cold, as indicated by permafrost indicators. However, we have to explain the lack of trees (i.e. the lowering of tree-line below today's sea level), as well as the presence of a wide variety of species of present day distribution from the Arctic to southern parts of Europe. The combination of species in the flora of the herb biozones is not one found today. The explanation will lie in the nature of the climate.

As discussed above, we have a situation in the Middle Devensian with a cold Atlantic Ocean, with the climate of the British Isles governed partly by this and partly by variation in the continental weather systems. This situation parallels the present, but must offer a completely different climatic regime to our area. We must view the climate of the Middle Devensian against this background, and against the evidence for the longitudinal zonation across northern Europe which we have already discussed. According to the evidence from flora, the climate must have had warm summers, but on flora alone it is difficult to estimate winter cold, since present distributions of northern plants are determined not only by temperature but also competition.

The position of the boundary between the tundra and boreal woodland is determined by a complex of factors, with the structure of the vegetation (e.g. its relation to albedo) and the climate playing an interlocking role (Hare & Ritchie 1972). The explanation of the treelessness is difficult to determine. The long period covered by herb biozones indicates a 'climax' of treelessness, which could be caused by a number of factors – low winter temperatures, low summer temperatures, soil instability, drying winds, waterlogged soils in the summer and so on. Perhaps persistent cool winds, with high evaporation, were an important cause. It is possible that the high albedo associated with snow cover and herb vegetation caused a shorter growth season in spite of the summer temperature, with the persistence of snow cover associated with the cool Atlantic. Such a combination would explain the presence of thermophiles in herb biozones, such as is found in the Middle Devensian. In the coldest parts of the sequence, when the polar front was far south in the Atlantic, the treelessness has a more obvious explanation in the increased severity of the climate.

An analogous situation may exist now where a cold ocean borders a continental mass. For example, in parts of Siberia, where the coastal vegetation is tundra, with taiga further south in more extreme climatic conditions, probably related to the median position of the Arctic front in the summer (Krebs & Barry 1970); or the treeless maritime tundra of the Aleutians and the Alaska peninsula (Hare & Ritchie 1972); or the barren lands of northern Labrador (57° N) where the cold Labrador current plays an important part in determining the climatic regime (Wenner 1947). We may perhaps envisage a climate with cold westerlies in the summer, possibly with low air humidity, and very cold anticyclonic conditions in the winter.

Further east, in south Poland, forest-tundra existed in the Middle Weichselian (Stillfried 'B' or 'Paudorf' Interstadial). The exclusion of trees from northwest Europe is probably associated with a climate dependent on the cold Atlantic, a hypothesis supported by the extension of 'tundra' in the Devensian far south on the French coast (figure 3; Vauville, Le Moura, van Campo 1969). Clearly a further study of the cold maritime climate of western Europe in the Devensian is required. At present we merely note that the occurrence of the mixture of species in the Devensian must relate to such a climate, vastly different from the climate of today.

Taking the Middle and Early Devensian as a whole, we see an early period with pollen-based interstadials giving way to a long period with herb biozones. The sequence gives the impression of an unbalanced situation achieving stability at the beginning of the Middle Devensian. In central and eastern northern Europe the fluctuations of the Early Weichselian are known from southern Poland, but in the Middle Weichselian a climate favourable to boreal forest growth was present in that area at times and further east there appears evidence at times for more thermophilous vegetation (Karaküla interglacial). It is perhaps these oscillations of Middle Weichselian climate, damped to the west by the stability induced by the Atlantic, which are expressed, not by the herb biozones, but by the thermophilous beetle faunas occurring in the Upton Warren beetle-based interstadial in Britain.

In the Late Devensian, after 30000 a B.P., with the expansion of the Devensian (and Scandinavian†) ice sheets herb biozones extend south in Poland and 'polar desert' occurred in the Netherlands. The evidence from well-dated floras in this part of the Devensian record is poor, but what there is suggests the presence of the typical herb biozone flora.

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† The later Weichselian ice advances of the Scandinavian ice sheets certainly include the Frankfurt and later stages, but the number and extent of early Weichsel ice advances is a matter for discussion (see Serebryanny *et al.* 1970).

5. Comparison with faunas

Here we will briefly note some comparisons of palaeobotanical data of environments with that from non-marine molluscs and insects. The molluscs associated with Devensian floras have been discussed by Sparks (West *et al.* 1974). Species of southern molluscs persist into the Early Devensian, with some species thought to indicate cold conditions. At Wretton, the faunas are associated with herb biozones alongside evidence of waste mantle structures requiring considerable cold. Even so some of the southern species are freshwater (e.g. *Planorbarius corneus*), but they range east into Russia and Siberia, and in such a distribution may lie the key to their presence in the treeless phases of the Devensian. They will apparently resist cold winters provided summers are warm, a conclusion compatible with that from the plants. The high percentages of *Pupilla muscorum* in the herb biozones at Wretton tally with these climatic indications, since the species is a characteristic dominant of European loess faunas. The molluscs indicate a continental climate. In the continental parts of the U.S.S.R. where Wretton species occur winter temperatures range from −10 to −20 °C, with summer temperatures of 10–21 °C. A general coldness and aridity is suggested by the Devensian (and Weichselian) mollusc faunas (Ant 1969).

The climate from the insect faunas of the Chelford Interstadial (Coope 1959) correspond with that inferred from the plant remains from Chelford. At Wretton, however, the insect faunas of the sediment with the Chelford woodland substage deposits was of a tundra type. The discrepancy has not been explained, but is probably the result of differing provenance of the pollen flora and the insect fauna, perhaps in terms of local variation in habitats of the sand plains of the R. Wissey floodplain at the time. A second type of variation between the floras and the insect remains is found in the assemblages from the Upton Warren Interstadial (acme *ca.* 42000 a B.P.) (Coope 1975*b*). Table 1 shows that several sites show the characteristic fauna of this time with thermophilous beetles, but the herb assemblage is similar, as far as we now know, to that elsewhere in the Middle Devensian. There is no sign of the development of forest. A possible explanation is that time was not sufficient to allow the development of forest-tundra or forest. However, there is no sign of increased representation of shrub or herb taxa which respond to the late-glacial amelioration, and in the absence of measurements of pollen deposition rate, which would indicate increased pollen productivity as a result of amelioration of climate, it is impossible to prove an amelioration of this type. It seems more likely that the climatic régime of the interstadial favoured the representation of thermophilous beetles, but did not affect the physiognomy of the vegetation. Climatic causes for this situation were discussed in § 4.

6. Conclusions

Difficulties in the interpretation of Devensian fossil floras in terms of vegetation and environment have been mentioned in the course of this discussion. When we consider that the vegetation we have described existed in Britain for 70000 of the last 80000 years, we realize the importance of resolving these difficulties for a proper appreciation and interpretation of environmental history. The desiderata for the solution of the problems are an increased knowledge of the ecology of the present day representatives of the species concerned, improved pollen morphological studies to gain a better knowledge of the Devensian floras and to reach a standard of identification similar to that reached for macroscopic fossils, and a better appreciation of the combined pollen, macro and sediment evidence from particular sites. Only with such studies can the taphonomy of the floras be better understood and so the vegetation and environment be better understood. The work must necessarily be complemented by studies of the origin of pollen and macro assemblages from vegetation at the present time. It is clear that sites must be investigated in this way, and must be reliably dated, across the longitude of northern Europe. We can then expect much further revelation of the remarkable vegetational and environmental history in the Devensian cold stage.

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Appendix. Pollen analyses from Four Ashes, Worcs.

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The stratigraphy of the gravel pits at Four Ashes, Worcs, has been described by A. V. Morgan (1973) and the insect faunas which occur in organic lenses within the sands and gravels at Four Ashes have been described by A. Morgan (1973). The sections showed up to 4.6 m of sand and gravel overlying Triassic sandstone and forming a terrace-like feature. The site provided a sequence of faunas from Ipswichian to Middle Devensian in age. The site has become the type site for the Devensian cold stage (Mitchell *et al.* 1973). Nine samples for pollen analysis were provided by Dr A. Morgan, five of which had finite dates. The locality numbers of the samples are those of Dr A. Morgan. The samples were prepared according to the schedule used in the Subdepartment of Quaternary Research, with final mounting in glycerine jelly.

The results of the analyses are shown in figures A 1 and A 2. Notes on the pollen morphology of some taxa are given below. The assemblages form three groups.

(i) Site 44. The assemblage shows high tree pollen (a.p.) percentages, with *Quercus*, *Alnus* and *Corylus* well represented. This spectrum is correlated with Ipswichian zone Ip IIb.

(ii) Site 10. The assemblage shows high a.p. percentages, constituted by pollen of *Betula*, *Pinus* and *Picea*. This assemblage is very similar to that from Chelford (Simpson & West 1958), and is therefore correlated with the Chelford Interstadial.

(iii) All the other assemblages show high non-tree pollen (n.a.p.) with up to 15 % *Betula* and below 7 % *Pinus*. The dominant n.a.p. taxa are Gramineae and Cyperaceae, with a wide variety of sparsely represented n.a.p. taxa.

Of the arboreal taxa, the frequency of *Betula* indicates the local presence of birch. In the absence of macroscopic fossils it is not possible to say whether this is dwarf or tree birch. The frequencies of *Pinus* are low and may result from long-distance transport rather than local growth. *Salix* pollen also occurs in low frequency. Its presence probably indicates local willow scrub. *Calluna*, and to a lesser extent *Empetrum* are represented by low pollen frequencies. Their local presence is uncertain.

Gramineae and Cyperaceae pollen form the bulk of the n.a.p. total. Their frequencies bear some relation to the sediment composition (see below). Pollen of aquatic plants is scarce but consistently present. *Caltha*, *Hippuris*, *Littorella*, *Myriophyllum alterniflorum* and *Sparganium* are represented. Spores of *Botrychium*, *Equisetum*, *Selaginella* and *Sphagnum* are present in low frequencies. *Selaginella* is the most abundant of these.

Figure A 2 shows the variety of n.a.p. taxa other than Gramineae, Cyperaceae and aquatics. They must represent plants from a variety of habitats in the region, both drier, open ground (*Armeria*, *Artemisia*, *Campanula*, Compositae, Liguliflorae, *Helianthemum*, *Plantago maritima*, *P. media/major*, *Rumex acetosella*) and local wetter habitats probably associated with the surface of the sand and gravel plain (perhaps *Ranunculus*, *Thalictrum*).

The left-hand columns in figures A 1 and A 2 show the composition of the sediment containing the pollen, using the major divisions of sediment type proposed by Troels-Smith (1955). The highest frequencies of Cyperaceae occur in samples 34 and 4, which show a Dh (detritus herbosus) element probably originating from local sedge growth. Sample 4 contained *Carex* nutlets. Even with this local representation, the analysis shows an accompanying high variety of other n.a.p. taxa. Sample 19, a highly inorganic sediment, showed low frequencies of *Picea*, *Ulmus*, *Quercus* and *Alnus* pollen, which may be derived with the inorganic sediment from an older horizon. In spite of the variation of sediment composition and so taphonomy of the assemblages, the Gramineae pollen percentages remain between 20 and 36 %, indicating regional vegetation with abundant Gramineae.

Notes on pollen morphology. The following notes are based on observations made on pollen of British taxa in the pollen reference collection of the Subdepartment of Quaternary Research.

Acer. Tricolpate, oval, 39 μm, striate, with long furrows. Five grains of this type were found in sample 44. In their larger size, thinner wall and whorled striae they resemble *A. monspessulanum* L. rather than *A. campestre* L.

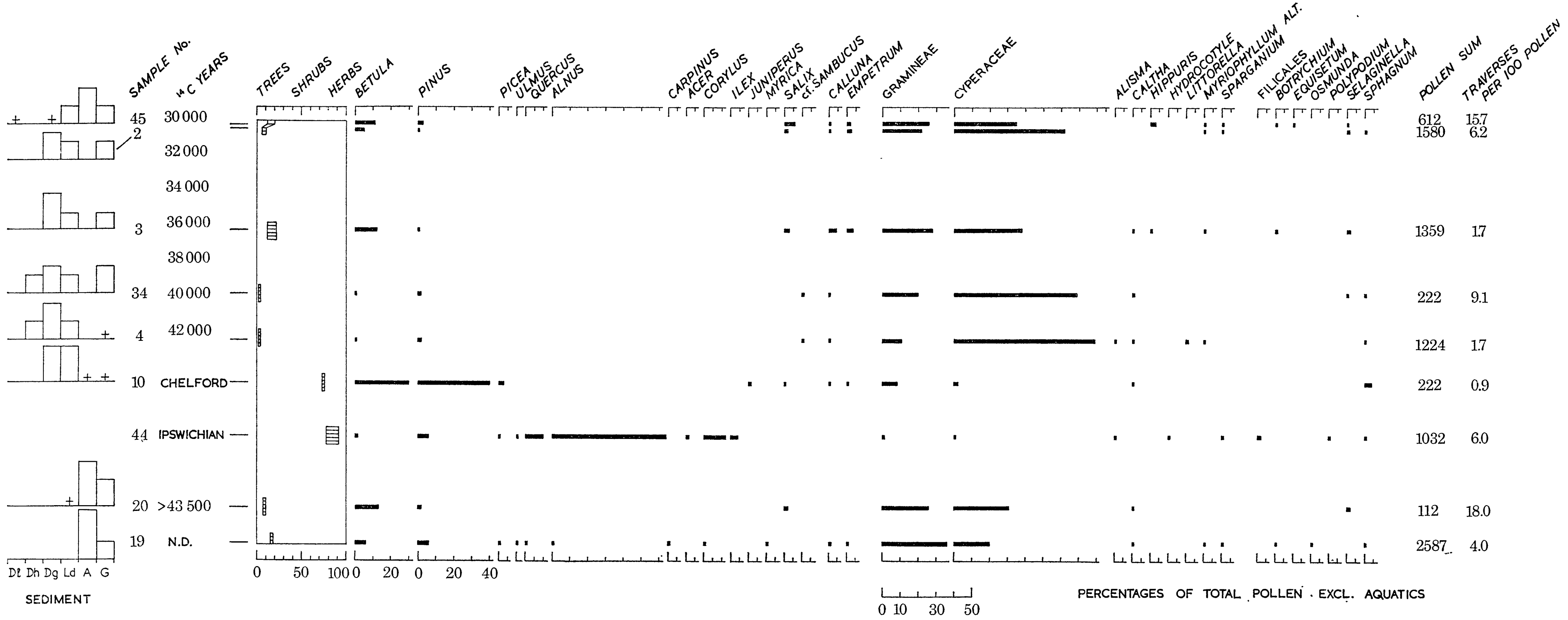

FIGURE A1. Four Ashes 1970: pollen diagram for arboreal, shrub, Gramineae, Cyperaceae and aquatic pollen, and spores.

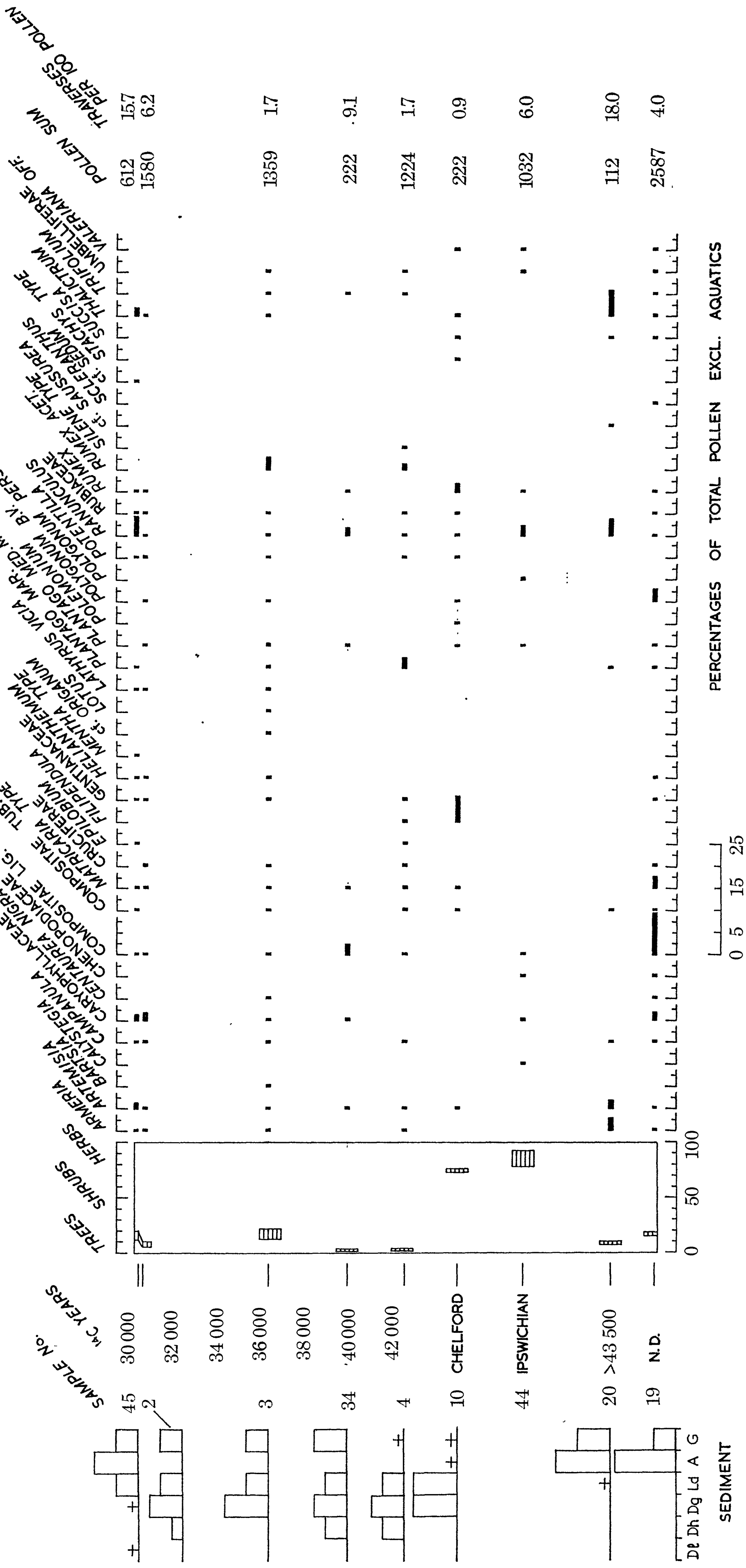

Figure A2. Four Ashes 1970: pollen diagram for non-arboreal pollen except Gramineae, Cyperaceae and aquatic pollen.

Bartsia/Euphrasia (*Bartsia* in figure A2). Tricolpate, spherical, 28–30 μm, very thin wall, very fine surface pattern, with long open furrows. Several grains found in sample 3 similar to *Odontites verna* (Bell.) Dum.

Bruckenthalia. Tricolpate, oval, 20 μm, thickened furrows, with crackling peculiar to many species of Ericaceae. One grain in sample 10.

Gentiana/Centaurium (Gentianaceae in figure A2). Tricolpate, oval 24–28 μm, thick wall, 'ladder-type' network, striae indistinct to nil. Grains of this type were found in sample 45 (1 grain), 2 (3 grains), 3 (15 grains), 4 (3 grains) and 19 (2 grains).

Hippuris. Sixteen grains found in sample 45 and two in sample 3, comparing well with the 5-furrowed grains of *Hippuris vulgaris* L.

Saussurea/Arctium (cf. *Saussurea* in figure A2). Tricolpate, spherical, 42 μm, thick wall, with coarse elements graduated in size towards the furrows, shallow broad-based spikes. One grain found in sample 20 similar to *S. alpina* rather than *Arctium* on account of smaller size and coarser elements in the exine patterns.

Lathyrus/Vicia. Tricolpate, oblong-oval, 27 μm, thin wall, short thickened furrows, large mesh shallow network. One grain in sample 45, two in sample 2 and one in sample 3.

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Discussion

G. Manley (3 *Whitwell Way, Coton, Cambridge*). Following Professor West's demonstration one can readily suggest an operative climate by analogy with today. With a prevailing westerly flow from a much colder North Atlantic in summer, one would expect winds to be strong, with diminishing cloud; moving inland over a warm surface towards the North German Plain (where the 'Lüneburg Heath' is still found) they would become increasingly dry. It suggests the likelihood of summer air temperatures averaging 10–13 °C, not unlike some of our windswept northern uplands today upon which trees at higher levels become established with difficulty. With a polar front where Professor McIntyre puts it, one might fairly expect more summer depressions than today to run along the Mediterranean and to curve northward across the Black Sea, or even across Hungary towards northern Russia. Even now this is far from uncommon. Warm humid air from the southeast, not forgetting the enlarged Caspian Sea, would carry the summer isotherms north, and encourage tree growth well into northern Russia. Might one hazard the further suggestion that among the herbaceous vegetation close to the ground the summer microclimate, with relatively dry air above, might be sufficiently warm to explain the presence of some of Dr Coope's beetles; but here I must confess ignorance of their habits. Moreover, under such marginal conditions of temperature, wind speed and evaporation linked with the slight local shelter provided by the shallow valleys, the development and spread of Professor West's forested episodes is understandable.